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INSECT POLLINATION OF CULTIVATED CROP PLANTS

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Agriculture Handbook No. 496

Agricultural Research Service
UNITED STATES DEPARTMENT OF AGRICULTURE

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FRONTISPIECE—Honey bee colonies distributed in almond orchard to pollinate blossoms. (Photograph courtesy University of California, Davis.)

INSECT POLLINATION OF CULTIVATED CROP PLANTS

By S. E. McGregor, *apiculturist*

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Agricultural Research Service
UNITED STATES DEPARTMENT OF AGRICULTURE

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FOREWORD

Insects play a vital role in the pollination of many plants, including some of our most important cultivated crops. This is well recognized by those knowledgeable of pollinating processes in plants. But, to many, this fact is not known, or if known it is regarded as a natural phenomenon that will take place without any effort on man's part. There is still much to be known about plant pollination and how to use the honey bee, wild bees, and other insects to achieve maximum efficiency in agricultural production. At the same time, the information we now have on the subject is not being utilized to the fullest extent for improving yields and quality of many kinds of fruits, vegetables, and field crops.

The publication entitled, "Biology and the Future of Man" (Oxford University Press, Philip Handler, editor), included this statement: "The upsurge in the growth of human populations constitutes the major problem for the immediate future of man." A world population projected to approach 8 billion people by the year 2,000 will demand maximum productivity from available land resources. While advances must be made in a number of agricultural practices in order to meet the increasing requirements for food, fiber, and other essential commodities, the question most relevant to the subject of this publication is the future role of the honey bee, wild bees, and other insects in crop production. How can agriculture make better use of domesticated and wild bees to help meet the increasing demands for food? This handbook deals with this question by providing information to growers on the crops that are dependent upon or benefited by insect pollination, what pollinating species are most effective, and how they can be utilized.

There has been a need to bring together the information developed by scientists, beekeepers, and by general agriculturists throughout the world on the role that the honey bee, the bumble bees, the leaf cutter bees, and other insect pollinators play in producing more and better quality crops. The compiling of such information is necessary to lay the foundation for maximum use of insect pollinators. However, the need for such information goes much further. It is necessary to identify gaps in our knowledge of plant pollination and to identify problems that must be resolved to assure maximum contribution of pollinators to food production.

S. E. McGregor, the author of this handbook, a classmate and associate in entomology, has devoted his entire professional career to apiculture. He taught beekeeping in one of our leading land-grant colleges in the South. He conducted research on almost every aspect of bee culture and management. He directed the bee research program of the United States Department of Agriculture for 4 years. But, he was also a practical beekeeper. He helped manage honey bees on his father's farm that were maintained to increase the production and quality of fruits, berries, melons, and other crops.

The author of this handbook recognizes the value of the honey bee as a source of an important food item enjoyed by many, as the livelihood of professional beekeepers, and as a satisfying hobby of many amateur beekeepers the world over. Yet, his overriding interest in bees and in beekeeping has been to advance this small but important industry so that it can make the maximum contribution to agriculture through crop pollination. He is eminently qualified to bring together the information on crop pollination by insects. I encouraged him to do this as his final major contribution to agriculture, to the bee industry, and to the public.

It would be a serious omission if attention were not called to certain problems that agriculture may face if adequate provisions are not made by society to develop and maintain a viable bee industry and to protect other insect pollinators from several adverse forces that are working against them.

In the past few decades, we have witnessed the development of an array of agricultural chemicals that have helped advance agricultural productivity to a level never before attained. As important as this development has been for the benefit of society, the use of these chemicals has had serious consequences for honey bees and other insect pollinators. Insecticides applied for controlling destructive insects often pose equal hazards to honey bees and to wild bees. Untold numbers of bee colonies are destroyed or weakened each year due to insecticide exposure. The use of herbicides that increase crop yields and production efficiency, that improve our livestock ranges, and improve the appearance of our roadsides, lawns, and parks are a boon to society. But, the use of these chemicals affects the honey bee and our natural pollinators to a degree that is difficult to assess. Moreover, as the demands for more food increase, we can anticipate more intensive monoculture that disrupts the continuity of plants needed to furnish adequate nectar and pollen for bees. In order to meet the future demands for food and living space, there will be fewer "idle" acres of land. However, these lands do not remain idle so far as pollinators and other beneficial insects are concerned.

These developments and trends raise a number of questions regarding the future of apiculture. How can the beekeeper, who depends on bees as a livelihood stay in business in the face of such adversities? Will the amateur beekeeper maintain interest and enthusiasm for a hobby if he cannot obtain at least some material reward for his efforts? For decades, thousands of bee

hobbyists assured the presence of large numbers of honey bees throughout our agricultural environments with great benefits to agriculture, and to the home gardener, but with little compensation to the keepers of the bees. What will be the effect on our agroecosystems if this source of bees disappears? Certainly, the nation must give due recognition to the value of the small but vitally important bee industry and take measures to keep it viable. One way to gain full recognition of the importance of this industry is to have a better understanding of the part insects play in plant pollination, which is the objective of this handbook. This treatise on plant pollination by insects should not only be of immediate value to the agriculturist but should clearly indicate the value of insect pollinators to our total environment and to our society.

E. F. Knipling
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PREFACE

The pollination of plants, essential in the perpetuation of most species, is so unobtrusively accomplished that it is often overlooked. The flower opens, then fades, after which it either sets fruit or it sheds, depending largely upon whether or not it was pollinated. Yet this option, often left entirely to chance, can mean the difference between profit and loss to the grower.

A low crop yield is often attributed to damage by harmful insects, plant diseases, cultivation techniques, or the weather. The problem may have been only that the male element of the flower, the microscopic pollen grain, was unable to fertilize the female element, the ovule, in the flower's own specifically prescribed way. On many crops this pollen transfer, or pollination, is performed by insects.

Many factors affect pollination—but most of them, negatively. Pollination can be prevented by cold weather, but the presence of warm weather alone will not cause the fruit to set. Fertility of the soil may influence the set of pollinated fruit, but soil fertility alone will not cause fruit to set. Interplanting of proper selections, harmful insect control, adequate irrigation or soil moisture, and other cultural practices may contribute to the effectiveness of insect pollination, but they alone will not cause the fruit to set. *Pollination is the critical factor.*

Plant pollination is complex and influenced by many overlapping effects. These effects are not limited to the target crop but are influenced by harmful insects and their control on nearby crops, herbicides applied to seemingly nonrelated weeds, overgrazing or improper pasture management, competing crops or plants, urbanization, water utilization, changing crops and cropping practices, size of the field, and even air pollution. Furthermore, Nature reveals her secrets with extreme reluctance, her sex life being no exception, and only by long hours of diligent and shrewd observations are these secrets revealed. We hope that crop and insect specialists will benefit from the material herein and obtain some clues that will help them in revealing more of Nature's secrets related to pollination of her flowers. In this way will the grower be further benefited.

Certain insect pollinators that were abundant a generation or so ago, when most farms grew a variety of crops, have succumbed in many areas to large-scale farming or other modern agricultural techniques. The grower, who recognizes this ecological change, realizes the importance of these pollinating agents, and learns to protect and successfully manipulate them, is almost certain to have a distinct advantage in the production of his crops. But he needs background knowledge of pollination in general, specific knowledge concerning the plants that he is growing that are benefited by insect pollination, and suggestions for the efficient use of such insects in maximum crop production. Such information is presented herein.

Many agricultural books tell the grower in detail how to prepare the seed bed; plant; fertilize; cultivate; irrigate; prune or thin the crop; control harmful insects, diseases, or other pests; and, therefore, bring the crop into the highest stage of flowering. Then the advice skips to the harvest stage. Usually little or nothing is said about the need for transfer of pollen from the male parts of the flower to the female parts—essential in seed or fruit production of many crops. This book is designed to fill that particular void.

The book is directed primarily to the grower who wants to achieve the highest possible economic production of those crops that are benefited by insect pollination. It should also be a useful reference book for specialists in agronomy, apiculture, entomology, and horticulture, and of special interest to beekeepers who supply bees to growers for pollination purposes. Because of the intriguing relationship of bees and pollination and the resultant impact upon food production, ecology, the natural beauty of a flowering landscape and nature in general, it should be of some interest to the public in general, although it is not designed for that purpose.

Only cultivated crops dependent upon or benefited by insect pollination are discussed. The majority of these are grown commercially within the United States, although a few important tropical crops, not grown commercially in this country, are included. The pollination requirements of ornamental plants are not included, even though many of them are cultivated as crops for the production of their seeds. This area could comprise another sizable book.

The relatively new term "cultivar," recommended by the International Code of Nomenclature for Cultivated Plants and defined by Gilmour et al., American Horticultural Society, 32 pages, 1969, is used instead of the somewhat less specific term "variety."

A cultivar is defined as "a group or assemblage of

cultivated individual plants that when reproduced sexually or asexually retain their distinguishing features that have been described morphologically, physiologically, cytologically, chemically or in other ways that have significant meaning to agriculture, horticulture, or forestry." It may be a clone, a line, an assemblage of individuals, or a uniform first-generation hybrid reconstituted in each generation by the crossing of two or more breeding stocks maintained either by inbreeding or as clones.

The term is derived from *cultivated variety*. It is more specific than a morphological variant of a botanical species, but in the sense of a *cultivated* variety the term cultivar and variety are exact equivalents.

The singular is abbreviated "cv." and the plural, "cvs." Capital initial letters are required for all words of a cultivar, the word or words placed in single quotes, for example, alfalfa (*Medicago sativa* L.), cv. 'Kansas Common'.

In the early 1920's, the Bee Research staff of the United States Department of Agriculture (USDA) began collecting and cataloging references on crop pollination by bees, along with other references on honey bees and beekeeping. This bibliography continued to grow in size, but was discontinued when the Bee Research Branch ceased to exist in 1972, at which time it comprised some 80,000 references. The items were derived from scores of beekeeping journals from all over the world as well as from other biological journals. Many of the references cited herein were translated or abstracted for this bibliography.

In 1949, the Bee Research Association of London, England, began abstracting world literature on apiculture and publishing the information as "Apicultural Abstracts." These are designated by code, such as AA-246/51. This identifies the material as Apicultural Abstract number 246 of the year 1951. Numerous citations herein are derived from that source.

The Bibliography of Agriculture, published by the USDA since 1944, was also the source of many citations. Other citations came from agronomy, entomology, horticulture, and related journals not included in the above sources.

Much of the literature on pollination by insects deals with individual crops or plant species, but a few publications deal with numerous plants. For example, Darwin's book in 1899 on "The Effects of Self and Cross Fertilization in the Plant Kingdom" dealt with the value of pollination by insects to more than 100 plant species, including the effect of cross-pollination on the growth and vigor of the plant's offspring.

The publication that contributed most to the thinking on the value of pollinating insects to crops other than fruits was issued by the USDA in 1942 as E-584, "The Dependence of Agriculture on the Beekeeping Industry—A Review." There were numerous reprints and revisions of this publication. It was unique in that it was assembled by bee specialists but was based entirely upon research by crop specialists. The information presented herein is based upon research not only by plant specialists but also by bee specialists, entomologists, zoologists, naturalists, and other biologists.

Attempts have been made throughout the book to arrange the material in alphabetical order. The crops are listed alphabetically by common name, followed by the scientific and plant family name. However, if the reader has only the scientific name, the common name of the crop can be located through the Index.

The information on each crop follows the same format: The name of the crop, its economic importance (derived from the 1972 USDA, Agricultural Statistics, unless otherwise noted), a brief description of the plant as it might relate to pollination, the inflorescence, pollination requirements, pollinating agents, and current pollination practices. Following each crop is a list of references that deal specifically with that crop. The material presented is derived primarily from published material, although some of my own unpublished data are also included. Only USDA photographs were used, except where otherwise noted.

The flower sketches were made by Mrs. Lucretia Brazeale Hamilton, for which appreciation is hereby expressed. Appreciation is also expressed to the many specialists on crops and insects both within the USDA and in numerous State agricultural experiment stations for their reviews and helpful suggestions relating to specific sections of the book. I could not conclude these expressions of appreciation without including the name of the late Frank Edward Todd, my friend and coworker, who stimulated and did much to sustain my interest in pollination and who encouraged me to prepare this book.

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INSECT POLLINATION OF CULTIVATED CROP PLANTS

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ECONOMICS OF PLANT POLLINATION

Worldwide, more than 3,000 plant species have been used as food, only 300 of which are now widely grown, and only 12 of which furnish nearly 90 percent of the world's food. These 12 include the grains: rice, wheat, maize (corn), sorghums, millets, rye, and barley, and potatoes, sweet potatoes, cassavas or maniocs, bananas, and coconuts (Thurston *1969*).[1] The grains are wind pollinated or self-pollinated, coconuts are partially wind pollinated and partially insect pollinated, and the others are propagated asexually or develop parthenocarpically. However, more than two-thirds of the world's population is in Southeast Asia where the staple diet is rice. Superficially, it appears that insect pollination has little effect on the world's food supply—possibly no more than 1 percent.

Within the United States, which accounts for only about 6 percent of the world's population, about 286 million acres were cultivated in 1969. About 180 million acres were devoted to the wind pollinated or self-pollinated crops, primarily barley, corn, oats, rice, rye, sorghums and wheat, grass hay crops, sugar beets, sugar cane, potatoes, sweet potatoes, and tobacco. About 60 million acres were devoted to crops that may receive some benefit from insect pollination but are largely self-pollinating (beans, cotton, flax, peanuts, peas, and soybeans). About 40 million acres were devoted to hay crops produced from bee-pollinated seeds (alfalfa, clovers, lespedezas). About 6 million acres were devoted to producing fruits, vegetables, and nuts—most of which are dependent upon insect pollination. Table 1 lists the cultivated crop plants, discussed herein, that are dependent upon or benefited by insect pollination. These plants provide about 15 percent of our diet.

The animal products we consume contribute about an equal amount to our diet. These include beef, pork, poultry, lamb, and dairy products—derived one way or another from insect-pollinated legumes such as alfalfa, clover, lespedeza, and trefoil.

More than half of the world's diet of fats and oils comes from oilseeds—coconuts, cotton, oil palm, olives, peanuts, rape, soybeans, and sunflower (Guidry *1964*). Many of these plants are dependent upon or benefited by insect pollination. When these sources, the animal and plant products, are considered, it appears that perhaps one-third of our total diet is dependent, directly or indirectly, upon insect-pollinated plants.

In addition, the insect-pollinated legumes have the ability to collect nitrogen from the air, store it in the roots, and ultimately leave it to enrich the soil for other plants. Without this beneficial effect, soils not fertilized by processed minerals would soon be depleted and become economically unproductive.

Another value of pollination lies in its effect on quality and efficiency of crop production. Inadequate pollination can result not only in reduced yields but also in delayed yield and a high percentage of culls or inferior fruits. In this connection, Gates (*1917*) warned the grower that, "he may fertilize, and cultivate the soil, prune, thin and spray the trees, in a word, he may do all of those things which modern practice advocates, yet without his pollinating agents, chief among which are the honey bees, to transfer the pollen from the stamens to the pistil of the blooms, his crop may fail."

With ample pollination, the grower may also be able to set his blooms before frost can damage them, set his crop before insects attack, and harvest ahead of inclement weather. Earliness of set is an often overlooked but important phase in the crop economy.

The value of pollination on the succeeding generation of crops is also frequently overlooked. The value of hybrid seed is not reflected until the subsequent generation. Vigor of sprouting and emerging from the soil is often a vital factor in the plant's early survival. Other responses to hybrid vigor include earliness of development, plant health, and greater production of fruit or seed.

Signs of Inadequate Pollination

There are numerous ways a grower, with little or no intimate knowledge of the life and habits of pollinating

[1] The year in italic after the author's name refers to Literature Cited at the end of each major section.

TABLE 1.—U.S. crops dependent upon or benefited by insect pollination—their estimated value, volume, and major States of production for 1971 (USDA Agr. Statis. 1972).

Crop[1]	Total value	Total production	Units of production	Major producing States with volume of production to nearest thousand				
	Millions of dollars	*Thousands*		*Thousands*	*Thousands*	*Thousands*	*Thousands*	*Thousands*
Alfalfa:								
Hay	2,000[2]	27,606	Acres	Wisconsin 3,017	South Dakota 2,456	Minnesota 2,240	Iowa 1,762	Nebraska 1,750
Seed[3]	40	487	--do--	South Dakota 90	California 86	Kansas 60	Idaho 39	Washington 35
Do.	40	116,891	Pounds	California 42,140	Washington 17,500	Idaho 16,380	Nevada 9,165	
Almond	85	134	Tons	California 134				
Apple	300	3,055	--do--	Washington 600	New York 462	Michigan 360	Pennsylvania 252	Virginia 240
Apricot	15	150	--do--	California 144	Utah 3	Washington 2		
Artichoke	8	11	Acres	California 11				
Asparagus	64	119	--do--	California 43	Washington 19	New Jersey 17	Michigan 16	Illinois 10
Avocado	29	47	Tons	California 28	Florida 19			
Bean, snap	100	326	Acres	New York 52	Wisconsin 50	Florida 35	Oregon 30	Michigan 15
Beet:								
Sugar	414	1,336	--do--	California 346	Idaho 164	Colorado 139	Minnesota 107	Michigan 82
Garden	14	4	--do--	Wisconsin 6	New York 4	Texas 2	Oregon 2	
Carrot	93	72	--do--	Texas 26	California 16	Michigan 6	Wisconsin 3	Arizona 3
Celery	78	33	--do--	California 18	Florida 12	Michigan 2	New York 2	
Cherry:								
Sweet	44	140	Tons	Washington 34	Oregon 33	California 32	Michigan 24	New York 6
Tart	28	139	--do--	Michigan 89	New York 20	Wisconsin 8	Pennsylvania 8	Utah 7
Citrus:								
Grapefruit	137	60,680	Boxes	Florida 42,900	Texas 10,100	California 5,160	Arizona 2,520	
Lemon	86	16,450	--do--	California 13,500	Arizona 3,150			
Lime	4	880	--do--	Florida 880				
Orange	445	189,560	--do--	Florida 142,300	California 38,600	Texas 6,200	Arizona 3,560	
Tangelo	5	2,700	--do--	Florida 2,700				
Tangerine	16	4,890	--do--	Florida 3,700	California 800	Arizona 390		
Temple	12	5,000	--do--	Florida 5,000				

See footnotes at end of table.

TABLE 1.—U.S. crops dependent upon or benefited by insect pollination—their estimated value, volume, and major States of production for 1971 (USDA Agr. Statis. 1972).—Continued

Crop[1]	Total value	Total production	Units of production	Major producing States with volume of production to nearest thousand				
	Millions of dollars	*Thousands*		*Thousands*	*Thousands*	*Thousands*	*Thousands*	*Thousands*
Cole Crops:								
Broccoli	35	43	Acres	California 36	Oregon 3	Texas 2	Arizona 1	
Brussels sprout	8	6	--do--	California 5	New York 1			
Cabbage	73	108	--do--	Texas 20	Florida 18	New York 14	California 10	Wisconsin 9
Cauliflower	27	25	--do--	California 19	New York 3	Oregon 2		
Cotton	1,439	11,471	--do--	Texas 4,735	Mississippi 1,325	Arkansas 1,140	California 742	Alabama 558
Cranberry	25	22	--do--	Massachusetts 11	Wisconsin 6	New Jersey 3	Washington 1	Oregon 1
Cucumber	85	175	--do--	North Carolina 34	Michigan 27	South Carolina 15	Florida 14	Texas 11
Date	3	20	Tons	California 20				
Eggplant	5	3	Acres	Florida 2	New Jersey 2			
Fig	4	44	Tons	California 44				
Flax	43	1,580	Acres	North Dakota 861	South Dakota 460	Minnesota 240	Texas 10	Montana 8
Grape	374	3,997	Tons	California 3,534	New York 200	Michigan 69	Pennsylvania 57	
Lespedeza seed	4	138	Acres	Kentucky 19	Tennessee 19	North Carolina 17	Kansas 15	Missouri 14
Lettuce	273	218	--do--	California 136	Arizona 44	Texas 9	Florida 5	Colorado 4
Lima beans	15	71	--do--	California 23	Delaware 16	Wisconsin 5	Washington 4	Maryland 2
Muskmelon:								
Cantaloup	82	102	--do--	California 52	Texas 19	Arizona 12	Georgia 5	South Carolina 4
Honeydew	13	12	--do--	9	2	1	0	0
Nectarine	11	69	Tons	California 69				
Olive	8	55	--do--	California 55				
Onion	105	100	Acres	California 27	Texas 24	New York 13	Oregon 7	Michigan 6
Peach	174	1,444	Tons	California 841	South Carolina 145	New Jersey 62	Georgia 60	Pennsylvania 52
Peanut	406	1,529	Acres	Georgia 510	Texas 297	Alabama 194	North Carolina 155	Oklahoma 119
Pear	63	701	Tons	California 309	Oregon 174	Washington 165	New York 19	Michigan 18

See footnotes at end of table.

TABLE 1.—U.S. crops dependent upon or benefited by insect pollination—their estimated value, volume, and major States of production for 1971 (USDA Agr. Statis. 1972).—Continued

Crop[1]	Total value	Total production	Units of production	Major producing States with volume of production to nearest thousand				
	Millions of dollars	*Thousands*		*Thousands*	*Thousands*	*Thousands*	*Thousands*	*Thousands*
Pepper	52	50	Acres	Florida 14	New Jersey 8	North Carolina 8	California 7	Texas 7
Plum and prune	65	296	Tons	California 232	Michigan 18	Oregon 17	Washington 16	Idaho 13
Red clover seed	12	432	Acres	Illinois 95	Indiana 60	Ohio 56	Missouri 33	Michigan 30
Soybean	3,465	42,409	--do--	Illinois 7,190	Iowa 5,456	Arkansas 4,305	Missouri 3,652	Indiana 3,400
Strawberry	116	51	--do--	Oregon 11	California 8	Michigan 6	Washington 4	North Carolina 2
Sweetclover seed	1	54	--do--	Minnesota 11	South Dakota 11	Kansas 7	Texas 6	
Tomato	444	395	--do--	California 181	Florida 38	Ohio 28	New Jersey 21	Indiana 17
Watermelon	68	257	--do--	Texas 60	Florida 50	Georgia 33	South Carolina 22	California 14

[1] The following crops, although discussed in the text, do not appear in the table because their value was either less than $1 million or complete data were not available: Acerola, Alsike clover, arrowleaf clover, ball clover, balsam-pear, berseem clover, blackberry, black medic, black pepper, blueberry, broad bean, buckwheat, cacao, carambola, caraway, cardamom, cardoon, cashew, cauliflower, celeriac, chayote, cherimoya, chervil, chestnut, chicory, Chinese gooseberry, chive, cicer milkvetch, clove, coconut, coffee, coriander, cowpea, crabapple, crimson clover, crotalaria, crownvetch, currant, dill, drug plants, endive, feijoa, fennel, gooseberry, guava, henequen, herbs, huckleberry, jujube, kale, kenaf, kidneyvetch, kolanut, kudzu, lavender, leek, litchi, loquat, lupine, macadamia, mamey sapote, mango, mung bean, mustard, niger, nutmeg, oil palm, okra, onion seed, papaw, papaya, parsley, parsnip, passionfruit, Persian clover, persimmon, pigeonpea, pimento, pomegranate, pumpkin, pyrethrum, quince, radish, rape, raspberry, rose clover, rutabaga, safflower, sainfoin, scarlet runner bean, sesame, sisal, squash, strawberry clover, subterranean clover, sunflower, sweetvetch, tea, tephrosia, trefoil, tung, turnip, vanilla, vegetable sponge, vetch, Welsh onion, white clover, white-flowered gourd, white gourd, white sapote, and zigzag clover.

[2] Estimated, based on value of all hay ($3,319 million) and the tonnage of alfalfa hay (76 million tons), which was more than half the total tons (131 million).

[3] Because of the differences in the production of alfalfa seed per acre in different States, both acres and pounds per acre are presented.

insects, can measure the effectiveness of the pollination of his crop. He would be wise to determine these ways in connection with the particular crop he is growing and learn to interpret their significance in terms of maximum production. He should remember that *no cultural practice will cause fruit or seed to set if its pollination is neglected.*

Fruit orchards without a strong hum of bees in them during flowering may not be amply pollinated. The actual number of bees per unit of flowers has not been determined in most instances; however, one bee per 100 flowers may be adequate.

In cotton fields with ample pollinator activity, all stigma tips will be well coated with pollen before noon. By midafternoon, the flower petals should be changing from white to pink and the corolla closed into a tunnellike tube. Cotton flowers not adequately visited by insect pollinators will have petals that stay white and open until sunset, and when they close they will fold flatly together. Day-old, well-pollinated flowers can be easily recognized by their tunnellike tubular corollas.

Melon and other cucurbit flowers should have one pollinator for each 100 flowers at about midmorning of a mild day. There should be a heavy set of fruit near the crown of the plant, and the fruit should be well developed and symmetrical.

Signs of Adequate Pollination

Inadequately pollinated alfalfa and clover fields have a "flower garden" appearance, but if the flowers are being pollinated about as rapidly as they are capable of being fertilized, the florets, which wilt soon afterwards, give the field a rusty-green appearance.

Other signs of adequate pollination include branches laden with symmetrical fruit, well-filled seed pods,

compact clusters of fruits or seeds, and uniform set. For example, adequate pollination is indicated by two or more muskmelons near the crown or base of the vine, or a majority of the apples developing from the king, or primary flower, at the tip of the cluster. In a watermelon field, adequate pollination would be indicated by a high percentage of melons in the number 1 class, that is, symmetrical, completely developed throughout, and of satisfactory weight.

Ecological Relationships

The value of insect pollination, the only type of pollination upon which man can exert much influence, is not limited to the cultivated crops. Bohart (*1952**)[2] pointed out that the most drastic effect of the absence of pollinating insects would be in uncultivated areas, where, as a result, most soil-holding and soil-enriching plants would die out. He also mentioned that springtime would be bleak indeed without the usual gay flowers.

Baker and Hurd (*1968*) also recognized this important ecological relationship, for they stated that "insect pollination is still extremely important among the forbs of the grasslands, in the shrub and herb layer of the temperate forest and in the desert. It remains undiminished in the tropics."

A simultaneous warning of disaster was recently issued because of our disregard of the importance of pollination. Abelson (*1971*) stated, "We have developed extraordinarily productive farm crops, but monoculture and the use of limited strains of plants makes the food supply vulnerable to plant enemies such as the southern corn leaf blight." He reminded us that plants are constantly involved in complex chemical warfare not only with pests but also with each other. The slightest weakening may give the enemy the advantage. Likewise, Harlan (*1971*) reminded us that "The post-modern era has seen spectacular increases in yield, and a virtual genetic wipe-out, with whole continents planted to one or a few related populations. These narrow genetic bases and loss of gene pools are invitations to disaster." Cross-pollination can be one means of preventing such a disaster. This vulnerability to disaster was enlarged upon by Horsfall et al. (*1972*), who cited such examples as the chestnut blight at the turn of the century, the Bengal famine of India in 1943, and the Irish famine of the 1840's.

The somewhat related warning by Tinker (*1971*) that one plant species in 10,000 or 20,000 species faces extinction is indicative of the growing problem of a continual adequate food supply of the pollinators. That such changes are actually having an impact on pollinators now was pointed out by Oertel (*1966*). He maintained certain colonies of honey bees on scales at Baton Rouge, La., and recorded the gain or loss in weight throughout the season from 1929 to 1963. His data (table 2) showed that over the years the weight of the colonies decreased from an average gain of 7 pounds to an average loss of 24 pounds during the period September to November. This loss, he deduced, was related to weed sprays, better pasture care that in general reduced the fall honey flow from goldenrod, a reduction in cultivated crops attractive to bees, along with increased plantings of soybeans that are relatively unattractive, and urbanization. Similar reports from commercial beekeepers across the continent are common. Oertel (*1966*) stated that lack of an adequate fall crop of honey caused the colonies to be less productive the following spring. According to Wearne et al. (*1970*), this decreased pasturage was also associated with bee losses.

Table 2.— Average gains (+) or losses (−), in pounds, for colonies (of honey bees) on scales for 5-year periods between 1929 and 1963, Baton Rouge, La.[1]

Years	July	August	September	October	November
1929-33	+14	− 1	−16	+32	− 9
1934-38	+11	− 5	− 7.6	+17.6	− 6
1939-43	+13	− 4.4	− 9	+18.4	− 8
1944-48	+38	− 4	− 8.5	+ 2	− 6
1949-53	+38	[2]+11	− 7.6	+ 2.5	−10
1954-58	+11	−11.4	−11.2	− 5.3	− 8
1959-63	+21	−11	−14	− 4	− 6

[1] Source: Oertel (*1966*).

[2] A net gain of 50 pounds in August 1950 was responsible for this exception to the usual August losses. An average net gain of 312 pounds was obtained in 1950: net gains were recorded each month from March to October.

Hawthorn and Pollard (*1954,* p. 56*) related this detrimental effect on colony condition to our costs of vegetables when they stated:

> In recent years there has been an increasing accumulation of data to indicate that seed yields of insect-pollinated crops may often be lower than they need be, not because of climate, soil, or cultural factors, but simply because the population of certain insects is low.
>
> With a planting of many acres there may not be enough insects such as honey bees to visit the millions of flowers normally present. Even native pollinating insects may be somewhat scarce because the very activity of preparing and cultivating such a large area of land may have destroyed some of their nesting places. Finally, to control some injurious insect the operator may have sprayed the entire planting with an insecticide which has killed many beneficial insects as well as the harmful ones.

Such action is reflected in the economy of beekeeping, as pointed out by Crane (*1972*) who stated:

> In many parts of the world beekeeping hangs in the balance and the scales are tipped against the bees and the beekeepers . . . the very change in land use which now seems to be bringing about the end of beekeeping may lead to its recognition as an essential part of agriculture, because of its importance for crop production.

Bruner (*1966*) studied the purely business aspect of vegetable production in northwest Mexico. He noted that the weakness of the "Mexican dictatorial-paternalistic method of farm operation" precluded obtainment of the best technically trained men and new ideas. Bruner considered the lack of proper "saturation-pollination" by bees and protection of beneficial insects from pesticides to be two major reasons for low agricultural production in certain areas. Some larger operations in our country tend to fall into a similar category.

[2] The year in italic followed by an asterisk indicates that the publication is cited numerous times, but the complete citation is given only once in the General Literature Cited, p. 382.

Farms are likely to continue to increase in size because of increased efficiency of operations. Blosser (*1960*) showed that the average cost of crop production on 640-acre farms was 9.5 to 15.1 percent less than on 160-acre farms that were producing the same crops.

Swift[3] reported on the impact of a changed pest control program on the insect pollinators and indirectly on the community. Because of the DDT residue in milk, the California Pest Control Program was changed to include numerous other insecticides, which were much more toxic to honey bees than DDT. The impact of this change was disastrous to the honey bee industry, with 40,000 to 80,000 colonies killed annually. The indirect result was that in 1968 the almond growers, who depend upon honey bees for the pollination of their almond crop, were short at least 26,000 colonies. Swift pointed out that this change to protect the milk had an unanticipated adverse effect on beekeeping, an industry not associated with the dairy industry, and this in turn affected the almond producers, who were still less associated. Swift further pointed out that California crops, valued at $300 million, were dependent upon insect pollination, primarily by honey bees.

The value of insect-pollinated crops in the United States was reported by Metcalf and Flint (*1962*) to be $4.5 billion. Crops dependent upon insect pollination were valued by Levin (*1967*) at $1 billion, with additional crops benefited by bee pollination valued at approximately $6 billion. The honey and beeswax produced were valued at about $45 million. In other words, honey bee colonies are worth roughly 100 times as much to the community as they are to the beekeeper.

The aesthetic value of pollination to ornamentals, wild flowers, and forest and range plants in terms of beauty of the landscape is recognized for specific plants (Alcorn et al. *1962*, Grant and Grant *1965*, McGregor et al. *1962*, and Meeuse *1961**) and in general (Kerner *1896–97**, and Knuth *1906–09**), but it cannot be measured. Nor can we measure the related ecological value in terms of seeds, fruits, and nuts produced, which are used as food for various forms of wildlife, but this value, too, is doubtless considerable.

Pollinators other than honey bees are also extremely valuable although their value is difficult to estimate. Within recent years, a few insect species have been managed by man for their pollination service. Bohart (*1952**) estimated that the value of the wild bee industry was well over $1 million per year in terms of expenditures and benefits. It had expanded considerably by 1972. No doubt numerous other unmanaged and generally unrecognized wild bees exceed Bohart's estimate. He dealt largely with the gregarious leafcutter bee (*Megachile pacifica* Panzer),[4] and the equally gregarious alkali bee (*Nomia melanderi* Cockerell). Bumble bees are excellent, although generally unmanageable, pollinators (Holm *1966*). Unfortunately, in many intensively cultivated areas, they have largely been eliminated.

[3] SWIFT, J. E. UNEXPECTED EFFECTS FROM SUBSTITUTE PEST CONTROL PROGRAMS. Presented at a symposium on The Biological Impact of Pesticides in the Environment, Oreg. State Univ., Corvallis, Aug. 18–20, 1969, 16 pp. 1969. (Mimeographed.)

[4] Formerly known as *M. rotundata* Fabr. (Holm and Skou *1972*).

Commercial Pollination Potentials

In a study of the beekeeping industry, Anderson (*1969*) concluded that the decline in the number of colonies of honey bees from 5.9 million in 1947 to 4.8 in 1966 was attributable to the low rate of return on the invested capital. Some beekeepers have tried to increase production by moving their colonies from one honey flow to another, a practice started as early as 1895 (Zierner *1932*). At that time, apiaries in California were moved by wagon from the desert sage and wild buckwheat to the cultivated lima bean fields. Today, thousands of colonies are moved hundreds of miles each year to several different floral sources. Anderson reported that others have tried to supplement their honey sales through the placement of their colonies in fields for pollination, but few could indicate that a profit was made.

If the need for insect pollination is increasing, one would assume that the number of colonies of honey bees should also be increasing to help meet this demand. Such is not the case. The number of colonies in the United States has been decreasing steadily for more than two decades. Furthermore, in contrast to earlier recommendations that every farm keep a few colonies of bees (Tyler and Haseman *1915*), the colonies are no longer present on almost every farm. They have either shifted to the suburbs, where they are operated by hobbyists who have short workweek employment, or they are operated by large-scale commercial beekeepers. This situation has disturbed the more or less even distribution of pollinators across the countryside, and even created a serious deficiency in some areas.

In some instances, this lack of an adequate supply is made up by the beekeeper renting colonies to the grower. An estimated 1 million colonies are rented for pollination of crops in the United States annually (there are no concrete figures on the number of such colonies). In some instances, the rental fees are no greater than those of five decades ago. There are several reasons for such low fees. There is almost no organized use of bees for pollination. Each beekeeper sets his own price. Sometimes the bees are supplied almost as a favor in exchange for apiary locations throughout the year, or for favorable consideration in relation to pesticides applied near the bees. The beekeeper may be hesitant to ask for higher fees for fear another beekeeper might undercut his price or move into his "territory."

Unfortunately, when the beekeeper operates the colonies at a low pollination fee, he tries to make up his fee elsewhere—a practice that may not be to the best interest of the grower. An inadequate number of colonies for maximum pollination may be supplied, the colonies may not contain the desired population of worker bees, or they may not be appropriately managed or distributed throughout the field to be pollinated.

A population of bees necessary for maximum set of fruit or seeds on the crop may be far greater than the location will support for honey production or colony maintenance.

There appears to be a potential market for many more properly maintained and managed colonies of honey bees for pollination of present and anticipated crops than can be mobilized. However, the beekeeper is

reluctant to go to the extra expense and labor of moving his colonies into an overstocked area unless he can collect an adequate fee for his trouble and have some assurance that the colonies will not be damaged by pesticides. He frequently finds himself in no position to bargain for these considerations. This points up the need for an organized pollination service staffed by experts acquainted with the needs and problems of both the grower and the beekeeper and capable of bargaining fairly for both. (See "Pollination Agreements and Services.")

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FLOWERING AND FRUITING OF PLANTS

Some basic knowledge of the structure of seed-forming plants, and particularly of the flower, is essential to visualize the marvelous contrivances and unique requirements for the union of the sex cells which give rise to the viable seed. Although each has a basic pattern, their intricate and diverse modifications permit plant life in some form to survive over much of the surface of our globe.

The Plant

Roots, stems, leaves, and even flower parts are sometimes concerned with asexual or vegetative reproduction. Particular sections of different plants are frequently preferable for vegetative reproduction, for example, the runners or *stolons* of the strawberry, the *tuber* of the potato, the *bulb* of the onion, the *corm* of the iris, the *nodes* or joints of the sugar cane, and the leaf of a violet. Reproduction in garlic is by *bulbils*, sometimes called cloves, that form in the flower head. Bulbils also form in the inflorescence of some agaves.

Asexual reproduction in plants has certain advantages. The asexual offspring of a plant, usually referred to as *clones*, are genetically identical. An example would be cuttings taken from a grapevine, rooted and used to

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create an entire orchard of a single clone. The plants would be uniform in appearance, vigor, flowering time, fruit ripening time, and fruit quality. Asexual reproduction can be made at any time, even before the plant is mature enough to produce seeds, or with plants such as the sweet potato or sugar cane that normally set no seed under our climatic conditions.

Asexual reproduction has some disadvantages. If there is a degree of self-sterility in the parent plant, this cannot be overcome by cross-pollination between the plants unless another compatible cultivar is interplanted. The use of asexual parts is sometimes bulky or otherwise less convenient than the use of seeds. Diseases and insects are more likely to be transferred on asexual parts than on seeds. Some plants cannot be easily or economically reproduced asexually.

Some plants reproduce both asexually and sexually, and both types of reproduction have certain advantages from the plant standpoint. Sexual reproduction, in which insects or other external agents sometimes play a part, concerns the development of seed in the flower. The external agent's contribution depends upon construction of the flower and the compatibility of the flower with its own pollen.

In sexual reproduction, cross-pollination can occur, leading to higher production or quality through more complete fertilization. It can also lead to hybrid vigor, or *heterosis*, from the crossing of two unlike plants to produce a more vigorous one. Such mixing of genes may also enable future generations to adapt to different environmental conditions, insuring their survival, as they have apparently done in the past (Leppik *1970a*, *b*). Almost two centuries ago, after Knight (*1799*) had studied the effects of self-fertilization in plants, he concluded that no plant can maintain itself with self-fertilization for an unlimited number of generations. In a figurative sense, it would seem as if Nature abhors self-fertilization and constantly strives ingeniously to achieve cross-pollination within the species. In numerous plants, selfing is permitted only after all efforts at cross-pollination have failed. Selfing is the plants final attempt to survive until favorable opportunity for crossing can occur. Again, figuratively speaking, Nature orders the plant: "Become fertilized, cross-fertilized if you can, self-fertilized if you must."

The Flower

The flower has a simple basic pattern, but with seemingly infinite variations. Typically, the flower (fig. 1) is composed of the *sexual organs*, protected by delicate colorful *petals* that form a tube or crownlike *corolla*, and which in turn are supported and partially protected by the usually green, more durable *sepals*, collectively called the *calyx*. The calyx and corolla combined are referred to as the *perianth*. There may be leaflike *bracts* just below the sepals.

The *male* part (or *androecium*) of the sexual organs are the *stamens*, which consist of the hairlike *filaments* bearing the pollen-producing *anthers* on the extremities. At the appropriate time, these anthers *dehisce* or split open and disgorge the male element, the numerous microscopic and usually yellow grains of *pollen*. The size of pollen grains varies from 4 to 6 microns for the little forget-me-not (*Myosotis sylvatica* Hoffm., family Boraginaceae) (Meeuse *1961**) to the relatively gigantic 350-micron grain of *Cymbopetalum odoratissimum* Rodr., family Annonaceae (Walker *1971*), or the 2,550 by 3.7-micron tubelike grain of the water-pollinated eel grass (*Zostera marina* L., family Naiadaceae) (Wodehouse *1935*). The size of the majority of pollen grains is in the 25- to 50-micron range.

The shape and sculpturing of pollen grains is even more diverse, and their characteristics are used in the identification of the plant source of the pollen (Wodehouse *1935*, Zander *1935*, *1937*).

The amount of pollen produced per flower varies from only 32 grains in the four-o'clock (*Mirabilis jalapa* L., family Nyctaginaceae) (Kerner *1897**, *v. 4, p. 98*), to several spoonfuls in the blossom of the Abyssinian banana (*Musa ensete* G. Mel., family Musaceae) (Pryal *1910*).

The *female* part (or *gynoecium*) of the flower is the *pistil*, consisting of the *ovary* with one to numerous *ovules* and, extending from the ovary, the *style* with the receptive portion, the *stigma*, on or near the tip. The pistil may be composed of one or more *carpels*. The ovary produces the fruit and the ovules the seeds.

The fruit on some plants—for example, certain citrus or bananas—may develop without viable seeds. Some flowers, like that of the coconut, produce only one seed. A watermelon may contain 1,000 seeds. The extreme example seems to be the orchid (*Cycnoches chlorochilon* [=*C. ventricosum* var. *chlorochilon* (Klotsch) P. H. Allen]) with 3,770,000 sporelike seeds only 470 to 560 microns long (Ames *1946*, Marden *1971*).

Typically, the ovary, with its style and stigma, occupies the central portion of the flower, which is surrounded by the stamens.

The size of the flower varies from 1.5 to 2.0 mm for *Pilostyles thurberi* Gray, family Rafflesiaceae (Munz and Keck *1959*) of southwestern United States, to 1,000 mm or more for the jungle flower of Sumatra in the same family (*Rafflesia arnoldii* R. Br.), which weighs almost 25 pounds (Kerner *1896**, *v. 1, pp. 202–204*).

The flower may be open only a few hours, for example, chicory and lettuce, which open after daybreak and are closed before noon. They may also be open for an extended period, for example, certain orchids that stay open if not pollinated for as long as 80 days (Kerner *1897**, *v. 2, p. 213*).

Flower petals vary in color through all shades from black to white, but they are rarely green. They vary in shape from that of the simple spring beauty (*Claytonia virginica* L.) to the intricately ornate orchids. Likewise, flowers vary in aroma from the seemingly odorless pomegranate to the highly aromatic sweetclover or the repulsive *Rafflesia arnoldii*.

The stalk or stem on which a cluster of flowers develop is referred to as the *peduncle*. In the cluster, the stalk of an individual flower or *floret* is called the *pedicel*. The end of the pedicel on which the flower parts rest is called the *receptacle*. Depending upon the arrangement of flowers within the floral cluster or *inflorescence*, they may be referred to collectively as a *catkin*, *corymb*, *head*, *panicle*, *raceme*, *spadix*, *spike*, or *umbel*.

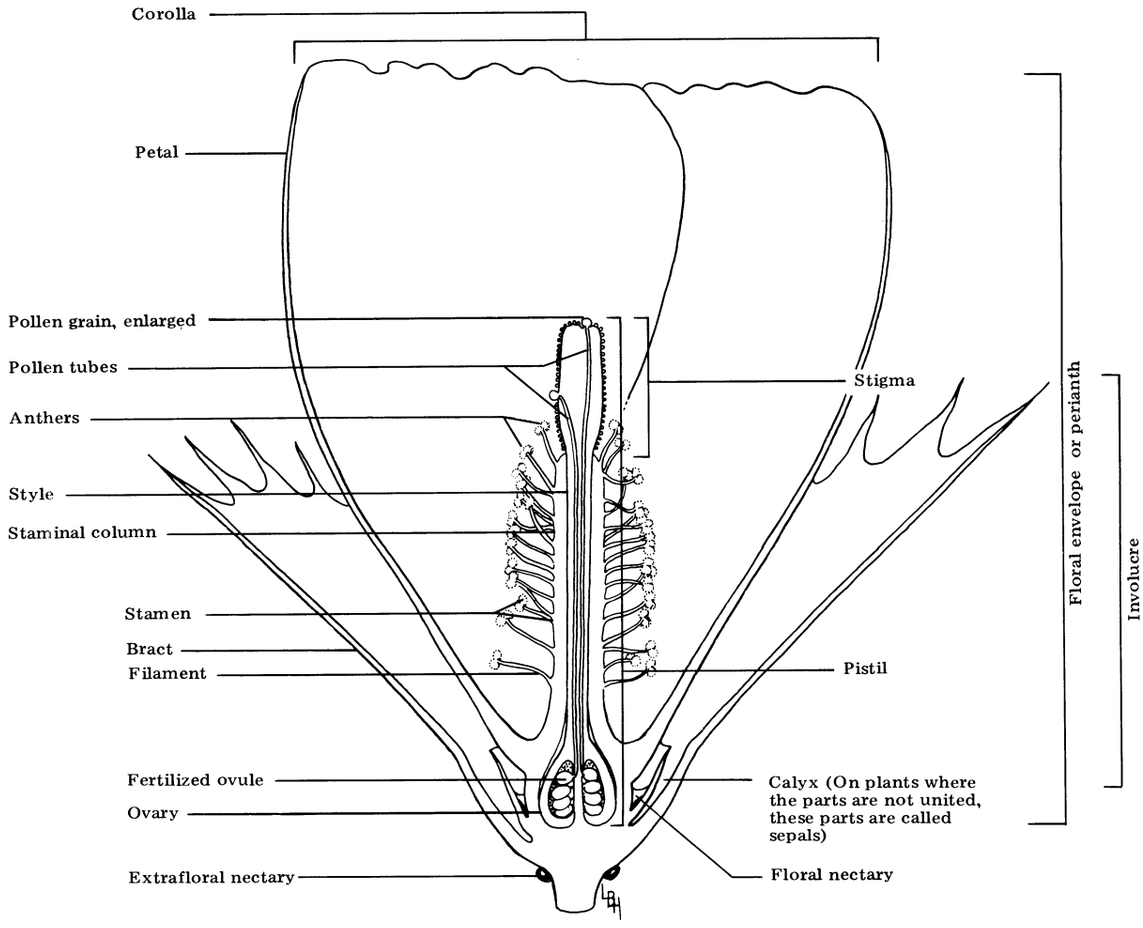

FIGURE 1.—Generalized longitudinal section of a cotton flower (*Gossypium* spp.), ×2, showing nectaries, pollen-laden anthers, and growth of a pollen-tube (further enlarged) down the style to the ovary and into an ovule.

A flower with both pistil and stamens present is called a *complete*, *perfect*, or *hermaphrodite* flower. Frequently, one or more of the sexual parts will be missing, vestigial, or nonfunctioning. If this is the case with the male elements but the pistil is normal, the flower is referred to as *pistillate* or *female*. If the pistil is in any way nonfunctional but the stamens produce viable pollen, the flower is referred to as *staminate* or *male*. If both pistillate and staminate flowers are on the same plant but distinct from each other, the plant is said to be *monoecious*. Corn, with its pollen-producing stamens (the tassel) on the top of the plant and the pistils and ovaries (silks and grains) several feet below, is a common example of a monoecious plant. If some of the flowers are perfect while others on the same plant are unisexual, the plant is referred to as *polygamous*. If the two sexes are on separate plants within a species or variety, it is referred to as *dioecious*.

In some plants, the stamens mature before the pistil is receptive to pollen. Such plants are referred to as *protandrous*. If the pistillate part matures and ceases to be receptive to pollen before the anthers of the same flower release the pollen, the flower is referred to as *protogynous*. Plants that are both protandrous or protogynous are referred to as *dichogamous*. The avocado is a dichogamous plant that has both types of flowers but on different cultivars.

A few plants have complete flowers, some of which never open. The pollen is released directly onto the stigma within the closed flower and self-fertilization results. Such flowers are referred to as being fertilized in the bud or *cleistogamous* flowers. The lemon has both completely normal and cleistogamous flowers.

Finally, within some species, there are differences in arrangement of the sexual parts, for example, one flower will have high anthers and a low stigma, whereas other flowers, sometimes in the same cluster but more often on different plants within the species, will have low anthers and a high stigma. Such plants are referred to as *heterogamous*, and such flowers are referred to as *pin and thrum* types.

Some plants are receptive to their own pollen; however, within the individual flower the pollen becomes mature either before or after the stigma is receptive. For pollination to take place, the pollen must be transferred from one blossom to another. In still other plants, their own pollen is unacceptable as is pollen from other plants of the same variety. Only pollen from another variety of the same or closely related species will cause set of fruit and seed. The mode

of transfer of pollen from one plant to another or within the flower depends upon the species of plants.

There are many more characters that flowers possess, essential for botanists in plant identification, but which do not contribute directly to plant pollination and are not included here.

The flower usually opens early in the morning although in some plants (for example, alfalfa, citrus) opening occurs throughout the day, in others (for example, evening primrose) opening occurs late in the afternoon to twilight, and in still others (for example, the saguaro cactus) opening occurs during the night (McGregor et al. *1962*). Some (for example, chicory and lettuce) only remain open a few hours; some (for example, cotton), from several hours to most of the day; some (for example, avocado), for 2 days; and some (for example, apple), for several days. The maximum time for a flower to remain open is probably reached in certain orchids which, if not pollinated, remain fresh 70 to 80 days (Kerner *1896*, v. 1, p. 395*).

Nectaries and Nectar Secretion

Flowers frequently have one or more *nectaries*, although nectaries are rarely mentioned in botanical descriptions of plants. Nectaries vary in size from microscopic to the 11-inch nectary of the orchid (*Angraecum sesquipedale* Thou.) (Darwin *1877**). The nectary is most often located within the flower, usually at the base of the sexual column inside the circle of petals. In cotton, however, there is a nectariferous ring just outside the base of the petals on the inner base of the calyx. Nectaries are also found outside the flower, on the stem or leaves. Nectar secretion within the flower usually starts about the time the flower opens and ceases soon after fertilization. Secretion of nectar on the stems and leaves is not influenced directly by flowering and may continue for several weeks.

The amount of nectar secreted varies from infinitesimal in numerous species to more than an ounce in the orchid *Coryanthes* spp. (Kerner *1897*, v. 2, p. 172*) and in *Protea mellifera* Thunb., which natives in Africa reportedly remove and drink (Langstroth *1913* and Holmes *1963*). Nichol (*1952*) reported that the nectar of the *Agave parryi* Engelm. flower stalk was gathered by Indians in the Southwest and used as a sirup. Numerous bee specialists have calculated the amount of nectar produced in the flowers of various crops. For example, McGregor and Todd (*1952**) calculated that the cantaloupe flowers on 1 acre produced 1.7 pounds of nectar in 1 day, whereas alfalfa flowers on 1 acre produced 238 pounds in 1 day.

Pollination and Fertilization

Certain words associated with pollination are frequently, but sometimes incorrectly, used. For example, a plant may be spoken of as *self-fertile* or *self-compatible* if it can produce fruit without the need for the transfer of pollen to it from another cultivar so that no interplanting of cultivars is necessary. Such a plant may not necessarily be self-pollinating. An external agent, such as the wind or insects, may be necessary to transfer the pollen from the anthers to the stigma within the flower or between flowers on the same plant. If the plant is not receptive to its own pollen, it is *self-sterile*. Even self-pollinating plants are frequently benefited by *cross-pollination*, the transfer of pollen from one flower to another. They may also benefit from having the pollen more thoroughly transferred and distributed over the stigma at the most receptive period. A plant is *cross-compatible* if it can normally be pollinated with pollen of another cultivar, but it is *cross-incompatible* if it is not receptive to pollen of certain cultivars.

Horticulturists have sometimes based their decision on the pollination requirements of a cultivar by bagging one or a few branches of the cultivar. If the set of fruit within the bag was somewhat comparable to that of open branches they concluded that the cultivar was self-fertile. In such a test, a 5- to 15-percent difference would most likely not be detected, yet such a difference could be of great economic importance to the grower of the crop.

When the stigma is receptive to pollen, it is coated with a colorless, relatively tasteless stigmatic fluid. If viable, compatible pollen comes in contact with this moist stigma, it adheres, germinates, and sends a pollen tube bearing the tube nucleus and the two sperm nuclei down through the style into the ovary and, finally, into one of the ovules. *Fertilization* follows this *pollination* process by the sexual union of one of the two sperm nuclei of the pollen grain and the egg nucleus of the ovule to form the fertilized egg or zygote. Through this process of sexual union, a viable seed is formed that is capable of producing another complete plant.

In general, the sooner pollination can occur after a flower opens the greater the likelihood that fertilization of the ovule and seed development will occur. As time elapses, the pollen may be lost to insect foragers, wind, gravity, or damage by heat, moisture, or drying out. Also, processes may set in that result in the shedding of the fruit.

Unlike asexual reproduction, which produces a plant basically identical to its parent plant, in fertilization following pollination each nucleus bears the genes of the plant from which it was derived; therefore, when they are combined the seed may not produce another plant exactly like that of either parent. For example, if the strawberry breeder is not satisfied with the type of plants he is obtaining asexually, he can transfer pollen from another variety to the stigma of an individual floret of the strawberry blossom of different selections, then save the particular seed that develops from that union to grow and be tested as a mature plant, which he studies for new and improved varieties. There is no way a breeder can forecast which cross will have improved qualities.

The manner of sexual reproduction is one of the plant's most interesting characteristics. In some instances, the likelihood of successful reproduction and survival of the plant species through centuries of time seems extremely remote. For example, the yucca plant of the Southwest depends for its survival on a particular species of tiny moth that visits the blossoms (fig. 2) at night, collects the pollen from the anthers, and transfers it to a depression in the tip of the stigma. After the pollen is packed into place, the moth lays a single egg on

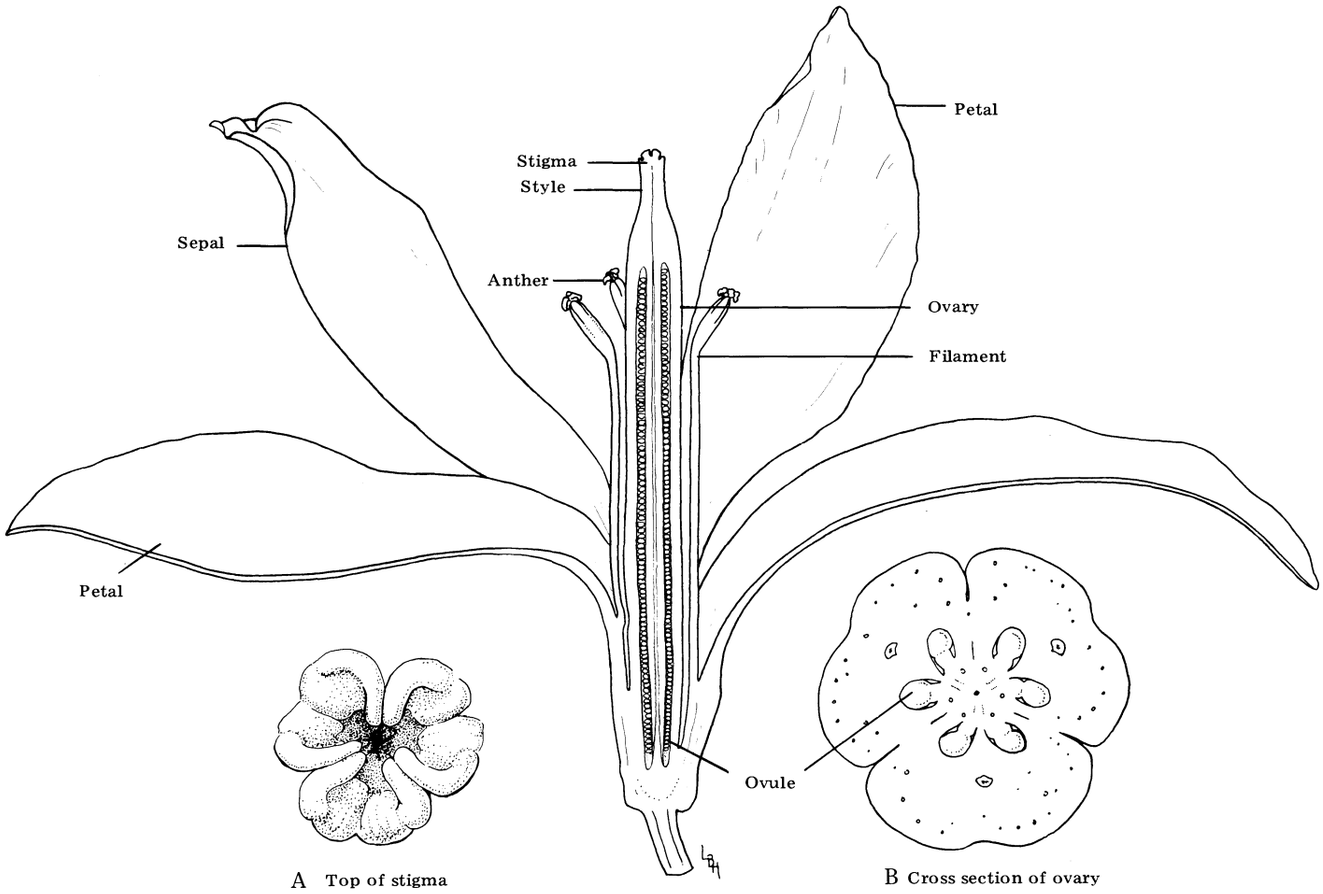

FIGURE 2.—Longitudinal section of the banana yucca, ×1. *A*, Tip of stigma, ×9; *B*, cross section of the ovary, ×7.

the side of the ovary. The pollen germinates, sends pollen tubes down through the style to the ovary, and fertilizes the ovules. About the time the ovules begin to form seeds, the larva hatches from the egg, burrows down through the style into the ovary, and begins to feed on the developing seeds, but it never consumes all of them. Some seeds survive, drop to the ground, and eventually produce new plants. The larva also reaches full size before the seeds mature. It burrows through the side of the seed pod, drops to the ground to pupate in the soil, and emerges as an adult the next year to pollinate new yucca flowers. Each is entirely dependent on the other for survival of the species (Riley *1878*). This is an example of sexual reproduction brought about through insect pollination. The elimination of either this insect or this plant could result in the disappearance of the other.

In other plants, the insect merely needs to crawl across the anthers and stigma of a flower to transfer pollen and cause fruit to set. In the cantaloupe, the pollen needs to be transferred only 1 or 2 mm to produce a fruit. If this transfer is not made, fruit is not produced. In the saguaro, or giant cactus of the Southwest, pollen must be transferred from the flower of one plant to a flower on another saguaro plant, sometimes several hundred meters away (Alcorn et al. *1961*). In the incompatible fruit tree varieties, pollen must be transferred to them from the row or tree producing compatible pollen.

If the ovary is divided into segments or locules, the styles and stigmas are also made up of corresponding *lobes*, *carpels*, or segments. When a pollen grain falls on one carpel, the pollen tube usually grows down it into its connecting locule of the ovary and fertilizes an ovule to form a seed. If for example, pollen fails to land on one of the three to five lobes of the cotton flower stigma, the corresponding *locule* or *lock* of the developing fruit will contain no seed—and consequently no lint that forms on a seed. Because each locule may contain about 10 ovules, at least 10 pollen tubes must safely penetrate them for complete development (Arutiunova *1940*). The watermelon may have 1,000 ovules in its three locules. This means that at least 1,000 pollen grains must land appropriately distributed on the three stigmas, at the proper period of receptivity, if a perfectly formed melon is to develop. Because all pollen grains may not be fertile, or may not land at the appropriate time, many more than 1,000 should be desired by the grower. Mann (*1943*) observed that a few watermelon pollen tubes crossed from one carpel to another, because the watermelon has no stylar canal within a carpel. However, where the pollen was not well distributed over all the carpels, the fruit was frequently asymmetrical, especially at the blossom end. In most

instances, pollen tube growth is limited to the carpel on which it originated.

The rate of pollen tube growth depends upon its compatibility with the style. In some cases, the flower is not receptive to its own pollen but is receptive to pollen from other plants of the same cultivar (for example, alfalfa). In other instances, the pollen must come from another compatible cultivar (for example, numerous cultivars of apples). Frequently, when the plant's own or self-pollen is compatible, the rate of its tube growth is less rapid than that of foreign pollen tube growth.

In many plant species, as soon as fertilization occurs the stigma and style wither and the petals begin to fade in color and close. As an example, the alfalfa floret wilts within a few hours after pollination but may remain fresh more than a week if not pollinated. Some flowers close at night and reopen the following day, repeating this process for up to several days (McGregor and Alcorn *1959*), but usually when the flower closes it never reopens. It either sheds or its fertilization stimulates fruit development.

The Fruit

Not all fruits develop simply as a result of ovule fertilization. In a few plants, the ovary will enlarge into a "fruit" without the stimulation of pollen. Such fruit development is referred to as *parthenocarpic* development. Parthenocarpic fruits are usually seedless, although not all seedless fruit arise parthenocarpically. For example, fertilization of the ovule may be necessary to prevent shedding even though the ovule may later disintegrate. Certain hormonal sprays will cause some plants to set seedless parthenocarpic fruit.

Some citrus fruits are *polyembryonic* with one fertilized embryo and sometimes several other nonfertilized embryos that are stimulated to develop adventitiously within the same ovule. This is referred to as *apomyctic* development or *apomyxis.*

The matured ovary, along with its contents and other structures intimately associated with it, is called the *fruit.* The fruit may be as varied as a grain of wheat, a walnut, an apple, a strawberry, or a watermelon. Fleshy fruits can be divided into types such as a berry, a drupe or stone fruit, or a pome fruit. A *berry* is defined as a fruit with a fleshy pericarp or ovary wall, surrounding one or more seeds. The grape, tomato, or watermelon can therefore be classed as berries. A *pome* fruit has a fleshy part surrounding a papery core. The apple is a common pome fruit. A *drupe* or stone fruit is one-seeded with a fleshy outer part and a stony inner part. The almond, cherry, olive, and peach are stone fruits.

The strawberry is an *aggregate* fruit type, with each pistil developing into a tiny achene, and the entire mass, including the enlarged fleshy receptacle, developing as a unit. In the raspberry, the pistil develops into a drupelet. The receptacle of the raspberry does not enlarge, and upon harvesting of the ripe fruit it is not removed from the plant. This leaves the well-known hollow space in the raspberry.

Development of the Knowledge of Plant Pollination

The transfer of the male sex cells to the female portion of the flower, and the fusion of the cells in the ovule is a critical period in the life of a plant. In the manipulation of pollinating agents, man contributes to the efficiency of this fusion and to the insurance that the plant will be productive of fruit or seeds to his benefit.

The basic principle of sex differentiation in plants may have been known as early as 1500 B.C. Goor (*1967*) stated that the Hebrews learned the value and art of date pollination from Egyptian and Babylonian experts. An Assyrian architectural relief of that period shows two divine creatures, each presumably holding a male date inflorescence over a female inflorescence (Faegri and van der Pijl *1966**). Kerner (*1897*, v. 5, p. 555*) stated, "When we consider that from time immemorial, Chinese and Japanese gardeners have produced asters, camellias, chrysanthemums, peonies, pinks, and roses, of which the majority are the results of crossing, we may assume with certainty that the practice of dusting flowers of one species with pollen of another species first came into use in those countries." Werkenthin (*1922*) quotes the Arabic writer, Kazwini, who died about 682 A.D., as saying that the date is the only tree that is artificially fertilized. Growers of dates today use this method to assure a set of dates in their groves (see "Dates"). However, if this indicated a recognition of sex in plants, the idea was not carried over to other plants. It was not until 1682 that a botanist, Nehemias Grew, stated that pollen must reach the stigma to insure the development of seeds. Apparently, however, he assumed that the stamens of a flower shed their pollen directly onto the stigma of the same flower (Dowden *1964*).

In 1694, Rudolph Jacob Camerarius published a letter, "De sexu plantarum epistole" (Werkenthin *1922*, Grant *1949*), in which he stated that based upon his experiments there are two different parts of the flower, the stamens and the pistil, and that they must work together to produce ripe seed. He concluded that these two parts represented true sexual organs (Faegri and van der Pijl *1966**). Actually, these had been recognized, and even the union of the two sexes was reported on centuries earlier by the Greek philosopher, Theophrastus (*300 B.C.*), "The Father of Botany" (Dzhaparidze *1967*).

In 1750, Arthur Dobbs, communicated to the Royal Society of London that the pollen was the male element which, after falling upon the stigma, was capable of fertilizing the ovary. He further concluded that the pollen must come from its own species (Grant *1949*). Watson (*1751*) reported that he transported date pollen 20 miles and pollinated a previously fruitless tree. In 1761, Koelreuter who is usually regarded as the discoverer of sexuality in plants, concluded that bees are agents in the transfer of pollen from the male to the female elements of the flower (Grant *1949*). He was the first to cross-pollinate and produce a hybrid between two plant species (Sinnott *1946*). In 1763, Arena also wrote rather fully on the subject of cross-pollination in plants and noted that it was carried out by insects (Lutz *1918*).

Sprengel (1793), however, was the first to really explore sex in plants, the important part played by pollinating insects, and the significance of cross-pollination in plant life. His work stimulated future work on

sex in plants and the part played by insects. Thomas Andrew Knight (*1799*) showed the value of cross-pollination between plants and hybrid vigor: ". . . nature intended that a sexual intercourse should take place between neighboring plants of the same species." He noted that the location of the pollen within the blossom was ". . . generally well adapted to place it on the bodies of insects; and the villous coat of the numerous family of bees, is not less well calculated to carry it." The value of cross-pollination was later supported by Herbert (*1837*).

Not until 1830, however, was the observation made by Amici on the formation of the pollen tube and its passage down the style and into the ovule. This was soon followed by recognition of the fact that there is sexual fusion between gametes in the ovule (Sinnott *1946*).

It was left for Darwin (*1889**) to prove conclusively and to dramatize the importance of pollination in perpetuation and vigor maintenance of the plant species. He studied scores of species, using both hand and insects to pollinate the plants on which he measured the value and significance of cross-pollination. Much of the work on plant pollination since his time is based upon the theories he promulgated. Little has been added to the knowledge of pollination requirements of some plant species since his work was published.

The first contribution of great importance on pollination from the United States was the discovery by Waite (*1895*) of self-sterility in pears and the need for insect-transfer of pollen between varieties. This initiated a new wave of interest particularly in fruit pollination, although many contributions on the value of pollination had already appeared (Crane *1876*, Hutchinson *1886*, Müller *1883**), and the various apicultural journals were beginning to extoll the virtues of the honey bee as the best pollinating agent. Benton (*1896*) recommended ". . . 4 or 5 well-populated hives of honey bees for every hundred large apple trees, the hives to be placed in or near the orchard." The renting of colonies for orchard-pollination service had its beginnings the first decade of this century (Beuhne *1909*, Stricker *1971*).

The acute need for legume seed that developed during World War II stimulated our Congress to establish the USDA Legume Seed Research Laboratory at Logan, Utah. The combined efforts at this laboratory established the value of honey bees in the pollination of alfalfa for seed production (Utah Agr. Expt. Sta. *1950*). As a result, several hundred thousand colonies of honey bees are currently being used to pollinate this crop alone.

The latest stage of development in the management of pollinating insects in production of crops is the large-scale use of wild bees, primarily the gregarious ground-nesting alkali bee (*Nomia melanderi* Cockerell) and the equally gregarious tube-nesting leafcutter bee (*Megachile pacifica* Panzer) (Bohart *1972*, Stephen *1959*). (See "Wild Bees.")

Some other sources of information on pollination should be mentioned. Clements and Long (*1923*) spoke in general terms about pollination of numerous plant species. Hooper (*1921*), Hutson (*1926*), Kenoyer (*1916*), and Wellington et al. (*1929*) discussed the pollination of several specific crops, and Farrar (*1931*) became concerned about the strength of colonies of honey bees used for pollination. Other smaller but key papers published in the United States include those by Bohart (*1960**), Bohart and Todd (*1961**), Eckert (*1959**), Hambleton (*1944*), Todd and McGregor (*1960*), and Vansell and Griggs (*1952**). Some broad spectrum publications in other countries include: (Australia) Gale (*1897*); (England) Butler and Simpson (*1953*), and Free (*1960*); (India) Krishnamurthi and Madhava Rao (*1963*); (Italy) Giordani (*1952*); (Jamaica) Chapman (*1964**), and Purseglove (*1968**); and (Russia) Krishchunas and Gubin (*1956**), Gubin and Khalifman (*1958*), and Kasiev (*1964*).

For up-to-date knowledge and completeness, none of these surpasses the recent excellent publication by Free (*1970**). He dealt thoroughly with the pollination needs and the management of pollinating insects to supply those needs for each family of plants he considered to be benefited by such pollination.

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HYBRID VIGOR IN PLANTS AND ITS RELATIONSHIP TO INSECT POLLINATION

Hybrid vigor, or *heterosis*, describes the increased vigor of plants or other organisms when compared with parents that were unlike in one or more inherited characters. Although there is no single, fully acceptable genetic definition of hybrid vigor (Ashton *1949*), it may be observed in the offspring in terms of increased size, uniformity, volume, quality in earliness, or resistance to unfavorable environmental factors.

Plant breeders express the degree of hybrid vigor of an agronomic character in different ways; the percentage increase over the *best* parent, over the *midparent* or average of the two parents, or over the best *commercial cultivar* in the area. The way the breeder chooses to express the hybrid vigor determines the percentage. For example, a cotton selection or line '*A*' may produce 800 pounds of lint per acre, and line '*B*' may produce 1,000 lb/acre. When crossed, the offspring or F_1 (first filial generation) produces 1,200 lb/acre. The best commercial cultivar in the area also produces 1,200 lb/acre. Depending upon which way the breeder chooses to express the hybrid vigor, it may be 33 percent (over the midparent), 20 percent (over the best parent), or 0 percent (over the best commercial cultivar based on yield, but because the F_1 or hybrid between '*A*' and '*B*' sets its crop of cotton on the stalk 3 weeks earlier than the commercial cultivar, thereby reducing irrigation and harvesting costs and insect pest problems, the hybrid is preferred. This undefinable earliness factor and, likewise, other intangible factors not measurable by yield alone may be ascribed to heterosis or hybrid vigor.

Neither hybrid vigor nor its qualities can ever be predicted. They can only be established or proven through testing of the F_1 for each parental combination. Hybrid vigor cannot be maintained at its maximum because it starts reducing with the first generation in which self-pollination may occur. For maximum vigor, it must be created anew each season.

The potential use of hybrid vigor in plants is always tantalizing to the breeder because it promises a new plateau of productivity. The problem is, first, the finding of this factor then, second, the development of a method of utilizing it economically under commercial conditions. In contrast to hybrid vigor, the inbreeding of a normally cross-pollinated plant not only results in an isolation of biotypes but also in a loss of vigor of the individual plant (Hawthorn and Pollard *1954**), which can make it more susceptible to unfavorable environmental factors. The inbreeding effects on a normally cross-pollinated plant are roughly the opposite of hybrid vigor.

The classic example of the use of hybrid vigor in plants is in hybrid corn production. The monoecious characteristic of corn makes it a simple plant for use in this manner because the male part, the tassel, and the female part, the ear, are widely separated on the plant, and, more importantly, the pollen is transported by wind. The only steps necessary after an appropriate cross is decided upon is to alternately plant rows of the two parental selections, then mechanically remove the tassels on one of the rows before flowering begins. Pollen may then be carried by the wind from the row with its tassels intact to the silks of the ears of the detasseled row. All of the grain produced on the detasseled row will be hybrid seed, and, likewise, the grain on the pollen-producing row will provide inbred seed for the next production season.

Unfortunately, in most other plants, the male and female parts are intimately associated within the same flower (complete flower) rather than being separated as in corn. When the male parts cannot be removed with dexterity, other means are explored for fertilizing the flowers of a plant with the desired pollen. One method is to use a *self-incompatible* parent with a suitable combiner. In incompatibility, which is widespread among

plant families (Lewis *1949*), the pollen and the ovules of both plants are independently functional, but because of some incompatibility between the maternal tissue and the pollen tube development, the pollen nuclei fail to unite with the egg nucleus and thus complete fertilization (Allard *1960*). If plants possessing the genetic mechanism based on incompatibility are wind pollinated or *anemophilous*, the only action required to produce a hybrid is to interplant rows of the two cultivars and all the seed will be F_1. If they are insect pollinated or *entomophilous*, arrangements must be made to have sufficient pollinating insects available to transfer the pollen. If pollen falls upon the stigmas of flowers of its own maternal origin, no fertilization occurs. If it falls upon compatible flowers, a hybrid results.

Male Sterility

Within recent years, a simple method has been found for obtaining 100 percent cross-pollination on a large scale in plants that normally have both sexes within the same flower. The method utilizes *biological emasculation* of the plants, in which the pollen grain either fails to develop or is not viable. Such plants are referred to as being *male-sterile.* Male sterility of some form has been found in many crops, and breeders are always on the alert for such plants among their selections. Male-sterile plants appear unexpectedly even in long-established commercial cultivars.

Two types of male sterility have recently become economically significant, and are used by plant breeders: *cytoplasmic male sterility* and *genetic male sterility* (Duvick *1967*). In the former, sterility is carried in or influenced by the cytoplasm. In the latter, it is carried in or influenced by the germ plasm of the nucleus, which contains the genes or hereditary characters. Because of their importance and relationship to insect pollination, they are discussed below in some detail.

Cytoplasm is the material of a cell that is transmitted from parent to offspring only through the egg, or the maternal side, independent of the cell nucleus. Characters influenced by the cytoplasm respond the same as in the female parent. Cytoplasmic male sterility is, therefore, carried through the maternal side of the line. The genes present in the nucleus are derived from both parents; therefore, genetic male sterility is influenced by both parents.

One explanation of cytoplasmic male sterility (used as a teaching device by L. S. Stith, personal correspondence, 1972) is shown in fig. 3 and is similar to the explanation given by Briggs and Knowles (*1967*). Here the ovule of the milo group (female) of *Sorghum vulgare* L. [=*S. bicolor* (L.) Moench] is fertilized with pollen from the kafir group (male) of the same species. The cytoplasm and half of the genes in the nucleus are thus from the milo (female) and half of the genes are from kafir (male) in the F_1. However, in the presence of the milo cytoplasm, the kafir genes produce sterility and approximately 50 percent of the F_1 are male-sterile. When these male-steriles are backcrossed to kafir, a higher ratio of sterile-fertile plants appear. Likewise, by the sixth backcross generation, near complete male sterility (99 percent) is established. Fertility can be

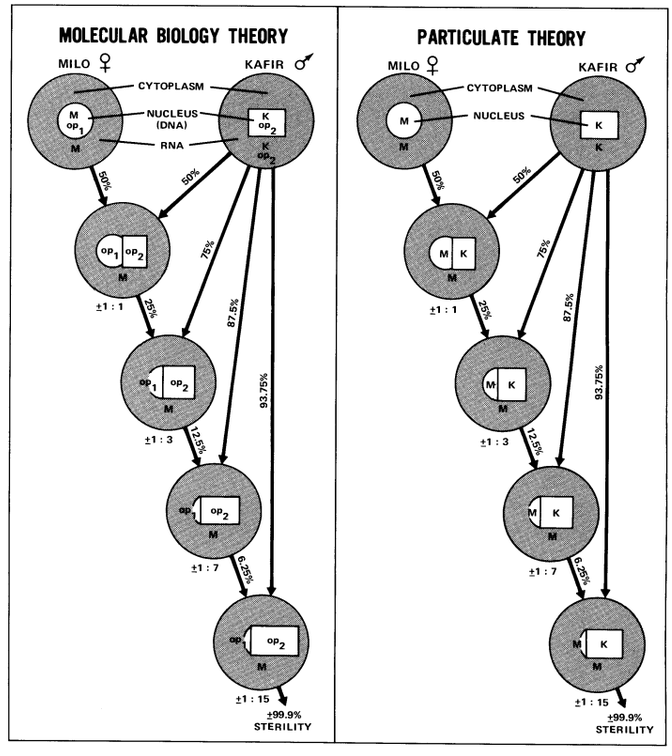

FIGURE 3.— Probable inheritance of cytoplasmic male sterility in the Milo (M. ♀) group of *Sorghum vulgare* L. [=*S. bicolor* (L.) Moench.] when its ovule is fertilized by the sperm in pollen of the Kafir (K. ♂) group. Explanation: op= operon or operator gene—a genetic unit consisting of adjacent genes that function together under the joint control of an enhancer and/or a repressor factor: bc= backcross. Ratios indicate probable proportion of fertile to sterile genes. (After L.S. Stith, personal commun., 1972.)

restored at any time by reversing the mating and backcrossing the sterile plants to milo.

The teaching device may leave something to be desired as an explanation for plant breeders or geneticists, but it does visually demonstrate incompatibility between nucleus genes (represented by a square) and plasma genes (represented by a circle). An explanation based on the DNA-RNA concept is simple and easily understood if one assumes that the Operon and structural genes controlling sterility are not identical in the milo and kafir group. By continual backcrossing to kafir, sterility is increased but fertility is restored when the plant is backcrossed to the milo group. The DNA-RNA molecular system simply explains partial sterility because DNA may be carried in organelles in the cytoplasm.

Cytoplasmic male sterility, therefore, is concerned with the incompatibility between factors in the cytoplasm of the cell and the genes of the nucleus.

Genetic sterility is that form involving only the genes in the nucleus of the cell, independent of the cytoplasm. The gene contribution is from both parents, with male sterility being the result of homozygous recessive genes or factors.

The cytoplasmic-genetic male sterility is the result of an interaction between the genetic and cytoplasmic systems. Under this system of male sterility, the double

recessive genes (*ms ms*) in the nucleus produce fertile progeny (*F*) in normal cytoplasm but produce sterile progeny (*S*) when acting in a cytoplasm that has undergone change (Briggs and Knowles *1967*).

The *cytoplasmic-genetic male sterility* system differs from cytoplasmic male sterility in that the offspring of the male-sterile plants may be male-fertile when crossed with certain selections that merely change the cytoplasm. Again, based on the molecular theory, the male sterility becomes a function of the DNA code in the nucleus of one parent being unable to activate the RNA system in the cytoplasm of the other parent.

Jones and Davis (*1944*) were the first ones to report the use of male sterility in the production of a commercial crop (onion seed), and they used the cytoplasmic-genetic system. After finding a male-sterile 'Italian Red' onion, which was propagated by its bulbils until the system could be understood, crosses and repeated backcrosses were made between the 'Italian Red' and a 'Crystal Wax' cultivar until the sterility was transferred to that commercially desirable cultivar.

The breeding research revealed two types of cytoplasm—fertile (*F*) and sterile (*S*). Those plants that had the (*F*) factor produced viable pollen, those with (*S*) cytoplasm did not. When a restorer gene (*R*) was introduced from the male parent, the dominant gene (*Ms* or *Rf*) action produced fertile progeny, thus both genetic and cytoplasmic inheritance were involved. In commercial production of onions, 4 to 12 rows are planted with a male-sterile type for each one to two rows of male-fertiles (fig. 4), and they must both flower at the same time. Bees transfer the pollen to the male-sterile heads, and the hybrid seed is produced on these heads. The male-fertile flowers may be destroyed or harvested separately after pollination is completed. The seed that is harvested, being hybrid, produces an onion superior both in yield and flavor.

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FIGURE 4.— Hybrid onion seed production. Note the 2 pollinator rows (center, with larger flower heads), which supply pollen for 6 male-sterile rows (3 on each side) to produce the cross-pollinated onion seed.

Future Possibilities and Problems in the Use of Bees to Pollinate Male-Sterile Crops to Utilize Hybrid Vigor

The utilization of hybrid vigor is enticing. For example, its use was estimated to increase the yield per acre of corn by 35 percent (Jenkins *1936*). In cotton, Stith (*1970*) estimated that production might be increased 20 to 25 percent by use of hybrid vigor, which he estimated would be worth $275 million per year to our growers, or the same annual production could be obtained from 20 percent less acreage. He believed this would result in no additional expense to the grower except for the increased harvest cost. Corn is wind pollinated but insects, primarily honey bees, would be required to cross-pollinate cotton.

Kinman (*1970*) reported the discovery of a fertility-restoration gene for cytoplasmic sterility in sunflowers. This, he believed, was the final step required in the development of hybrid sunflowers. In personal correspondence, Kinman indicated that this male sterility and its restorer in sunflowers could result in doubled production of current cultivars. The effect of such an increase in production and potential profits on the future of this crop in the United States is unpredictable but will doubtless be great. Bees would be required to transfer this pollen from the fertile to the male-sterile plants.

Hybrid onions now command the bulk of the onion market. Growers use honey bees almost exclusively in transferring the pollen of the fertile plants to the male-sterile ones. Because there is no pollen for the bee to collect on the male-sterile plants, it visits the blossoms only to collect nectar. Onion growers frequently complain that honey bees are reluctant to visit the male-sterile flowers solely for the nectar. To produce hybrid seed, the flowers on the male-sterile onion row must be visited by nectar-seeking, pollen-coated bees that have previously visited the fertile rows.

The above discussion illustrates the need to consider the attractiveness of the plant to nectar- and pollen-collecting insects during the process of developing a male-sterile plant. It must be recognized that bees may visit a flower for its pollen, its nectar, or both, and in male-sterile plants only nectar is available. Bee breeders have made selections of bees that show preference for alfalfa pollen (see "Alfalfa"), but no selections have appeared that show preference for nectar. The plant breeder might approach the problem from another angle—by selecting plants that produce more nectar or, at least, more attractive nectar for the bees. Cooperative work between bee and plant specialists in this area may prove valuable.

Caviness (*1970*) stated that hybrid soybeans as a commercial crop was intriguing, but he doubted that it would ever materialize because the flowers were small and unattractive to bees, and had other discouraging characteristics, including the sparsity of nectar and pollen and the relative concealment of the flowers by the foilage. Male sterility has, however, been found (see "Soybeans") in soybeans. Also, other breeders are looking for ways to utilize hybrid vigor in this $2 billion crop because the potential profits are great with only a minor increase. The primary problem seems to be the relative unattractiveness to bees. Already there are leads in that area. Some plants show greater attractiveness than others.

The discovery of a strain of beans highly attractive to bees or the development of a way to attract bees to the flowers could almost assure utilization of hybrid vigor in

this crop. This is an example of a crop on which cooperative research between bee specialists and plant specialists can no doubt make advances of benefit to both.

Rubis (*1970*) indicated that hybrid safflower was feasible based on differential separation of male and female parts, which he called *functional male sterility*. In this crop, the male-sterile plant produces pollen on the anthers inside the anther tube. The anthers release the pollen only after the style has elongated and pushed the stigma beyond reach of the anthers. Bees visit these flowers freely for nectar, bringing pollen from stigmas that have pushed pollen before them and out of the anther tube. In their collection of the nectar, they may also transfer pollen from the anther tube to the stigma of the same flower.

Davis and Greenblatt (*1967*) have reported the discovery of cytoplasmic male sterility in alfalfa with a restorer gene. Hybrid alfalfa is produced on a limited scale now, and the discovery of cytoplasmic male sterility may greatly enhance the use of hybrid vigor in this important crop. Because alfalfa is a perennial crop, the male-sterile plants could be used for several seasons.

Foster (*1967*) reported that hybrid muskmelons produced twice as much fruit as the commercial lines. Foster (*1968*) reported the discovery of male sterility in muskmelons. The plants are entomophilous and are freely visited by bees for nectar, so the future commercial use of male sterility and hybrid vigor in melons is bright.

Nieuwhof (*1969, p. 231*) stated that genetic male sterility had been found in Brussels sprouts, cauliflower, and sprouting broccoli, but a laborious task of thinning would be required to remove the (roughly 50 percent) male-fertile plants. He doubted that commercial utilization of hybrid vigor in this group was likely. Other breeders are searching for cytoplasmic male sterility in these crops through which complete sterility might be obtained. The cole crops and numerous other vegetable crops are insect pollinated.

An economical way of producing hybrid tomato seed is highly desirable. The few bees that visit current cultivars of tomatoes do so only to collect pollen. A male-sterile strain would therefore be of no interest to such bees. Possibly some of the primitive species of this family group produce nectar. If such a species could be found and this characteristic transferred to a commercial male-sterile cultivar, it would then attract the insect pollinators, and insect cross-pollination could be achieved. Here again, cooperative research between exploratory botanists, plant breeders, and entomologists might be productive to the public.

Regardless of the type of male sterility—incompatibility, or cytoplasmic, genetic, cytoplasmic-genetic, or functional sterility—if insect activity is involved, specialists should cooperate to utilize all factors in the development of more productive crops.

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POLLINATING AGENTS AND THEIR COMPARATIVE VALUE

Although this handbook principally concerns insect pollination, other pollinating agents should be recognized and their relative value considered.

Wind Pollination

Insofar as it benefits man's existence, wind is probably the most important pollinating agent. The majority of the forest trees, for example, alders, birches, conifers, hickories, junipers, oaks, and poplars are wind pollinated. Within the grasses and grains, corn is largely dependent upon wind for its pollen dispersal. Although many of the grasses are self-pollinated, any cross-pollination that occurs is usually caused by wind or gravity.

Many plants that cause discomfort to man in the form of respiratory allergies are also pollinated by wind. Some examples of these are various grasses, junipers, pigweeds, and ragweeds.

Immediately after the pollen from some of these plants is exposed to the air and while it is still moist, it may be collected by bees and utilized as food. Some cross-pollination of wind-pollinated plants can occur in this way and doubtless does so as a result of bee activity. Later in the day, the wind also distributes the pollen, and the relative effect of the two different agents cannot be separated.

The flowers of wind-pollinated, or anemophilous, plants are usually small and unisexual. The anthers are numerous, and they produce large amounts of light, dry, usually round and smooth grains of pollen. The corollas are small and inconspicuous, the petals sometimes absent, and the stigma is often large or feathery. Corn is a common example of a monoecious wind pollinated plant. The female element, the ear, is near the center of the plant. The ear consists of numerous pistillate florets with stigmas, the silks, as much as 12 inches long. The pollen grain falls on the silk, sends its pollen germ tube down the inside of the silk to the female nucleus, and, upon fertilization, the grain on the cob is formed.

The common cattail (*Typha latifolia* L., family Typhaceae) produces pollen in such abundance that it is harvested by the Apache Indians of the Southwest and sold to the Navajos for use in rituals (Durham *1951*) and harvested by one commercial operator and sold to beekeepers for bee feed.

Water Pollination

Water serves to transport the pollen of certain hydrophyllous plants. For example, in *Vallisneria americana* Michx. (family Hydrocharitaceae), the boat-like staminate flowers break off at the stem and float about on the surface of the water with the pollen-bearing anthers extending over the side. The pistillate flowers develop and open on the surface of the water. Eventually, the anthers bump against a receptive stigma, pollen is transferred, and fertilization results (Kerner *1897*, v. 4, pp. 130–132*). Pollination under water is much less frequent (Knuth *1906*, p. 68*).

Raindrops also contribute to the transfer of pollen from the anthers to receptive stigma of Piperaceae flowers (see "Black Pepper").

In general, most pollens are rendered useless upon contact with water, and the number of water-pollinated plants is limited.

Snails and Slugs

A few plants are adapted for pollination by snails and slugs, which feed upon the more succulent areas of the plants such as the flower parts. Plants so adapted are usually closely crowded, they grow in water or moist places, and the stigmas and anthers do not protrude far out of the corolla. Plants listed by Pammel (in Pammel and King *1930*, pp. 892–894*) that benefit by such pollination include duckweeds (*Lemna* spp., family Lemnaceae), *Philodendron pinnatifidum* (Jacq.) Knuth (family Araceae), *Rohdea japonica* Roth (family Liliaceae), and similar plants.

Spiders and Mites

Knuth (*1909*, p. 542*) listed one family of mites (Acarida) and two families of spiders (Araneida) as flower visitors, but apparently they are of no significance.

Birds

Various kinds of birds are effective pollinators of flowers. Meeuse (*1961*, p. 96*) stated that about 2,000 species of birds belong to about 50 families that visit flowers more or less regularly, two-thirds of them being "specialists" that rely upon flowers for most or all of their food. Grant and Grant (*1965*) considered that numerous species of the wild-flowered phlox family were pollinated by hummingbirds. Alcorn et al. (*1961*) reported on the effectiveness of the white-winged dove (*Zenaida asiatica mearnsii* (Ridgway)) in pollinating the saguaro cactus (*Carnegiea gigantea* (Engelm.) Britt. and Rose, family Cactaceae) and mentioned numerous other occasional visitors to these flowers, including the cactus wren, Gila woodpecker, gilded flicker, and the thrasher (fig. 5).

Bird-pollinated flowers are usually colorful, because birds locate the flowers by their excellent vision rather than by their relatively poor sense of smell. Also, the bird-visited flowers usually have an abundance of nectar,

FIGURE 5.— Whitewinged dove feeding upon nectar in the flower of saguaro cactus.

FIGURE 6.— Bat feeding upon nectar of agave flowers.

which is necessary to compensate the bird for its visit to the flower.

Hummingbirds were observed by the author on one occasion visiting flowers of the cotton plant, but this visitation is so rare as to be of no economic significance. Visitation to wild flowers and numerous ornamentals is much more common (Grant and Grant *1967a,b*).

Mammals

BATS

Several mammals are considered to be pollinating agents of flowers. The bat *Leptonycteris nivalis* Saussure) feeds upon the nectar and pollen of the saguaro and certain agaves (fig. 6) (Alcorn et al. *1961*). Pollen found in its stomach indicates that it feeds on numerous other night-flowering desert and tropical plants. Because this bat seems to survive largely, if not wholly, upon nectar and pollen, it might aptly be dubbed a "mammalian honey bee." Other bats, referred to as flying foxes (*Cynopterus* spp.), also visit certain tropical flowers and probably serve to cross-pollinate them.

Insecticides are apparently detrimental to bats also. Cockrum (*1969*) studied the bat populations in a cave near Morenci, Ariz. He estimated its population at in excess of 25 million individuals in 1963, but only 30,000 in 1969. This species ranged far enough to reach the cultivated areas where insecticides were applied. However, another species in the same area with only a short foraging range suffered no reduction in population; therefore, he concluded that the reduction in bat numbers resulted from the effect of insecticides.

MONKEYS

Although there seems to be no written reference to monkeys as pollinating agents, R. J. Knight, Jr., (personal commun., 1971) stated that the tropical plant *Bombacopsis* spp. (family Bombacaceae) produces much nectar, which is sought after by small monkeys. He stated that in the process of feeding upon the nectar these animals would seem to become agents in cross-pollination of these flowers.

KANGAROOS

The kangaroo was proposed as a possible pollinator of the Australian *Dryandra* spp. (family Proteaceae) by Kerner (*1897*, v. 4, p. 230*) although the proposal has been questioned by K. M. Doull (personal commun., 1972).

Mechanical or "Artificial" Pollination

Previously mentioned pollinating animals, including insects, transfer pollen purely by chance as they go about foraging for food. Man has also become a pollinating agent of great significance, but he intentionally transfers pollen. In his plant breeding work, man intentionally applies pollen of a known specific source to a specific stigma to create improved cultivars. He also applies pollen to entire flowering fields or orchards to create increased set of certain fruit or nuts.

Pollen of such crops is routinely harvested, sometimes the season before it is used, then mechanically distributed by various means onto the stigmas to be pollinated. Pollen may be applied by a tiny brush onto the stigma of individual flowers, it may be dusted over clusters of flowers by hand, or diluted with a carrier and mechanically blown amongst the flowers by shotgun blast, bomb, power duster, helicopter, or fixed-wing airplane.

The commercial vanilla crop is completely dependent upon hand pollination (see "Vanilla"). Our date crop and some of the cherimoyas (see "Cherimoya") grown in the United States are regularly produced by hand pollination.

As a pollinating agent of individual flowers, man is exhorbitantly expensive. Shemetkov (*1960*) calculated

that in the pollination of greenhouse cucumbers one colony of honey bees was as effective as 300 men.

One or two companies harvest specific pollens and market them using intricate methods of storing and handling the pollen. This pollen is only used on high-value crops such as apples, cherries, prunes, and walnuts, and then only if pollinating agents are inactive because of inclement weather, a compatible cultivar is nonexistent, or the flowering periods do not coincide.

The pollen is usually collected from buds rubbed across screen wire to mutilate the anthers and release the pollen, which is then removed and refrigerated. Bee-collected pollen has been tested for its fertility, but it is usually unsatisfactory (Griggs et al. *1950, 1952**).

Beehive Inserts

A combination man-insect pollination technique is also used in which hand-collected pollen is placed in a metered dispenser on beehive entrances. By this method, outgoing bees have the pollen, usually diluted with *Lycopodium* spores, sprinkled on their bodies, and they carry it to the flowers (Burrell and King *1932;* Griggs et al. *1952*;* Griggs and Iwakiri *1960*; Johansen *1955*, *1956*, *1957;* and Townsend et al. *1958*). This method, which was thoroughly reviewed by Free (*1970* pp. 413–416*), has met with only limited success. The metering devices must operate only when the bees are flying, which may be only a few hours or on intermittent days; therefore, a considerable amount of man hours is required to see that they operate properly.

When there is no alternative to failure in setting a crop of fruit because the usual source of pollen is lost or delayed and any effectiveness is better than none, the inserts should be used. If conditions become ideal for their use, a normal crop may be set.

Insects

As compared to insects, the previously mentioned pollinating agents, with the exception of wind, are insignificant in the pollination of our cultivated crops. Almost every order of insects has been mentioned in connection with the pollination of some plant. Insects vary in size from tiny midges scarcely a millimeter long to giant butterflies with a wingspread of almost 200 mm. Those insects that have been mentioned in connection with the pollination of our commercial crops include: ants, aphids, bees (honey bees and other colonial, gregarious, and solitary bees), beetles, butterflies, flies, midges, mosquitoes, moths, thrips, and wasps. The bees are by far the most important of the insects.

Entomophilous or insect-pollinated flowers are relatively colorful, and the pollen grains are fewer in number than in the anemophilous plants. They are sticky and tend to adhere to each other in clusters. In some plant species, the grains seem to be heavily coated with a viscid material. Most of the insect-pollinated flowers have one or more nectaries within the flower, usually at the base of the corolla. Meeuse (*1959*) reviewed the value of beetles as pollinators. Even mosquitoes pollinate the orchid *Habenaria obtusata* Richards (Stoutamire *1968*).

Bees provision their nests with nectar and pollen. They methodically and rapidly go from flower to flower in collecting this food, usually in no way injuring the flower (fig. 7). Occasionally, certain bumble bees learn to cut small holes in the base of the corolla and collect the nectar without entering the blossom. The only discernible damage is that they and other pollinators then "rob" this nectar from the flower without making contact with the sexual column and effecting pollination. The body of the bee is covered with branched or plumose hairs to which the pollen clings and is transported from flower to flower.

Bees are usually considered to be visitors to the plant in that they spend a short amount of time in the flowers then return to their nest elsewhere. However, Tsyganov (*1953*) stated that bees are not guests but "thoroughly adapted symbionts, because they feed and rear their young on the products gathered from the flowers." Symbionts may be described as two dissimilar organisms living together in some intimate mutually beneficial relationship. In this case, the bee benefits by obtaining the pollen and nectar, which is its sole source of food. The plant benefits by being cross-pollinated without which it might become extinct. (For more details on the bees see "Wild Bee Culture" and "Beekeeping in Relation to Pollination.")

Insects other than bees usually benefit only specific crops, frequently only at specific times, and often only to a minor degree. This may be due to their anatomy, habits, or mode of reproduction. For example, *moths* and *butterflies* are covered with scales, somewhat like roof shingles, instead of with hairs. As a result, few pollen grains are likely to adhere to their bodies. They only consume nectar for their bodily requirements as an energy food and do not provision their nest. Usually, the proboscis is relatively long and delicate so it is unlikely to transfer much pollen. Frequently, the remainder of the body does not contact the pollen.

The *wasp* is interested only in the nectar of the flower. It provisions its nest with caterpillars and

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FIGURE 7.— Honey bees collecting pollen from flowers of saguaro cactus.

occasional droplets of nectar, presumably for adult food. Its body is sparsely covered with rather coarse spines, not adapted to the transfer of pollen as are the hairs of the bee. Where the wasp forages for nectar, it is unlikely to become pollen coated as does the bee. Wasps of the family Scoliidae are effective pollinators of alfalfa. When they collect the nectar, they trip the flower in the process. When collecting cotton floral nectar, Scoliid wasps are also excellent pollinators of the blossoms. In general, however, wasps are of little significance as pollinators. An exception is the tiny fig wasp (see "Figs"), which enters the opening in the end of the fig and crawls over the flowers in search of a suitable place to deposit its eggs. The fig is pollinated in the process.

Beetles frequently feed upon pollen as well as the anthers and other flower parts. They are at times of some value in the pollination of certain crops, but, on the other hand, they can be equally destructive. Often the presence of beetles within the flower repels other more beneficial pollinating insects. Pollen is unlikely to cling to the slick chitinous covering of beetles and be transported to other flowers in sufficient quantity to set a commercial crop of fruit.

Midges and *thrips* are sometimes listed as important pollinating agents, although they are inclined to get into a flower and stay for considerable periods. Nor does their presence within the flower insure its pollination even if it is self-fertile. For example, when flowering muskmelons were caged to exclude larger insects, such as honey bees, practically no marketable melons were produced, although thrips were numerous within the flowers at all times (McGregor and Todd *1952**). On the other hand, thrips are considered to be the primary pollinating agents of cacao (see "Cacao"). These insects are of little significance in pollinating U. S. Crops.

Aphids feed upon the plant sap and seldom become involved with the pollen of the flower. For that reason, they are of no significance as pollinating agents.

Ants, as well as aphids, midges, and thrips, have been given credit for pollinating cacao (see "Cacao"). The ants, being unable to fly, would be required to crawl down the trunk, across the intervening space to another tree, up its trunk, and into the flowers to effect cross-pollination. This accomplishment appears highly unlikely. Besides, ants are only sparsely covered with spines to which pollen is unlikely to cling. The honey ants of the Southwest gorge themselves with nectar or honey dew, collected by other ants, and become helpless "honeypots" hanging from the roof of the nest. The effectiveness of these ants in pollinating the plants from which the nectar is obtained is unknown.

Flies of numerous families, genera, and species are of considerable importance in pollinating some of our cultivated crops, especially the Umbelliferae and some of the Cruciferae. Blowflies of various species have been used for years in pollinating specific onion plants (Jones and Emsweller *1934*). Flies are considered to be highly important in pollinating mangos (see "Mangos"), and have been mentioned in connection with the pollination of apples, avocados, berries, cherries, pears, and numerous other crops. They offer some promise in the pollination of strawberries.

The number and kinds of pollinating agents are so numerous that these agents may seem to be present everywhere, but they may not necessarily be present in sufficient numbers to provide the grower with sufficient pollination for the maximum crop production that he desires.

In summary, pollinating agents other than wind and water vary enormously in size, kind, and efficiency from tiny midges and thrips scarcely a millimeter long to giant butterflies almost 200 mm in wingspread, from hummingbirds and bats to flying foxes and pollination application by airplane. (See "Beekeeping in Relation to Pollination" and "Wild Bee Culture.")

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BEEKEEPING IN RELATION TO POLLINATION

When the grower decides that his crop must be insect-pollinated but he does not have enough pollinating insects to provide this service, he may decide to rent colonies of honey bees from a beekeeper. If he plans to do this, he should have some basic knowledge about bees and beekeeping. This would be helpful in determining if the colonies he rents are as specified in the contract with the beekeeper, and if they will provide the service he desires. He may even determine if, under his particular situation, the beekeeper's rental fee is adequate, exorbitant, or even insufficient for him to provide adequate service and maintenance of the colonies.

This section is directed to such growers. It is not intended for those who desire to become either hobbyists or commercial beekeepers. The information they would want can be found in USDA Agriculture Handbook 335, "Beekeeping in the United States;" USDA Home and Garden Bulletin 158, "Beekeeping for Beginners;" or various other Federal or State Agricultural Experiment Station or Extention Service pamphlets on beekeeping. There are also numerous books and journals on bees and beekeeping.

The Beekeeper

When renting bees, the grower will find that he must first deal, not with bees but, with the beekeeper. Usually a few local pollination contractors or beekeepers act as contact agents for a few neighboring beekeepers. The majority of the bee rentals, however, are personal arrangements between the grower and a local beekeeper.

The uniqueness of his occupation tends to isolate the beekeeper from other agricultural enterprises to the point that communication falters, even when there is a demand for and a supply of bees for pollination.

The grower, for example, may consider only the fee and the potential value of the insects to his crop, along with the problems of having the beekeeper, his vehicles and crew, and the colonies on his premises.

The beekeeper views the deal from an entirely different point of view. The advantages include the fee, which holds promise of being more certain than a honey crop, the possibility of sandwiching the pollination deal between honey crops, and the possibility of the bees finding better forage than had they been kept in their permanent location. There is also the possibility that the deal may result in his obtaining a better permanent location, which he is always seeking.

The disadvantages to the beekeeper include the adverse effects on the colonies of overstocking the area, which may be necessary to provide the maximum pollination service that the grower desires. Also, the fear of damage to the colonies by pesticides constantly hangs over the beekeeper when he concentrates his colonies on a cultivated crop. Frequently, the pollination services of the bees are needed at the same time that the major honey flow occurs in the permanent location, so if the bees are moved the primary honey crop for the year may be lost. When the hives are moved from a location, there is always the possibility that another beekeeper will take it over. It then may be permanently lost because of the temporary pollination deal. Other factors include increased chances that colonies may become infected with bee diseases carried by other colonies in the new area, wear and tear on the colonies and the equipment during the process of moving, problems that always seem to arise with the moving of bees at night into a new location, and, finally, problems associated with collecting the pollination fee after the service has been rendered.

These divergent viewpoints frequently prevent frank discussion between the two parties. A better knowledge by the grower of the beekeeper's viewpoint and of some of the problems associated with the rental of bees for pollination may be of value in improving communication, leading to a more stable pollination service.

The Honey Bee

All honey bees belong to the genus *Apis* of the superfamily Apoidea of the order Hymenoptera. There are four recognized species in the world, three of which are found only in the Orient. Two of these, the little honey bee (*A. florea* F.) and the giant honey bee (*A. dorsata* F.), occur only in the wild. The Indian honey bee (*A. cerana* F.) is maintained in small hives but produces little honey. The most productive species is the common or domestic honey bee (*A. mellifera* L.), which is now distributed throughout much of the world. There are no "native" or "wild" honey bees in this country. Our honey bee was brought over from Europe by the early colonists.

There are numerous races of the common honey bee,

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the more important of which are the Italians (*A. m. ligustica* Spinola), the Caucasians (*A. m. caucasica* Pollman), the Carniolians (*A. m. carnica* Pollman), the European bee (*A. m. mellifera* L.), and the Africans (*A. m. adansonii* Latrielle). The first three races are found in the United States today. The Italians are most common.

A few queens of the African bee were transported from Africa to Brazil in 1956. Their progeny escaped, increased, and spread rapidly. Because of their irascibility, they became a serious problem in several South American countries. They may even reach the United States within a decade. If this should occur, their impact upon American beekeeping could be serious (McGregor *1970*).

The Colony and the Beehive

Regardless of the strain of honey bees involved, the nest structure and general activities are basically the same. The cluster or colony, whether in a manufactured hive, a rock cave, or as a swarm suspended from a tree limb (fig. 8), is normally composed of one queen, from 5,000 to 100,000 worker bees, and, depending upon conditions, from none to several hundred drones—their numbers varying with the extensiveness of the flowers upon which the colony has been foraging. The wax combs over which the bees cluster are used for food storage and broodrearing.

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FIGURE 8.— A swarm of honey bees, after it has left its parent colony and settled on a tree limb before proceeding to a new domicile.

"Brood" refers to the immature stages of bees. The worker bee develops from a single, tiny, white egg deposited in the bottom of a cell of the comb by the queen. Three days later, the egg hatches into a larva, which is intensively fed by adult bees for 6 days (fig. 9). The cell is then sealed, and the larva changes into a pupa (fig. 10) and emerges from the cell as an adult bee 21 days after the egg was laid. Drone bees require 24 days to develop, and the queen requires about 16 days (fig. 11).

The amount of food material stored in the combs depends upon many factors—the available flora, weather, colony strength, bee strain, and available comb space. There may be only a few pounds of honey present, or there may be several hundred pounds. There may be no pollen stored in the cells, or there may be several hundred square inches of comb space filled with it. These amounts can change rapidly. For example, a colony may find a new source of nectar and store 100 pounds or more within a week or two. At the same time, a new source of pollen may become available and fill several combs.

Water, which is essential for the welfare of the colony, is collected only when it is needed to cool the cluster or dilute honey consumed by the bees. Colonies can sometimes be seriously damaged if they are deprived of water for only a few hours on a hot day. Conversely, they can form a tight cluster and survive temperatures below 0° F for more than a month (Owens *1971*).

Pollen is collected when it becomes entangled with the dense branched hairs on the bee. Then it is combed into pellets on the bee's hind legs. This may occur while the bee is collecting nectar or when it is deliberately "scrabbling" within the flowers for pollen. Pollen is as necessary in the rearing of bees as nectar. Honey stored in excess of the needs of the colony is removed by the beekeeper for his own use.

Normally, bees forage in decreasing numbers with increasing distance from their domicile, although the relative attractiveness of the flowers and the competition by bees and other insects in the area that feed on nectar and pollen will alter the foraging pattern. The bees will fly over a less attractive field to a more attractive one, but they tend to conserve their energy and usually store food in proportion to its ease of availability, attractiveness, and distance from their home. Under extreme circumstances they have been known to go as far as 8.5 miles (Eckert *1933*), but the bulk of their foraging is often within one-fourth mile of the domicile.

Time and energy are expended by the bees when they transport food and water to the cluster. The grower using the services of the bees would profit by having the hives placed within or as close to the field (and to a source of water) as possible.

Early American beehives were made of 10-inch boards. They held different numbers of frames, in which the comb is built, but the 10-frame size became the most popular. Because of the weight involved, some beekeepers made lighter units out of 6-inch boards. These, with variations, evolved into our "deep" and "shallow" hive parts. The majority of U.S. beekeepers

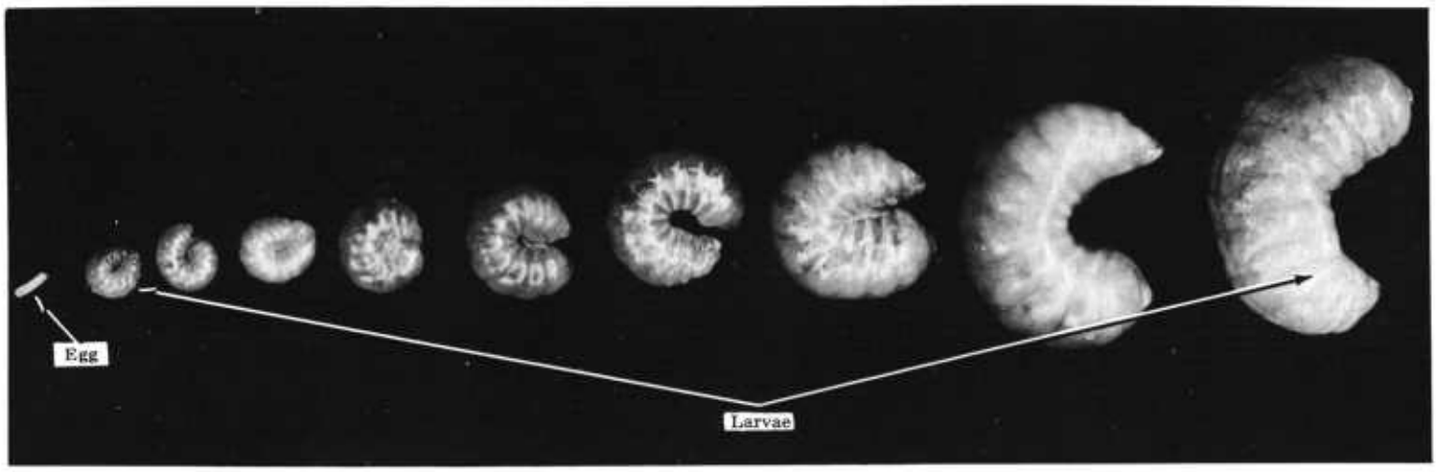

FIGURE 9.—Successive stages in development of honey bee from egg to 9-day-old larva, ×3.

use the 10-frame deep hive (fig. 12). When these units are stacked upon each other, the upper ones are referred to as "supers." Because of the tendency of the bees to have the brood toward the bottom of the cluster, the lower unit is usually referred to as the "broodchamber." Some populous colonies may have so much brood or the broodnest may be so poorly organized that it extends through two or three supers. There may be several honey-filled supers above this.

The number of supers per hive may be determined by the strength of the colony. However, a beekeeper may place more of them on the hive than are required by the colony, merely to have the bees protect the combs from damage by wax moths or other pests. The actual strength of the colony (population) cannot always be determined by counting the number of supers.

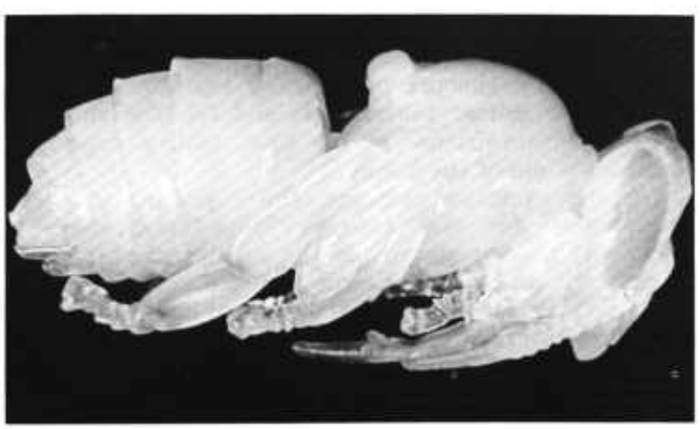

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FIGURE 10.—Honey bee pupa, enlarged.

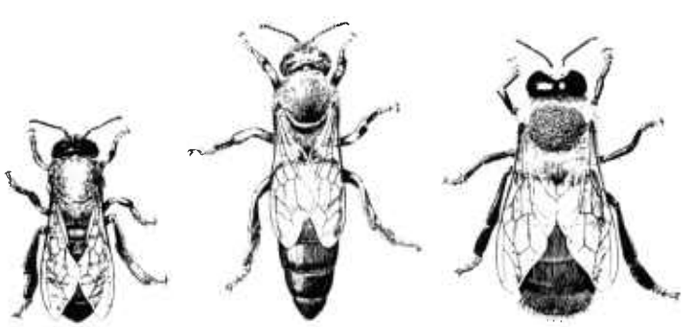

FIGURE 11.— Worker, queen, and drone honey bees (left to right).

Manipulation of the Colonies by the Beekeeper

When the pollination deal is made, there are usually specifications as to the cluster size, frames of brood, and size of hive that houses the colony. After delivery, the colonies may change rapidly and may deteriorate in quality unless proper attention is given to them. The frequent visits to the colonies by the beekeeper to keep them in proper condition are sometimes perplexing to the grower. He may dislike having "outsiders" coming onto the property so frequently. He may believe that the beekeeper is merely harvesting a crop of honey on each visit, or he may feel that disturbing the colonies so

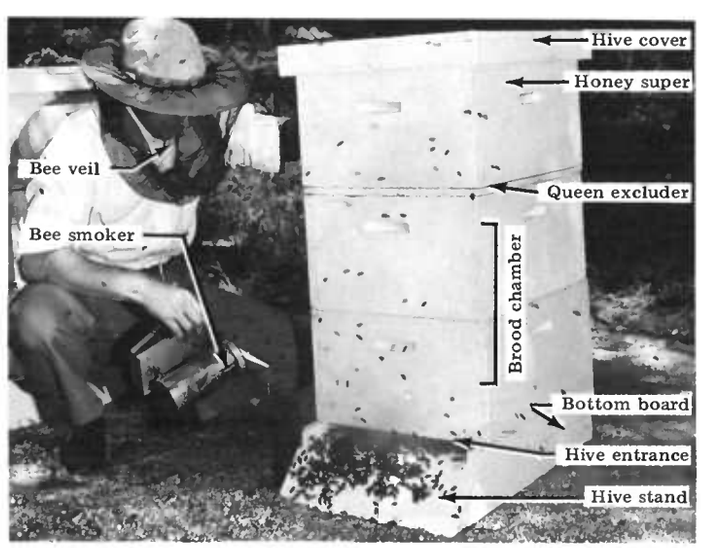

FIGURE 12.— Beehive, consisting of 2 supers that comprise the brood chamber and 1 honey super above the queen excluder.

frequently may decrease their effectiveness as pollinators, as well as increase the chances that the farm workers may be stung.

To understand what the beekeeper is doing and why the colony manipulations are advantageous to the grower requires some knowledge of bees. Only the significant points associated with the manipulation of the colonies while they are used for pollination will be mentioned.

THE CLUSTER

The colony cluster may be considered as a pulsating organism. It contracts as the temperature drops and expands as the temperature rises. The population also changes, increasing when nectar and pollen are available and decreasing when there is a dearth of fresh food.

The emerging brood (fig. 13) may add as much as half a pound of young bees per day to the cluster. One or more combs may be filled with honey per day. Other combs may be filled with pollen (fig. 14). Still others may contain a combination of honey, pollen, and brood (fig. 15). Thus, a colony having ample room when delivered may become overcrowded within a week. Unless the beekeeper rectifies this condition, the colony's efficiency as a pollinating unit is lowered. If there are no open cells, the queen has no place to lay eggs so broodrearing declines, food collection diminishes, and flowers remain unpollinated. Crowded conditions cause swarming, When the colony swarms, the old queen and much of the working force leaves, and the efficiency of the colony is further reduced.

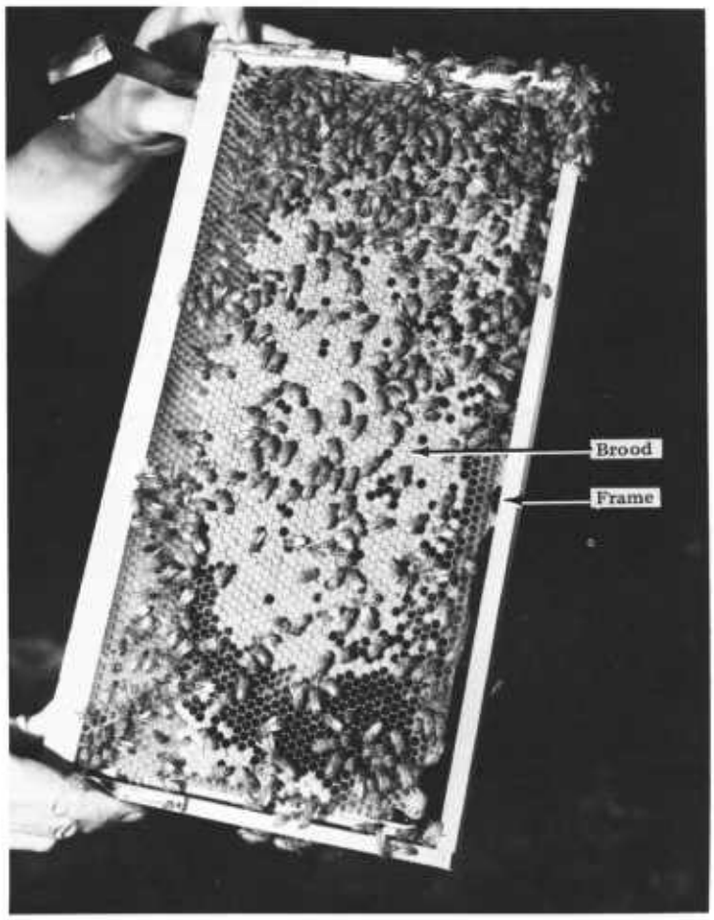

FIGURE 13.—Wood frame containing wax comb. The center area is filled with about 60 in² of sealed cells of brood—the developing worker bees. (An equal area of brood may be on the opposite side.) Adult worker bees remain on the comb while it is being examined.

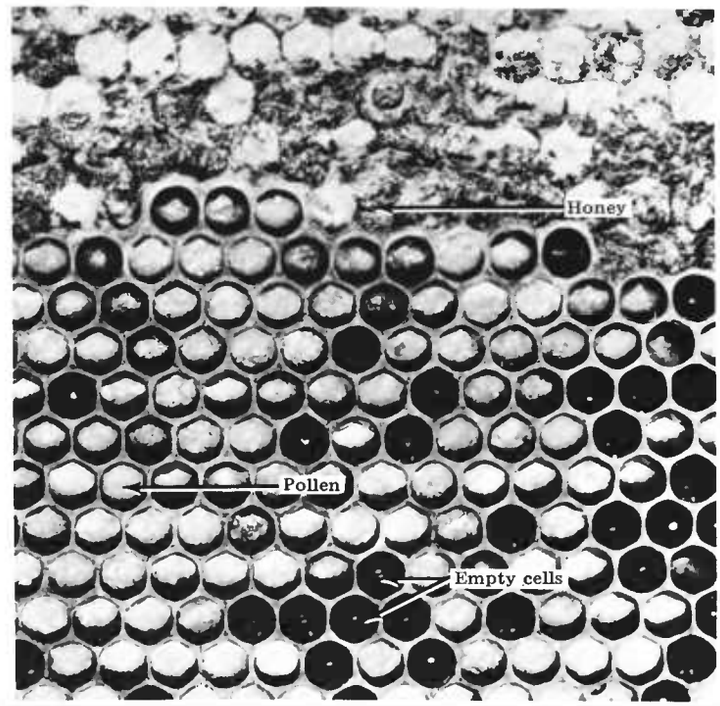

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FIGURE 14.—Part of a comb well filled with stored pollen or bee bread.

When the beekeeper periodically examines the colonies, he recognizes the changes and rectifies them by shifting certain frames in the hive, adding supers, or removing some of the honey.

On the opposite extreme, the conditions may be unfavorable for the colony. More food may be consumed than is stored, so the surplus diminishes or completely disappears. Feeding of the colony may be necessary. This is usually in the form of combs of honey placed in the hive in exchange for empty combs. The colony may also be damaged by pesticides to the extent that the working force and pollinating value are lost. Under such conditions, the removal of the colonies to a better floral pasture may be necessary to save them. New, strong colonies then must be brought in to continue the pollination of the crop.

ROBBING

When bees are unable to find fresh nectar, they are highly attracted to exposed honey—a condition leading to what beekeepers refer to as "robbing." Once robbing has started, the bees will try to get to the honey that is inside other colonies, despite the resistance by guard bees at the entrances. At times, fighting between these robbing bees and the "defending" bees results in thousands of bees being killed. If all the bees in a colony are killed, the robbers remove all of the honey. The attack then turns to another and yet another colony. Many colonies in an apiary can be destroyed in this way, and all may suffer heavy loss from the fighting. Because of the robbing characteristics of bees, the beekeeper

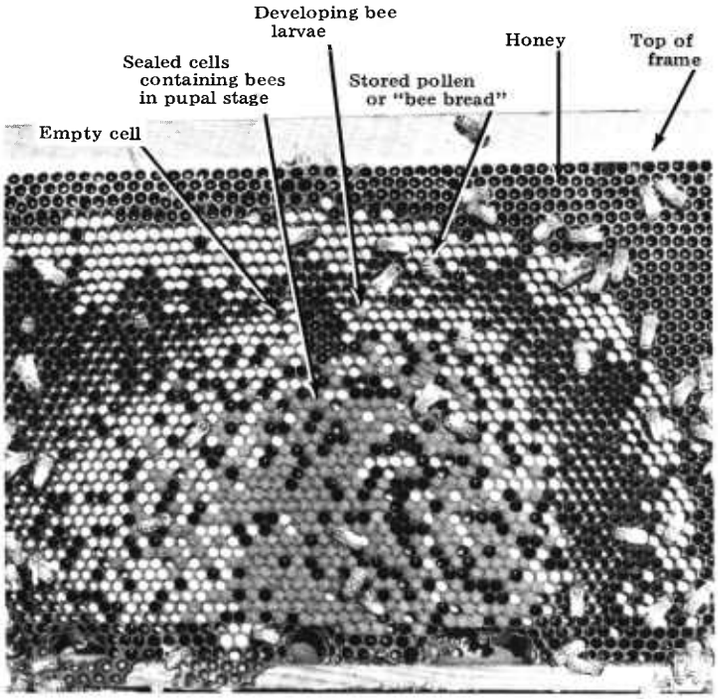

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FIGURE 15.—Comb containing honey, pollen, open brood, and sealed brood. Empty cells scattered through the brood area sometimes indicate that the egg-laying ability of the queen is failing, and that she should be replaced by a younger more productive queen.

refrains from opening the hives when there is no nectar flow.

DRIFTING

Honey bees normally return to the entrance of the hive from which they departed. If they stray into the entrance of another hive, when no food is being stored, they are likely to be killed by the guard bees.

When numerous colonies are placed close together without orientation landmarks, the bees may drift from the central hives to those nearest the edge of the group. Drifting is likely to be more severe if the hives are in open or windswept areas. Drifting reduces the efficiency of the colonies as pollinators. Some become depopulated and ineffective while other become overcrowded, immediately filling all available space in the hive. The bees then cease foraging and usually swarm.

For the colonies to be most effectively used in pollination, all possible steps should be taken to prevent drifting. It is to the grower's advantage for the bees to be distributed in smaller groups of no more than a dozen in or around the field. Orientation landmarks near the colonies should be used when practical to aid the bees in locating their own domicile.

The Apiary

The place where the colonies are kept is referred to as an apiary. The area in which the apiary is located before the bees are used as pollinators determines their effectiveness. Such a place should have a succession of flowers producing pollen and nectar throughout most of the year with one or more periods when a particular species of plant produces nectar in great abundance. From this source, the beekeeper obtains the honey crop. Usually, the surplus honey is stored during a brief period of the year, sometimes only during 3 or 4 weeks. The remainder of the year the colony looses weight as it consumes its stores or barely maintains its weight as it forages on minor floral sources.

Frequently, the major honey flow occurs at the same time the colonies are needed for their pollination services. Then the beekeeper must weigh the costs of harvesting and marketing the honey crop against the costs of transporting the colonies to and distributing them in distant, overstocked, and less desirable locations, for the pollination fee.

The beekeeper does not overstock the permanent location. Usually, a location is first tested with a few colonies. If they do well, their numbers are increased until additional ones would only cause a decrease in the storage per colony. Some locations will support only a few colonies, perhaps two dozen; others may support several hundred. Many beekeepers prefer locations that will support the number of colonies their vehicle can move on a single trip—the unit being a truckload of colonies. Others may place one-half of a load or even several loads in a location. For example, a California beekeeper may place several hundred colonies where there is a vast acreage of citrus in bloom, then place the colonies in groups of only 40 or 50 to forage on lima beans.

No beekeeper can positively determine the value of a bee location except by testing it over several years with colonies.

Migratory Beekeeping

Some beekeepers operate their colonies in the same location year after year. Others move their colonies from one to several times. Some migrate from along the Canadian border into California, the Carolinas, Georgia, Florida, or other States along the gulf coast. Others migrate in a more east-west direction; Texas to Colorado, or from the Rocky Mountain States into California. The north-south migrations are primarily for colony build-up in the South for Northern honey crops, although some Southern honey crops—for example, citrus—are obtained. East-west migrations are primarily between honey flows.

Powered hive-hoists have been developed by the beekeepers (fig. 16). These hoists permit one man to load 100 or more heavy hives onto large flat-bed trucks, transport them hundreds of miles, and unload them alone. One man equipped with such a truck can move and handle 1,500 colonies of bees—with a skilled helper, 2,000 colonies (Huston *1967*). Most of the hives are handled singly in this way, but from two to six on a common pallet are also moved.

The development of migratory beekeeping for honey production made the transition to migratory beekeeping for pollination much simpler for the industry. Now, when the grower contracts with a beekeeper for pollination services, the colonies can be rapidly transported to the site at the appropriate time.

One of the most serious difficulties encountered in

FIGURE 16.— Powered hive hoist for moving beehives.

the use of large trucks in transporting the bees to the site is that of maneuvering the vehicle within the field or orchard when the colonies are being distributed. The soil may be wet from heavy rains or irrigation or soft from recent cultivation, the driveways in the field or orchard may be difficult to negotiate, and the bridges and culverts may be inadequate to support the load. Beekeepers frequently state that they prefer a 500-mile haul of a truckload of bees on the highway over the last mile or so of distributing the bees over poor or muddy driveways within the field (fig. 17).

Most beekeepers begin the move after nightfall when all the bees are in the hive. The entrances of the colonies can be closed for the period of the move, but usually they are left open. The entire load is usually covered with a plastic screen to prevent escape of any bees while enroute.

Few bees attempt to leave the entrance of the hive while the truck is in motion, but if the truck stops during daylight hours, some bees may begin to leave. To a degree, this can be prevented if the truckload is sprayed with water. Most beekeepers carry sufficient motor fuel so they will not need to refuel enroute. Many beekeepers deliver colonies at night so that the bees will remain inside the hive while it is being positioned in the field. However, unfamiliarity with the area combined with poor nighttime visibility can prove hazardous for the beekeeper.

If there is a vehicle breakdown or other delay in the distribution of the colonies within the field until after daybreak, the bees begin to fly from the entrances. On a warm day the screen soon becomes filled with these bees. Unless they are released, they soon die. However, with removal of the screen they quickly orient to the location and begin to forage. Then, when the truck is moved and the colonies are distributed within the field, the bees forage and return to the site of their first release. This loss of workers decreases the efficiency of the colonies, and the concentration of disoriented bees may create a hazard to livestock or people.

A simple, safe, fast method of distributing the colonies within the field to which they have been delivered would alleviate or greatly simplify a complex problem in the use of honey bees for crop pollination. Some growers contribute in this regard by providing a guide for the truck or a tractor and a trailer with driver to aid in distributing the colonies.

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FIGURE 17.— Rainy weather creates muddy roads and frequent problems in moving beehives into and out of fields for pollination.

"Disposable" Bees

One possible solution that has been proposed for the problem of distributing large and relatively heavy bee hives within the field is the use of queenless clusters of bees or clusters having infertile queens in light disposable containers. Research is in progress in the development of a disposable pollinating unit (DPU) by the USDA and the California Agricultural Experiment Station (Kauffeld et al. *1970*, Anonymous *1972*), although results are incomplete and inconsistent.

What the Grower Should Expect in Colonies Rented for Pollination

OUTSIDE APPEARANCE

The size of the hive does not necessarily indicate the strength of the colony within it. A hive may consist of several supers, but the cluster size might warrant only a single unit. It should be stressed that an accurate assessment of the pollinating efficiency of the colonies cannot be made merely by "counting boxes."

Some indication can be obtained by watching the flight activity of the bees at the entrances. On a bright warm day, dozens of bees should be constantly coming and going at each entrance (fig. 18). A lack of uniform activity between entrances would indicate that some of the hives are not as populous as others. It might also indicate that some of the hives are filled with honey, leaving no storage space.

INSIDE THE HIVE

An examination of the colony gives the best indication of its quality. If the grower wants to do this, but is fearful of the bee stings, even when he protects himself with gloves and a screen veil, he can have the

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FIGURE 18.—Intense flight activity at the hive entrances usually indicates that the colonies are populous or "strong."

beekeeper manipulate the colony while he makes observations through the glass windows inside a closed automobile, driven to within a few feet of the hives.

Have the beekeeper blow a few puffs of smoke into the hive entrance then immediately remove the cover. If no more than a dozen bees are present, the super space may not be needed. Have the super loosened and tilted upward so the bottoms of the frames can be seen. If bees are not present on most of them, the decision is strengthened that the space is not needed. Repeat the examination of all supers until the broodnest is reached.

Brood.—Ask the beekeeper to lift out for your observation all frames that have brood in the comb.

On the average, there will be about 100 in^2 of sealed brood per comb with sealed brood. Naturally, in an oval broodnest some will have more, some less, but if the frames with sealed brood are counted, the number multiplied by 100 will usually give a fairly reliable estimate of the number of square inches of sealed brood.

The brood cells on the comb should be compact. This indicates a healthy colony and a vigorous queen. The broodnest should also be compact and oval so the cluster can surround and protect it. There should be sufficient bees to do this, particularly if cold weather is likely to occur.

If the contract calls for colonies averaging 800 in^2 of sealed brood, there should be about eight frames with sealed brood.

Honey.—A satisfactory pollinating colony need not necessarily have much honey. Enough to tide it over any possible period of dearth or inclement weather—one or two combs—is usually sufficient. If the colony is likely to store a surplus, there should be ample storage space. The lack of adequate storage space or any condition that tends to form undue crowdedness within the hive is likely to stimulate swarming and reduce the pollination effectiveness of the colony.

When removal of the cover reveals fresh cells filled with honey built between it and the frames, this is a strong indication that storage space is inadequate.

The presence of queen cells either indicates that the queen has recently disappeared (the queen may be killed in an occasional colony during transportation) or that there is inadequate or improperly arranged space and that the colony may swarm shortly.

Pollen.—Pollen is usually rather promptly converted into brood. There is little the beekeeper can do to alter pollen storage other than to see that adequate space is available; however, the presence of pollen is good insurance that broodrearing is likely to continue. A preponderance of pollen with little brood, however, may indicate that broodrearing has not kept pace with pollen storage, a clue that the queen may be failing.

AN IDEAL POLLINATING COLONY

There is no definition of an ideal pollinating colony. Also, the ideal condition of a colony for one crop might not be ideal for all other crops. For most crops where the activity of the bees in collecting pollen is desired, the colony should be populous and expanding. An expanding colony should have one-fourth or more of its brood in the egg or larvae stage. This unsealed brood requires pollen and stimulates pollen collection by the adult bees. Where cross-pollination of male-sterile plants for hybrid seed production is desired, a populous colony is preferable but it should be more concerned with nectar collection than brood feeding. In every case, there should be adequate room for food storage.

If the colony is purported to be a "strong single-story colony," it should be so populous that when opened a blanket of bees immediately covers the tops of every frame (fig. 19). Such a colony is ready to have an extra super of empty combs added. Within its cluster, there should be four to six frames with brood, with the remainder of the combs largely filled with pollen or nectar. There should be brood to the top bars of some frames so that when the super is added the broodnest can expand into it without being divided by stored honey in the upper parts of the frames. When each frame is lifted out, it should have bees on almost every square inch of space.

If the colony is purported to be a "strong two-story colony," there should be numerous bees on the top bars of almost every frame when the hive cover is lifted (fig. 20). When the two bodies are divided, a blanket of bees should cover the top bars of the lower one.

There should be 6 to 10 frames of brood. Most of the brood should be in a compact area in the lower body and surrounded by pollen. The upper body may have some brood and honey, but if many of the combs have sealed honey they should be transferred into a third body and replaced with empty combs as near to the brood as possible.

A purported "strong three-story colony" should have 8 to 12 frames with brood located in the lower and central bodies (fig. 21). When the hive cover is lifted, a few bees should be on the top bars of every frame.

When the top super is removed, bees should be on almost every square inch of the top bars of the middle super, and a blanket of bees should be on the top bars of the bottom body. There should be honey storage space in the combs directly above the broodnest. Three to six frames with only foundation would be acceptable, but entire supers of foundation are rarely needed on colonies used for pollination. Sometimes, numerous frames of foundation act as a barrier to normal expansion of the colony and tend to create crowded conditions.

With the photographs and basic principles on bees and beekeeping discussed in this section, the grower should be able to determine the quality of colonies he has rented and the degree of care they receive.

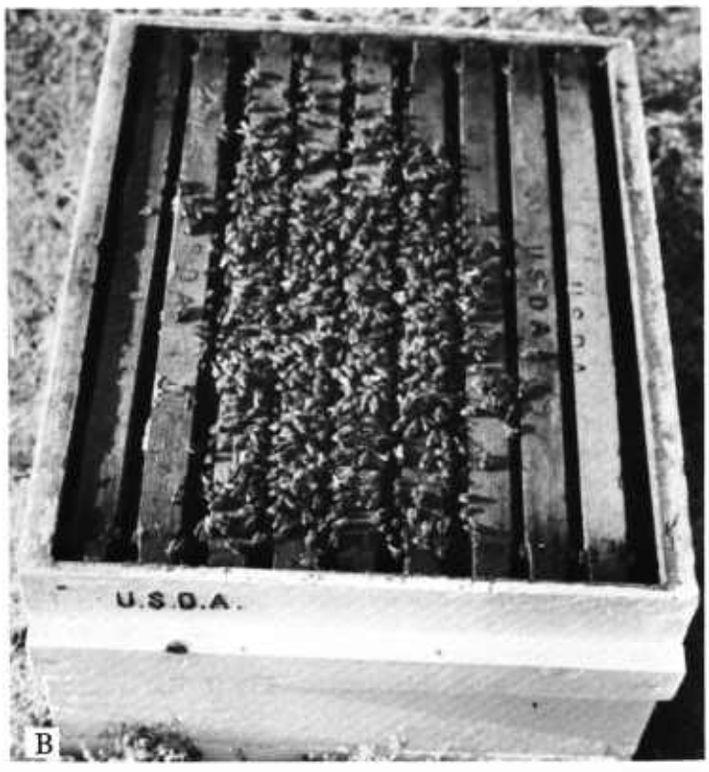

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FIGURE 19.—Single-story colonies. *A*, Cluster covers most of comb area, and should forage effectively on cool days, but population is not the maximum expected of a colony. *B*, Cluster covers about 4 combs. This colony is unlikely to forage extensively on cool days, so its value as a pollinating unit is low. *C*, This colony is useless as a pollinating unit. It was formed a few days previously with 2 pounds of bees and a queen.

Bee Stings

Some growers hesitate to use honey bees for crop pollination because they fear being stung. Some knowledge of the bee and its venom may reduce this fear.

The sting is the organ of defense for the colony. Anatomically, it is a modified ovipositor or "egg placer" of insects. A poison sac has evolved along with certain specialized muscles that force the venom from this sac out through the barbed sting. By involuntary action, these muscles drive the sting more deeply into the flesh even after the sting is torn from the body of the bee. The worker bee usually dies within a few hours after the sting is lost. The queen does not lose her sting, which is only used to destroy other queens. The drone, the male bee, has no sting.

PREVENTING BEE STINGS

There is no practical way to completely avoid bee stings while conducting normal activities on a farm,

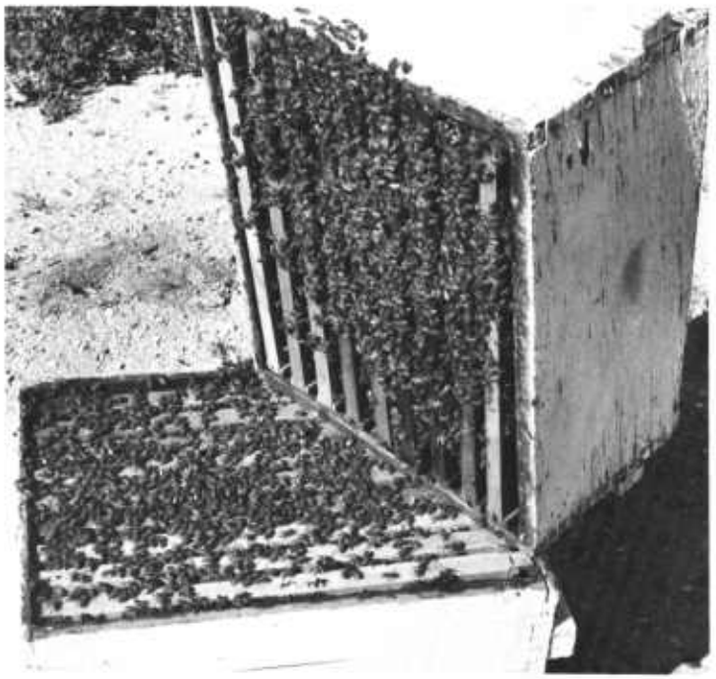

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FIGURE 20.—A strong 2-story colony. When supers are separated, a blanket of bees is seen covering the frames in both supers. An extra super may be needed within a few days to provide space for bee clustering and food storage. This is an acceptable pollinating unit.

particularly where numerous colonies are involved, but some steps can be taken to reduce the possibility of being stung.

Bees are usually much more inclined to sting a person who is near the hive entrance than if he is farther away. Even when protected from stings, a person should not stand in front of a hive because this disrupts the bees.

Bees are less inclined to sting smooth light-colored clothing. Rough, woolly, suede or leather clothing, particularly horsehide or any type of hair, seem to irritate bees. Certain hair oils, perfumes, and the odor of bee venom increase the chances that the bees will sting. They are also quite likely to sting areas where other bees have recently stung.

Moving objects or objects on the skyline are more likely to be attacked than stationary objects or those that blend into the background.

There is no evidence that bees detect fear or that they are more prone to sting one individual than another if the clothing and actions are similar. However, some people react differently from others, and rapid movement or similar evasive action may increase the likelihood of one being stung. It is well known that striking, swatting, or swinging at bees will increase the probability of being stung. Nevertheless, seemingly gentle bees will occasionally sting even the most careful beekeeper.

Specific recommendations for reducing the chances of being stung are as follows:

Recommendations to Reduce Chances of Being Stung by Honey Bees

- Do not bump, jar, or otherwise disturb the hive.
- Do not go within 50 feet of the hive entrance at any time.
- Do not go within 300 feet of the hives while they are open and being manipulated by the beekeeper or for the remainder of the day after they were manipulated.
- Do not swat or slap at a bee.
- When a seemingly irritated bee comes around, stand still and cup the hands loosely over the eyes, nose, and mouth—areas most likely to receive a sting and most seriously affected by stings.
- If practical, lie prone on the ground or hide in dense shrubbury until the irritated bee leaves the area.
- Blend into the background as much as possible.
- In approaching a beehive, determine where its entrance is and approach from the opposite side.
- Do not go near a hive while wearing fuzzy, woolly, or suede clothing or apparel made of horsehide.
- Do not go near the hive unless the head, particularly the hair, is covered.
- Obtain and wear a bee veil to protect the head and neck while working near beehives.
- If a bee gets into a moving motor vehicle, do not try to swat it. Stop at once. The bee usually flies to the glass after which it can safely be released.
- Do not try to move or handle a beehive at night or on a rainy day without help of an experienced beekeeper.
- If a hive is going to be opened, the safest time for the amateur or nonbeekeeper is during the middle of a calm day when the sun is shining and flowers are in bloom so that the bees are busily storing food.

REMOVE THE STING!

Because venom is forced into the flesh for some minutes after a sting is received, it should be removed as quickly as possible. Attempting to pick the sting out with the fingers is slow, and may press more venom out of the poison sac into the flesh. Instead, scrape or rub the sting away very quickly. An experienced beekeeper may be stung a dozen times but because of his instantaneous response by rubbing the sting away he may receive no more venom than an unaccustomed person after receiving one sting.

EFFECT AND TREATMENT OF STINGS

The local and general effect of bee venom in animals and man was reviewed in detail by Beck (*1935*). He reported that stings may be fatal to some individuals, while of no consequence or even beneficial in relieving certain arthritic effects in others. Normally, there is acute instant pain when the sting is received similar to that of a puncture with an extremely hot needle. This may last from a few seconds to several minutes.

Lehnert (*1967*) reviewed the effects of bee stings, and stated that symptoms in an allergic person usually appear a few minutes after the sting. Local swelling may be excessive, and a rash may break out over the body. There may be a sensation of choking, difficult breathing or asthma, and the lips may turn blue. Shocklike

symptoms, vomiting, and loss of consciousness may follow in rapid succession. Such persons should be provided with professional medical aid at once.

Normally, within a few minutes after the sting is received, a local wheal or whitish area appears at the site of the sting, surrounded by a reddening area. The size of this area will vary from less than an inch to several inches across, depending upon the susceptibility of the victim. The area may become slightly painful but is not sensitive to touch. The pain may be soothed with a cold, damp cloth on the site of the sting. This may be the extent of the effect, which may last a few to 24 hours in a normal person receiving his first or an infrequent sting. Beekeepers frequently state that the best treatment is to "forget it." Immunity usually develops after a few stings have been received.

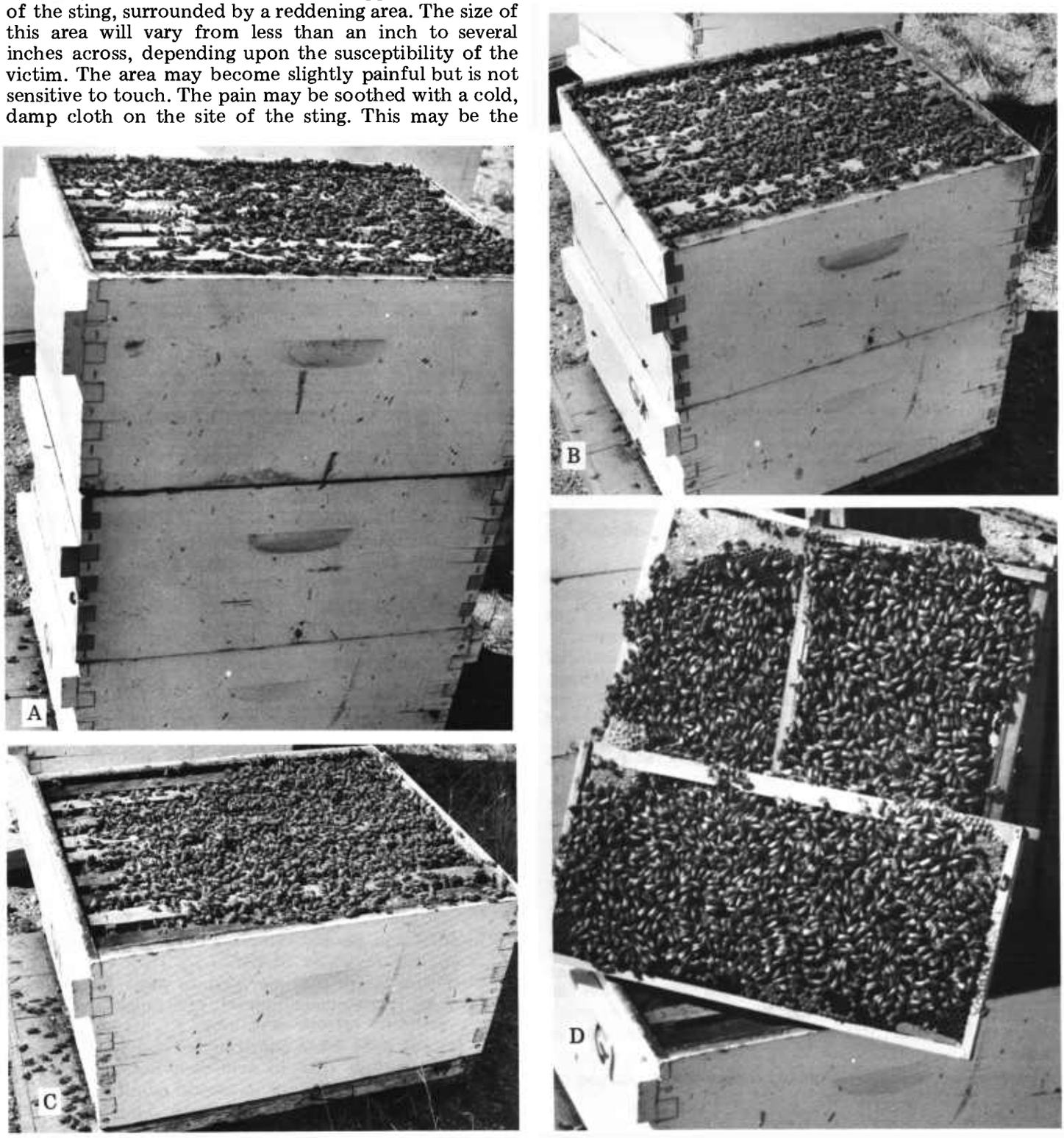

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FIGURE 21.—Composition of a strong 3-story colony. *A*, Cover removed, showing top bars of frames covered with bees. *B*, Top super removed, showing top bars of frames in middle super covered with bees. *C*, Middle super removed, showing top bars of frames in bottom super covered with bees. *D*, 3 frames removed from the broodnest, showing combs of brood well covered with bees. This colony is about maximum in size and strength as an efficient pollinating unit.

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WILD BEES AND WILD BEE CULTURE

A brief review of the classification of insects and their relatives may help the reader to understand the scope and magnitude of those insects referred to by the general term "wild bees."

All known animal organisms have been arbitrarily classified by specialists into phyla, classes, orders, families, genera, and species, with some subdivisions in between. For example, the phylum Arthropoda contains numerous classes including the Insecta, which is divided into numerous orders, one of which is the Hymenoptera, which in turn is divided into superfamilies, one of which is the Apoidea (bees).

Wild Bees

The Apoidea of America north of Mexico have been classified in different ways by different specialists, but Stephen et al. (*1968*) classified them into the seven families listed on this page. Also listed are the more important genera in each family.

Family[1]	*Important genera*
Short-tongued bees:	
Andrenidae	*Andrena, Panurginus, Perdita, Pseudopanurginus*
Colletidae	*Colletes, Hylaeus*
Halictidae	*Agapostemon, Dufournea, Halictus, Nomia*
Melittidae	*Hesperapis, Melitta*
Long-tongued bees:	
Anthophoridae	*Anthophora, Melissodes, Nomada, Xylocopa*
Apidae	*Apis, Bombus, Euglossa, Melipona, Trigona*
Megachilidae	*Anthidium, Lithurgus, Megachile, Osmia*

[1] Two relatively obscure families, Fideliidae and Oxaeidae, are omitted.

There are about 19,000 described species of bees in the world (Linsley *1958*). At least 5,000 species of bees are in North America (Bohart *1952**), and, with the exception of one species, *Apis mellifera* L., the domestic honey bee, all of them are grouped under the general term "wild bees."

Only to a limited extent has man learned how to manipulate a few species in a few genera of wild bees. He can construct nesting sites and transport immature stages of leafcutter bees (*Megachile pacifica*) (see "Leafcutter Bees") and alkali bees (*Nomia melanderi*) (see "Alkali Bees"). These bees are used in large-scale pollination of legume crops in the Western States.

Numerous species of the genera *Melipona* and *Trigona* are induced to nest in prepared domiciles, such as hollowed-out gourds, hollow tree sections, or manufactured hives, from which a few ounces to a few pounds of honey may be harvested. Some of these colonies are also placed near crops needing pollination (see "Stingless Bees and Meliponiculture").

Slight progress has been made in inducing numerous species of bumble bees (*Bombus* spp.) to nest in specially prepared boxes or nests that can be transported to fields to be pollinated (see "Bumble Bees").

Osmia bees (*Osmia* spp.) can be induced to nest in bamboo canes, which are then transported to fields to be pollinated (see "Osmia Bees").

Logs of softwood, in which carpenter bees (*Xylocopa* spp.) can construct nest tunnels, are provided near plantings of passionfruit (*Passiflora* spp.) to encourage these bees to nest near and pollinate the flowers (see "Carpenter Bees").

Other steps mentioned by Bohart (*1971*), which may have actually increased the wild bee populations at least in the eastern half of the United States, include:

1. Opening up of forested areas, which created more favorable conditions for bees.
2. Paving highways, which concentrated moisture along roadsides.
3. Introduction of "weeds" upon which the bees forage.

4. Growing numerous crops upon which the bees forage.
5. Bringing desert areas into bloom (with irrigation).

Plantings on which wild bees may forage or reproduce, are also made and protected from fires, floods, overgrazing, or insecticide exposure.

Otherwise, little is known about manipulation of the thousands of other species of wild bees.

Numerous species of wild bees, however, can be found almost anywhere plants grow, for example, the Melissodes bees (*Melissodes* spp.) in cottonfields (Butler et al. *1960*). Wild bees doubtless provide, in the aggregate, millions of dollars to the economy of agriculture. Their value to range, forests, fields, and ornamental flowers is impossible to measure, but it should not be overlooked. The demonstrated value of the few species over which man has learned to exercise some control is sufficient to support the claim that this group of largely overlooked insects is an essential segment of our agriculture as well as our general ecological environment. As such, more intensive study should be made of the various species to determine the practicability of their preservation, culture, and use on various insect-pollinated crops.

Although ants, beetles, butterflies, moths, and many other groups of insects contribute to the pollination of plants, Apoidea are of greatest interest and by far the most important as pollinators, especially in temperate regions.

The families of Apoidea have plumose or branched hairs at least on the top of the thorax, the first joint of the hind tarsi is enlarged, and they provide their young with a diet of nectar and pollen. This is even true of the "cuckoo bees" (several genera in various families), which lay their eggs in the nests of other bees. Male bees have 13 segments in the antennae; the females, 12.

The sting of the female (a modified ovipositor) or the exposed genitalia of the male readily identify the sex of the individual. Apoidea may be solitary, gregarious, or social.

A solitary species is one in which the female prepares and provisions the cell, deposits the egg, and then seals the cell completely unassisted. More than one cell may be constructed, but only one at a time. After the cell is sealed, no further attention is given it, and the adult may die within a few days.

Gregarious bees are solitary individuals that endeavor to nest in close proximity to each other. The alkali bee (*Nomia melanderi*) belongs to this category. It builds individual nests in the ground—as many as 100 nests per square foot of soil.

Social bees live together in a society and have divided duties. The queen is the sole or primary egg-laying individual. Her active life is relatively prolonged, and she maintains contact with at least some of her adult offspring. Ants, bees, wasps, and termites include species with the most highly developed insect societies.

The time of day that wild bees forage differs with the species involved. Those that feed only at dawn are referred to as *matinal* bees. *Crepuscular* bees feed both at dawn and near dusk. A few species are *nocturnal* in their foraging, but the great majority feed when the sun is shining, because that is when the majority of the flowers are open (Linsley *1960*).

The distance that the different species of wild bees may forage must vary enormously. Janzen (*1971*) reported that an individual *Euplusia surinamensis* (L.) returned to its nest from a distance of 23 km (14.3 miles). He calculated that another individual flew as much as 24.4 km (15.2 miles) to and from the foraging area. By comparison, the alkali bee (*Nomia melanderi*) may forage 4 or 5 miles from its nesting site (Stephen *1959*); whereas the alfalfa leafcutter bee (*Megachile pacifica*) usually forages within only a few hundred feet of the nest (Bohart *1962b*).

Visitation to plants by wild bees is highly variable. Some species visit many different families of plants, others visit only a few closely related families, and still others visit only a single species or closely related species. In different instances, each type of activity would be advantageous.

Wild Bee Culture

ALKALI BEES (*NOMIA MELANDERI* COCKERELL)

The alkali bee has been known for many years to be a highly efficient and effective pollinator of alfalfa, particularly in the area north and west of Utah. It is a highly gregarious solitary bee that nests in large numbers in saline soils with a silt loam or fine sandy loam texture.

The culture and utilization of this bee has been studied and promoted over the last two decades, particularly by Bohart (*1952**, *1958*, *1967*, *1970a*, *1970b*, *1972*), Menke (*1952a*, *1954*), Stephen (*1965*), and Stephen and Evans (*1960*). Much of the material presented herein was developed by these men.

Life history and habits.—Alkali bees are nearly as large as honey bees. They are black, with iridescent copper-green stripes across the abdomen (fig. 22*A*). The male bee has much larger antennae than the female. Being gregarious, alkali bees may construct 100,000 or more nests in an area 40 by 50 feet. Nesting sites with an estimated 200,000 nests have been reported (Bohart *1952**). The nest (fig. 22*B*), a pencil-sized (three-eighths inch) vertical tunnel, may extend 10 inches below the surface but is usually only 3 to 5 inches deep (Frick et al. *1960*). There may be 15 to 20 cells usually arranged in a single comb-shaped cluster. Each cell is an oval cavity, slightly larger than the main tunnel, about one-half inch long, lined first with soil and then with a waterproof transparent liquid applied with the bee's glossa. Each cell is provisioned with a 1.5- to 2-mm oval pollen ball, made up of 8 to 10 bee loads of pollen mixed with nectar. The soil removed from the tunnel is dumped at the tunnel entrance to form a conical mound 2 to 3 inches across.

The adult bees emerge from late June to late July, depending upon the location and season. The males appear a few days ahead of the females. Before emergence, each bee is confined to its natal cell for 3 days as an egg, 8 days as a growing larva, 10 months as a full grown dormant larva, 2 weeks as a pupa, and several days as a hardening, maturing adult (fig. 22*C*). During the approximate 1 month of her active adult life, the female

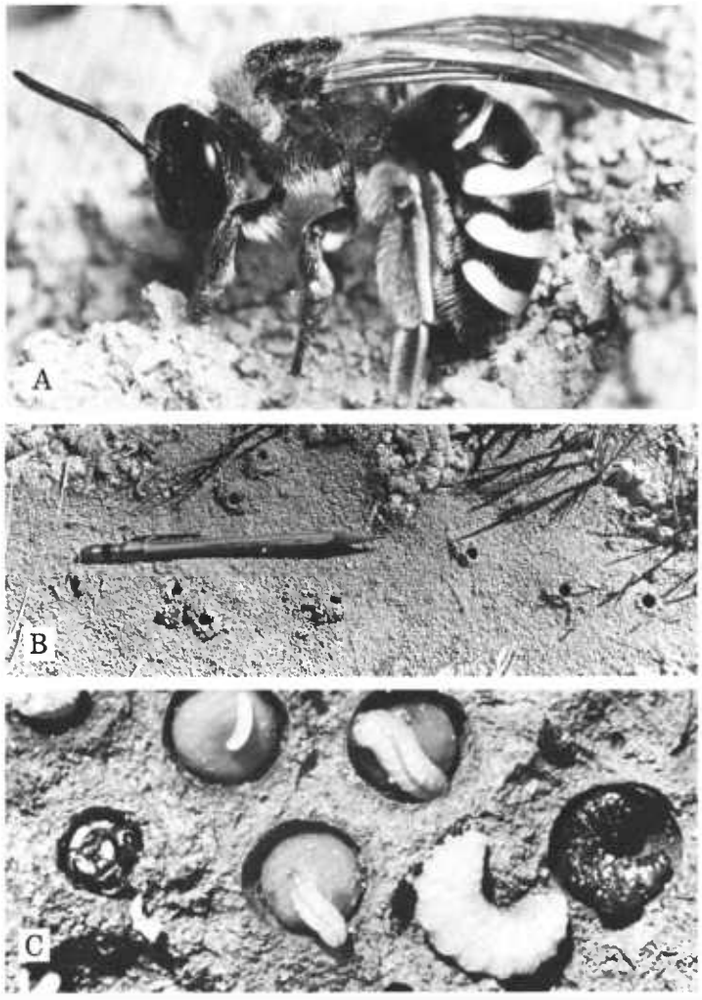

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FIGURE 22.—The alkali bee. *A*, Adult; *B*, nesting site; *C*, cells excavated to show immature stages.

constructs, provisions, and lays an egg in each of 15 to 20 cells.

Mating occurs during the 3 days the entrance tunnel is under construction, usually during the first day. The males patrol back and forth over the nesting site, and they will mate with any number of females; however, they rarely bother a mated female after she becomes actively engaged in constructing the nest (Stephen *1959*).

About the third day after construction starts, the first cell is completed. Pollen is then collected and formed into a pellet in the cell, an egg is laid on the pollen, and the cell is immediately sealed by a spiral ceiling and a soil plug. Then work is begun on the next cell, and no further attention is paid to the last one. Thereafter, the daily routine consists of fashioning another cell off the main tunnel, providing it with a pollen ball, depositing the egg and sealing the cell. About one cell is completed each day (Bohart and Cross *1955*). Usually only one nest is prepared and provisioned by a female. There is usually only one generation a year in the intermountain States, but in California two and sometimes three generations appear from May to September.

Food sources and feeding characteristics.—Alfalfa nectar and pollen constitute the primary source of food for most female alkali bees. They visit a few other plant species, for example, clovers, mint, onions, Russian thistle, salt cedar, and sweetclovers. In alfalfa seed producing areas, however, most of the nests are provisioned with nectar-moistened pollen balls derived from alfalfa.

While foraging, alkali bees do not trip the alfalfa blossoms as rapidly as do the leafcutter bees, but almost every blossom they visit is tripped. Because of the large number of flowers the females visit, they become highly effective. Bohart (*1952**) stated that two large nesting sites in Utah, one of which had an estimated 200,000 nesting females, "provided good pollination for the alfalfa-seed fields within a radius of at least 2 miles." The males visit flowers for nectar only and only occasionally trip the flowers.

Alkali bee nesting sites or "beds".—Within recent years, research by Bohart (*1958*), Bohart and Knowlton (*1952*), Frick et al. (*1960*), Fronk[5], Stephen (*1959, 1960*), and Stephen and Evans (*1960*) has resulted in the development of a dependable method of preparing and stocking nesting sites or bee beds for the alkali bee. Such beds can now be prepared and stocked successfully in areas where this bee had not previously occurred.

There are certain basic requirements of an acceptable bed. It must have a moisture supply capable of rising to the surface. This usually requires a hardpan layer a foot or more below a porous soil that tends to hold the moisture and permits its movement from the source of supply to the surface. Conditions should permit rapid drainage of surface water. The underlayer should range in texture from a silt loam to a sandy loam with no more than 7 percent clay-size particles. The surface should be firm but not have a hard crust. If some salt does not appear on the surface, about 1 pound of salt per square foot of surface should be raked into the first 2 inches. This seals the surface layer and thus slows down evaporation.

The bed should be kept relatively free of weeds. It should not be flooded during the active bee season or excessively disturbed by livestock or vehicles.

When bee beds are constructed by alfalfa seed growers, about 3 feet of soil is removed from the selected site. The flat-bottomed excavation is then lined with 0.006-inch plastic film. The excavation is backfilled with an inch of soil, a 10-inch layer of gravel, and 2 feet of appropriate soil. Salt is usually added to the surface as mentioned above. Water can be supplied through a piece of tile that extends from the gravel bed to several inches above the surface.

The size of the bee bed may be determined by the size of the plastic sheet. Bohart (*1952**) indicated that an acre of bee bed might be sufficient for 100 acres of alfalfa, but conditions vary so much that the only safe recommendation seems to be to have as many bees as the forage will support.

After the bed is prepared, alkali bees may find and migrate to it if other beds are within a mile or so. At greater distances, the bees must be brought in. One-cubic-foot blocks of undisturbed soil from

[5] FRONK, W. D. INCREASING ALKALI BEES FOR POLLINATION. Wyo. Agr. Expt. Sta. Mimeo. Cir. 184, 7 pp. 1963.

established bee beds may be transferred and imbedded at the new site during the winter while the bees are in the resting stage (Stephen *1965*). The bees can also be transferred as dormant larvae in individual containers (Bohart *1958*). Generally, attempts at transferring adults have not been successful.

Diseases and enemies.—Numerous diseases, pests, and other enemies inflict damage on alkali bees. Bohart (*1952**) mentioned insects, including ambush bugs, bee flies, chalcids, clerid beetles, conopid flies, cuckoo bees, meloid beetles, robber flies, tiger beetles, velvet ants, and wasps. Crab spiders are also a problem, but mites, although present, are of little consequence (Cross and Bohart *1969*). Vertebrate enemies include birds that feed on the adults and mice and skunks, which usually feed on the larvae. Bacterial and fungal diseases may suddenly strike and seriously diminish the population of a bee bed. Trampling of the nesting sites by livestock, traffic by vehicles, unwise use of pesticides, and flooding during the active bee season can also reduce populations or destroy the site.

Possibilities and limitations.—There is little doubt that where populous alkali bee beds occur the bees of these beds pollinate alfalfa in a highly efficient manner and contribute to the production of bumper seed crops (Menke *1952b*). According to Bohart (*1970b*), a 3,000 ft^2 bee bed cost about $600 to build and stock in 1970. Stephen (*1965*) stated that a well-populated, 1,500 ft^2 bed should provide adequate pollination for about 40 acres of seed alfalfa. At the same rate, the 3,000 ft^2 bed should take care of 80 acres for several seasons. At current honey bee colony rental rates, alkali bees would be much more economical than honey bees.

Alkali bees also have some strong limitations. Their services are confined to areas of the West where rainfall, particularly during the active season, is unlikely. The beds cannot be transported; therefore, the crop to be pollinated must be planted near the bed. The bed must be planned and constructed many months before its pollination service is expected. Finally, a bee bed may be lost—quickly and easily—to flooding, predators, parasites, diseases, or pesticides and other agricultural practices.

LEAFCUTTER BEES

Life History and Habits.—The alfalfa leafcutter bee (*Megachile pacifica* Panzer) is a relative newcomer to America, although there are many other leafcutter bees here. Hurd and Michener (*1955*) listed 124 species in California alone. Bohart (*1962b*) stated that *M. pacifica* was found "about 30 years ago" in the vicinity of Washington, D.C., possibly brought over from eastern Europe or western Asia. It spread rapidly across the Northern States to the Pacific coast. Bohart (*1972*) stated that "it occupies roughly the northern three-fourths of the contiguous United States." In many areas, the alfalfa leafcutter bee became the most important pollinator of alfalfa (fig. 23).

As its name implies, this highly gregarious solitary bee lines its nests with circular sections cut from alfalfa leaves (Stephen *1961*), although it will cut sections from petals of large ornamental flowers. The nests are in hollow tubes or tiny holes above ground (fig. 24). The charcoal-gray adult bee is only slightly larger than a housefly.

The female bee emerges from May to July (depending upon location), mates, and immediately searches out a nesting hole. She prefers a tube or tunnel into which she can barely fit (five thirty-seconds of an inch) but will accept a somewhat larger one when necessary. When one is found, she begins the construction of a cell in it. She builds the first cell at the base of the tube, using freshly

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FIGURE 23.—Alfalfa leafcutter bee collecting pollen from alfalfa.

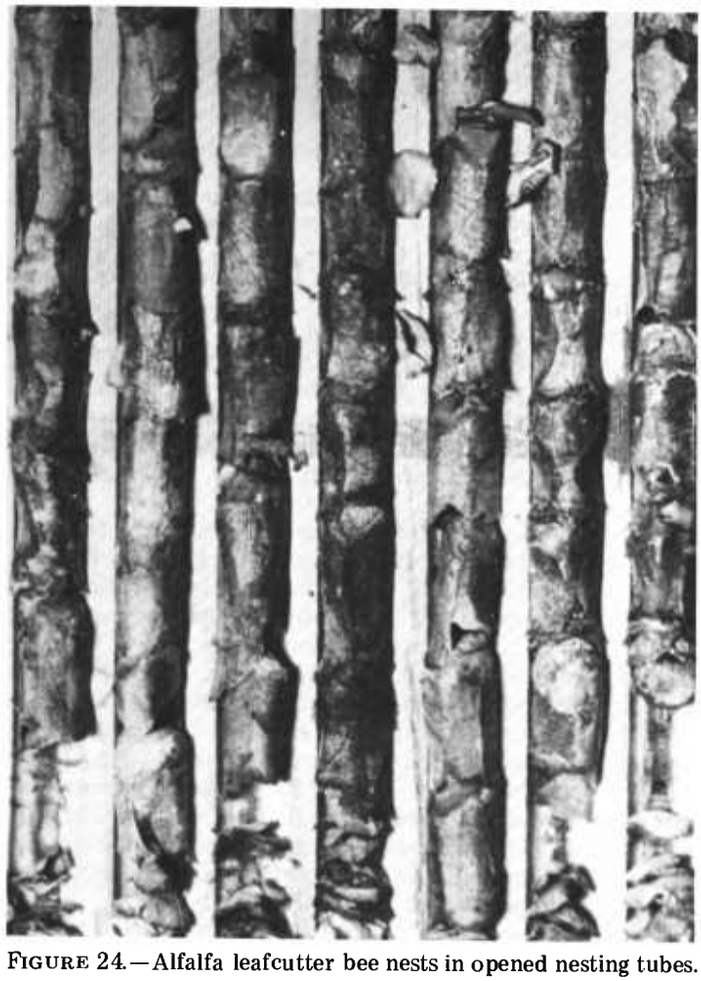

FIGURE 24.—Alfalfa leafcutter bee nests in opened nesting tubes.

cut oblong pieces of leaves. This cell is then filled about half full with a mixture of pollen and nectar. An egg is placed on the food, and the cell is capped with circular pieces of leaf. Another cell is immediately started directly above the first one, and the process is repeated until the tube is nearly filled with cells. After the final cell is sealed with a large number of circular leaf pieces, another tube is begun if pollen and nectar continue to be available.

A female may live 2 months and lay 30 or 40 eggs during her lifetime. About two out of three adults that emerge from the cells will be males. A theoretical increase of about tenfold per generation is possible if ample nesting holes are available and the bees are somewhat protected; however, Bohart (*1962b*) stated that a fivefold increase from year to year is probably optimistic. There is usually a partial second generation that may overlap the first, which would enlarge the expected increase.

The eggs hatch in 2 or 3 days, and the larvae feed on the food in the cell. Larval development is completed in about 2 weeks, and some individuals continue development and emerge as adults about 23 to 25 days after the egg was laid. Others remain without further development as larvae until the next year when they complete their development and emerge as adults.

The males emerge about 5 days before the females. As soon as the female emerges she mates, and although the males may mate many times, the females mate only once (Hobbs *1967*).

Leafcutter bees (as well as alkali bees) can be handled in complete safety. The female has a sting but rarely uses it and then it causes only slight pain. This enables an unskilled worker to handle these bees with assurance of safety, even when thousands are flying about.

Food sources and feeding characteristics.—The alfalfa leafcutter bee derives its food and nesting material primarily from alfalfa; however, it will forage on sweetclovers (*Melilotus* spp.), white clover (*Trifolium repens* L.), some of the wild mints (*Mentha* spp.), and a few other species. Goplen (*1970*) reported that this bee preferred purple alfalfa flowers to yellow flowers to a degree that influenced pod and seed set. The effect of this preference in commercial seed production has not been determined.

The adult does not forage at temperatures below 70° F (Hobbs *1967*). The female visits flower after flower in rapid succession, tripping almost every flower visited, 11 to 15 per minute. She forages no farther from her nest than necessary, usually within the field where the nest is located, and most often within a few hundred feet of the nest. The male visits flowers for nectar only and seldom trips a flower. Hobbs (*1967*) stated that alfalfa fields can be thoroughly pollinated in 3 weeks with about 40,000 females per acre. Klostermeyer (*1964*) indicated that at least 2,000 females per acre were necessary for each 500 pounds of clean alfalfa seed produced. Other figures fall between these extremes.

Rearing and utilization.—The tendency of the alfalfa leafcutter bee to nest in individual tubes in close proximity to hundreds of other nesting females enables man to use this bee to a highly profitable and satisfactory degree in the pollination of alfalfa fields. Growers have been rapidly adopting this bee since 1958 when a Utah grower began making thousands of nesting holes around his outbuildings so the bees could increase their population. Methods of rearing and manipulation have also changed as the widespread value of these bees has become accepted.

Special "bee boards" have been prepared to rear these bees—4-inch by 4-inch timbers about 4 feet long with closely spaced holes three-sixteenths of an inch in diameter bored 3.5 inches deep (fig. 25). These bee boards, with about 2,000 holes filled with leafcutter bee nests sold for about $40 (Bohart *1972*). The boards became so useful and sought after in alfalfa seed fields of the Pacific Northwest that bee board "rustling" became a problem until growers began branding their boards for easy identification.

Some growers used packets of 7/32-inch soda straws cut into 4½-inch lengths for their bee boards. The bases were dipped in paraffin, and the pieces were packed into small open-ended cartons.

Hobbs (*1964*, *1965*) stated that straws less than seven thirty-seconds of an inch produced more male bees but that about equal numbers of males and females emerged from larger straws. He was convinced that all tubes should be at least seven thirty-seconds of an inch in diameter.

Grooved laminated boards composed of wood, particle board, or polystyrene plastic can be clamped together to form nesting holes or tunnels but, most important, they can be taken apart, so that the cells can be examined for dead, diseased, or parasitized ones and the healthy ones removed and concentrated for winter storage or shipment. Bohart (*1972*) stated that the price for 10,000 healthy cells (1 American gallon) was $100.

Hobbs[6] reported that polystyrene grooved boards were being manufactured and used in Canada. He stated that they were more readily accepted by the bees and that bees using them worked longer hours than bees in wood boards. The machine-made polystyrene boards, being exactly alike in shape, could be easily assembled or put through the cell stripper, a device for removing the cells from the grooves. A polystyrene board filled with cells weighs 13 pounds as compared to 45 pounds for the cell-filled wood boards. However, the polystyrene material is delicate and must be handled carefully. Also, mice will chew the material to get to the cells. Finally, the cells sometimes mold because moisture given off by the pupa is not absorbed by the plastic. Plastic blocks with tunnels, plastic straws, and corrugated paper are also used to a limited extent.

Winter storage.—The cells can be left outside during the winter, but mortality for various reasons is high. For best results, they should be stored in a dry, cool place, about 30° to 40° F., then incubated the following spring to cause emergence as adults when desired. They can be stored in the bee boards just as they are brought from the field or they can be removed from the grooves

[6]HOBBS, G. A. FURTHER INFORMATION ON ALFALFA LEAFCUTTER BEEKEEPING. 9 pp. Canada Agr. Res. Sta., Lethbridge. 1969. (Mimeographed.)

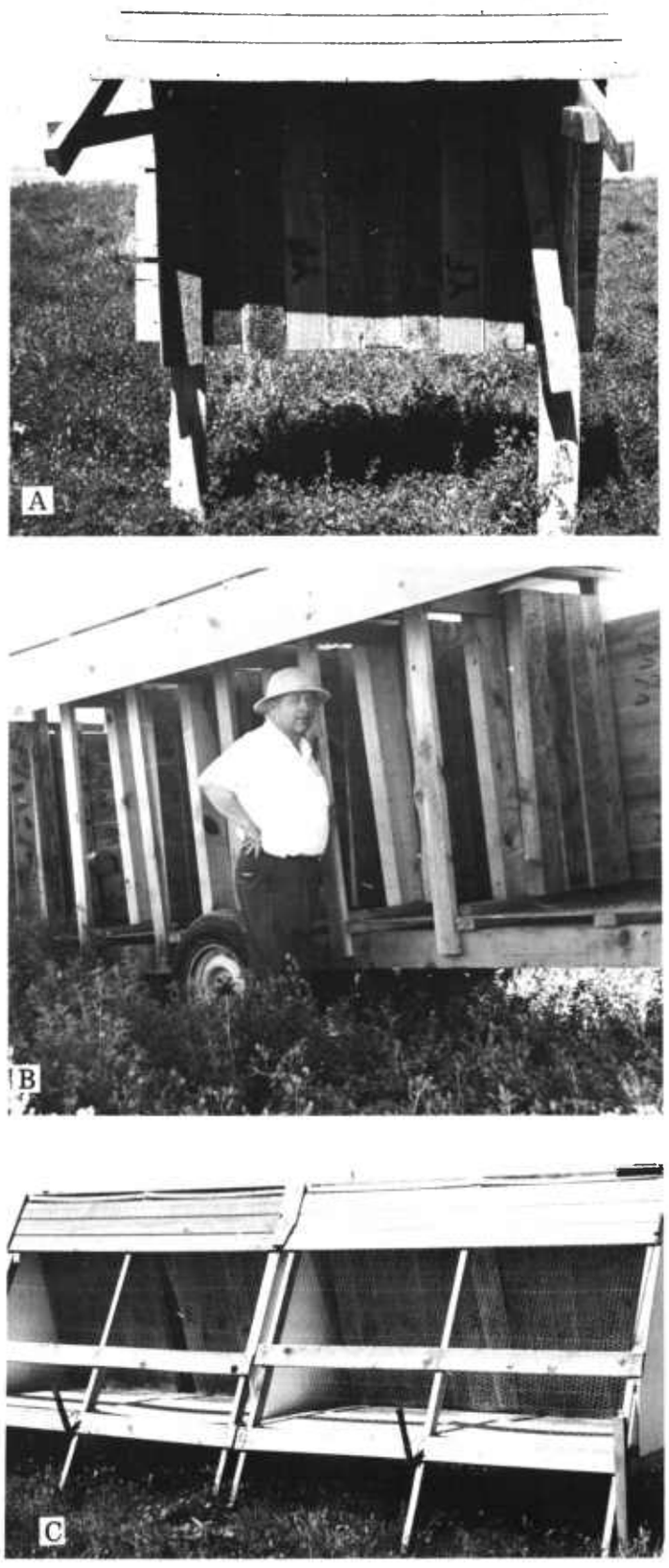

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FIGURE 25.—Alfalfa leafcutter bee nests and shelters. (Note use of brands on nesting boards to discourage theft.) *A*, Stationary shelter; *B*, portable shelter; *C*, stationary shelter with wire screen to protect nests from birds.

of laminated boards by the cell stripper. Storage in the bee boards increases the difficulty of controlling diseases, parasites, and predators but storage in loose cells increases the dangers of parasitism if no control measures are taken.

About 3 weeks before alfalfa is due to begin flowering, the cells are placed in trays in a storage room such as that described by Wilson (*1968*) where the temperature is held at 85° F. and the relative humidity, from 50 to 75 percent. There should be one cell for each tunnel to be used at the nesting site. About one-half of the adults will be males and some of the females will perish, but each surviving female should be expected to fill two or three nests. Pans of water with lights (preferably ultraviolet) shining on them should be placed beneath the trays. The parasitic chalcids and dermestids should emerge first, and, being attracted to the lights, they drown in the water (Waters *1966*). The males begin to emerge several days before the females. The females should be removed to the field about the 21st day after they are placed in incubation.

Usage and handling of nests and shelters.—Size and shape of shelters vary greatly. Some are no more than 4 by 4 by 4 feet, others are the size of a one-room dwelling. Johansen et al. (*1969*) suggested they be 4 by 8 feet in size and 140 yards apart, with about 20,000 filled nest tunnels at the start of the season.

Bohart and Knowlton (*1967*) gave the following specifications for a good shelter; it should—

1. Protect the nesting material against high-angle rays of the sun when the weather is hot.
2. Have an easterly exposure.
3. Afford some shelter from wind and rain.
4. Provide good ventilation.
5. Be large enough to be conspicuous for the bees and have plenty of nesting holes. (Yellow apparently increases conspicuousness, but black, green, and blue are most attractive for nesting.)
6. Be placed 2½ feet or more above ground.
7. Be built so that covers may be added for protection against birds or pesticides.

In addition—

- Shelters should be distributed in the field at the rate of one shelter with 10,000 nesting females for each 5 acres of alfalfa.
- Soil around the nesting site should be bare so that incoming bees may light on it and absorb heat before entering the nest.
- Ants near the nest should be controlled with a nonresidual insecticide, but the bees should be protected from this or other pesticides. Chicken wire should cover the front or openings to exclude bee-eating birds.
- Above all, shelters should be able to withstand wind that is likely to occur when they are in use.
- Shelters should be movable by winch, fork, rollers, or trailer.
- Land beneath the shelters should not be irrigated because the water may cool down the shelter, or the bees may fall into it and drown.
- When the first bees begin to emerge, the tray should be closed and taken to the field. There it should be opened just wide enough for the bees to escape but

not enough for mice to enter. The bee boards should be in place in the shelter before the bees are released.

- If 10,000 females are to be released at a shelter and the average bee board has 2,000 holes, there should be about 15 bee boards at each shelter.

Diseases and enemies.—When the alfalfa leafcutter bee began to increase in population, it seemed to have no important diseases, pests, or parasites. Within a decade, however, scores of natural enemies had appeared, some of which were serious. The tiny parasitic wasp (*Sapyga pumila* Cresson) first mentioned by Torchio (*1963*) as a potential threat was verified by Torchio (*1970*) as causing a high percentage (6.9 to 65.3 percent) of the cells to be parasitized. Torchio (*1972*) recommended trapping for satisfactory control of this wasp. Some degree of control has been devised for the other insect enemies. Birds can be screened away from the nests with chicken wire, and rodent control measures can protect the bees and their nesting materials from mice.

Insecticides sprayed over neighboring property are unlikely to be a problem, but if the alfalfa field is treated they can be serious. Alfalfa leaf material used in the nest can be toxic if treated with persistent insecticides even before the blooms appear or the bees emerge. Confining the bees for protection from pesticides is a poor solution but moving the bee boards at night to a cool dark place for a day or two may be feasible.

Possibilities and limitations.—There are many advantages in the use of alfalfa leafcutter bees. They perform excellently in the pollination of alfalfa. They can be handled safely without fear of the stings by the operator or the neighbors. They multiply rapidly. They forage primarily only in the field to which they are supplied. They can be transported easily and economically in the immature stage, in which most of the year is spent. They do not require constant nurture and manipulation like the honey bee requires. They can be supplied to any field where desired (fig. 26) unlike the alkali bee that is in a permanent nesting site. Their use is so practical and different that they now constitute a new entomological industry (Bohart *1970b*), and Bohart (*1970a*) urged honey beekeepers to become *leafcutter beekeepers.* The use of leafcutter bees can be combined with honey bee pollination. Williams (*1968*) listed 15 dealers who were marketing drilled boards in Idaho and Washington, and three who were marketing grooved laminated boards, one each in California, Oregon, and Utah.

There are some limitations to the bee. It is of economic value to few other plants besides alfalfa. Its usage has not been successfully adapted to the arid Southwest. A similar bee (*M. concinna* Smith) in the Southwest (Butler and Wargo *1963*) seems to be less gregarious, although Butler and Ritchie (*1965*) indicated that it might be reared artificially on bee-collected pollen and sugar sirup. Because of the newness of the leafcutter bee as a commercial pollinator, little is known about its diseases, parasites, and enemies and their long-term effect on it. For its use to be successful, a devoted leafcutter beekeeper would be required to look after its welfare.

Where this bee has been successfully used, the alfalfa seed growers have harvested bounteous seed crops, and, unless unforeseen disaster strikes, its use is likely to increase.

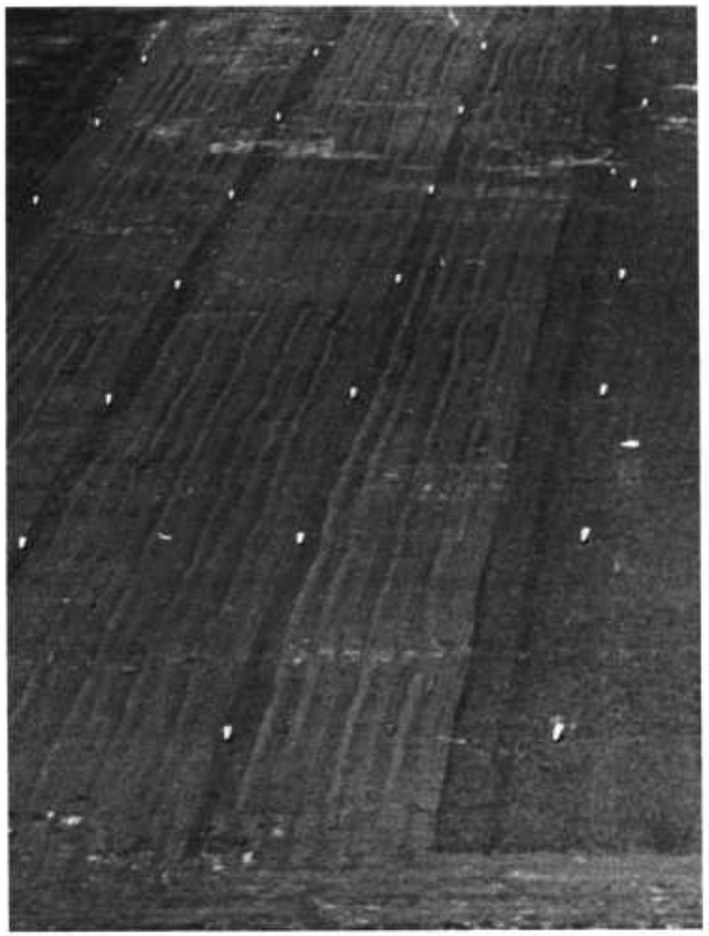

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FIGURE 26.—Alfalfa leafcutter bee shelters in alfalfa field.

STINGLESS BEES AND MELIPONICULTURE

Members of the Apidae subfamily Meliponinae or "stingless bees" are social insects. Some species have clusters of as many as 80,000 individuals; other species, less than 100. The two important genera are *Melipona* and *Trigona.* They do not occur in the United States but are present and of economic significance in Mexico as well as Central and South America. *Trigona* spp. also occurs in Africa, Southern Asia, and Australia. They are mentioned here because of their widespread distribution over the tropical and subtropical areas of the world, their value in the pollination of many crops, and their long-time culture for the production of honey and "wax".

These bees have been studied taxonomically by Schwarz (*1948*) and behaviorially by several men, especially by Nogueira-Neto (*1948a, b, 1950, 1951*), Nogueira-Neto and Sakagami (*1966*), Kerr (*1946, 1948, 1951*), Sakagami (*1966*), Sakagami and Oniki (*1963*), Sakagami and Zucchi (*1967*), and Zucchi et al. (*1967*). Meliponiculture was reviewed and discussed from the practical standpoint by Ordetx and Perez (*Ch. 5: 45-55, 1966*). The following discussion is drawn largely from the above references.

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The females possess weak or vestigial stingers but are unable to inflict pain with them, hence the term "stingless bees." Some species have mandibles sufficiently strong to inflict a mild bite or to pull hairs, or they may crawl into the ears or nostrils of the intruders. Others emit a caustic liquid from the mouth that, in contact with the skin, causes intense irritation. Most species, however, are not bothersome to man, and he may safely manipulate them with ease, even to having his face within inches of a *Trigona* nest containing many thousands of individuals.

Stingless bees were kept by man centuries before the arrival of Columbus or the common honey bee (Bennett *1964*). Some species produce an acceptably delectable honey, as much as half a gallon per colony per year. Others produce less desirable, thin (35 percent moisture versus half that amount in our domestic honeys), strongly acid honeys. One species (*Trigona (Lestrimellita) limao* Smith) produces a honey used to induce vomiting (Bennett *1965*). The most common species used in miliponiculture is *Melipona beechii* Bennett.

When the wax is secreted from the glands on the abdomen of stingless bees it is similar in appearance to that of *Apis mellifera*, but it is then mixed with propolis and the product, called cerumen or Campeche wax, is more or less black. Cerumen is used for waterproofing on farms and in villages, in ink and lithography, and in other restricted ways.

Originally, the colonies were kept in gourds, tree trunks, or similar cavities, but an improved hive has been developed that permits easy manipulation and transportation of these bees (fig. 27). This hive is about a cubic foot in volume—sufficient for the 3,000 to 5,000 bees in an *M. beechii* cluster. If necessary, additional space can be added for larger clusters. A nest of *Trigona clavipes* (F.) in a hollow tree, sketched to scale by Sakagami and Zucchi (*1967*), was 8 by 8 by 50 inches and had a worker bee population that "apparently exceeded several tens of thousands." It contained "at least 20" horizontal brood combs separated from the collection of pollen and honeypots. The size of hive acceptable to a colony of this size was not given.

Life histories and habits.—The size of stingless bees varies from 2 to 14.5 mm. *Trigona duckei* Friese is the smallest species of stingless bee known; *Melipona interrupta* Latrielle is the largest. *M. beechii* is slightly smaller than *Apis mellifera.* The colors of the different species vary from black to brown, red, orange, yellow, and white.

The nest entrance is frequently reduced to permit only a single bee to enter at a time. The nest may be covered by a membranous wax and propolis network, which envelops and protects the nest and brood. There may be a single or multiple layer of brood—the individual cells vertical in some species, horizontal in others —or the cells may be in a cluster like grapes. Some species use the brood cells only once, then they are destroyed and reconstructed. The honey and pollen are not stored in the brood comb but in irregular cells outside of the broodnest.

The queens of *Trigona* are reared in queen cells, similar to those of *Apis mellifera. Melipona* queens develop in cells that externally seem to be no different from those that produce drones and workers; usually one queen to three to six workers. The workers of *Melipona* fill the cell with food before the egg is deposited. Each colony has a single sovereign queen but tolerates numerous virgins. A 4,000 worker bee population of *M. beechii* may have 50 virgin queens living harmoniously with the mother queen. Mating occurs in the air.

Advantages of stingless bees as pollinators.

- Stingless bees do not sting, therefore they are not a hazard to man or animals nearby.
- They collect and utilize considerable nectar and pollen throughout most of the year, therefore, numerous flowers must be visited and pollinated.
- They can be manipulated in hives like honey bees.
- The hives are small, easily handled, and relatively inexpensive.
- The colony is unlikely to become hopelessly queenless.
- The byproducts of honey and cerumen are usable.

Disadvantages of stingless bees.

- Stingless bees cannot tolerate cold weather, therefore, they are limited to the tropical and subtropical regions.
- The byproducts are produced only in small quantities, and they are less desirable than those of the honey bee.

OTHER IMPORTANT BEES

Bumble bees.—There are dozens of species of bumble bees (*Bombus*) in the United States. Most of them are excellent pollinators of a wide variety of crops (fig. 28), although in some plant species they cut a hole in the base of the corolla and "rob" the nectar without effecting pollination.

Bumble bees start each spring in a new nest. A mated female, that overwintered in solitary hibernation, finds a suitable nest site in the spring, possibly an abandoned mousenest in a ditchbank or brush pile.

A wax cell is constructed and stocked with a mixture of pollen and nectar, upon which several eggs are laid. Soon the smaller sterile females (workers) emerge, and the nest is enlarged (fig. 29). These workers relieve the queen of all duties except egg laying, and colonial life emerges. During the summer, the colony grows and becomes more complex. Toward fall, males and sexually mature females develop and mate. Soon thereafter, the mated females abandon the nest and go into solitary hibernation, and the males and immature females die off (Medler and Carney *1963*).

The size of the nest varies with species of *Bombus* as well as with forage available. Michener and LaBerge (*1954*) listed the contents of a large *B. medius* Cresson nest in Mexico as follows:

1 queen
0 males
800 workers (sexually immature females)
28 eggs
126 immature stage

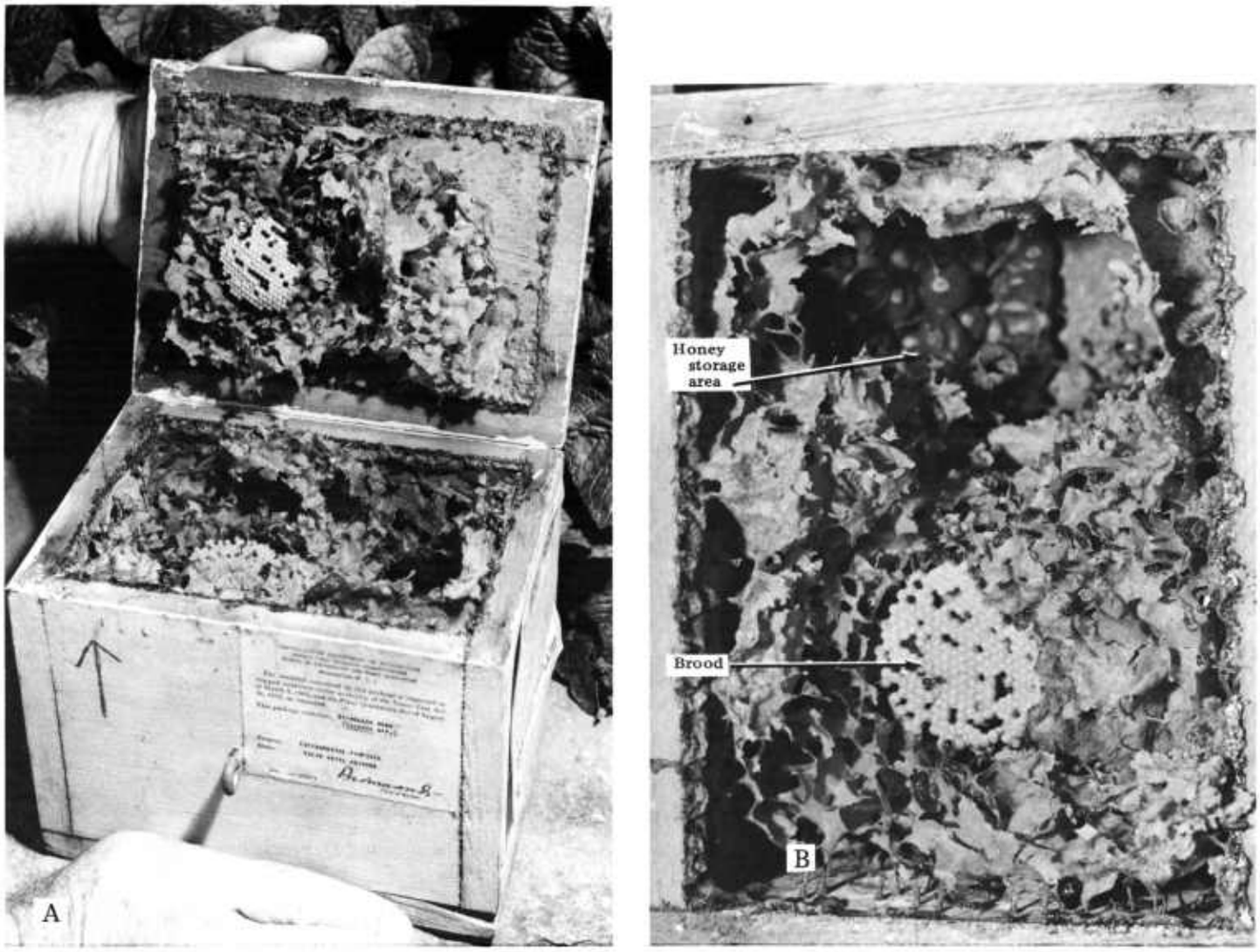

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FIGURE 27.—Stingless bees. *A*, Nest in a constructed hive; *B*, closeup of nest showing bees, brood, and honey storage area.

804 empty cocoons
1,227 cocoons filled with honey
23 pollen pots filled with pollen
27 empty pollen pots

They concluded that the queen had produced 2,183 offspring by June 21, when the nest was examined. Most nests have far less than this number. Holm (*1960*) recorded from 31 to 930 total cells in colonies of *Bombus terrestris* (L.), and from 41 to 600 in *B. lapidarius* (L.), at the end of the season. However, Westbury (*1971*) concluded that colonies are normally unlikely to exceed 400 adults with only 20 to 30 workers present at any one time.

Medler (*1958*) believed that bumble bees would soon be successfully managed, and suggested that "bombiculturists" be trained to culture and manage these bees for pollination. Because of the potential importance of these bees as pollinators if they could be managed, many research workers both before and since have studied them.

Bumble bees can be induced to occupy manmade nests or hives, such as the 6-inch cube hive used by Hobbs (*1966*) and hives, cans, or tile used by Fye and

PN-3765

FIGURE 28.—Bumble bee collecting nectar from a wildflower (*Colutea arborescens* L.).

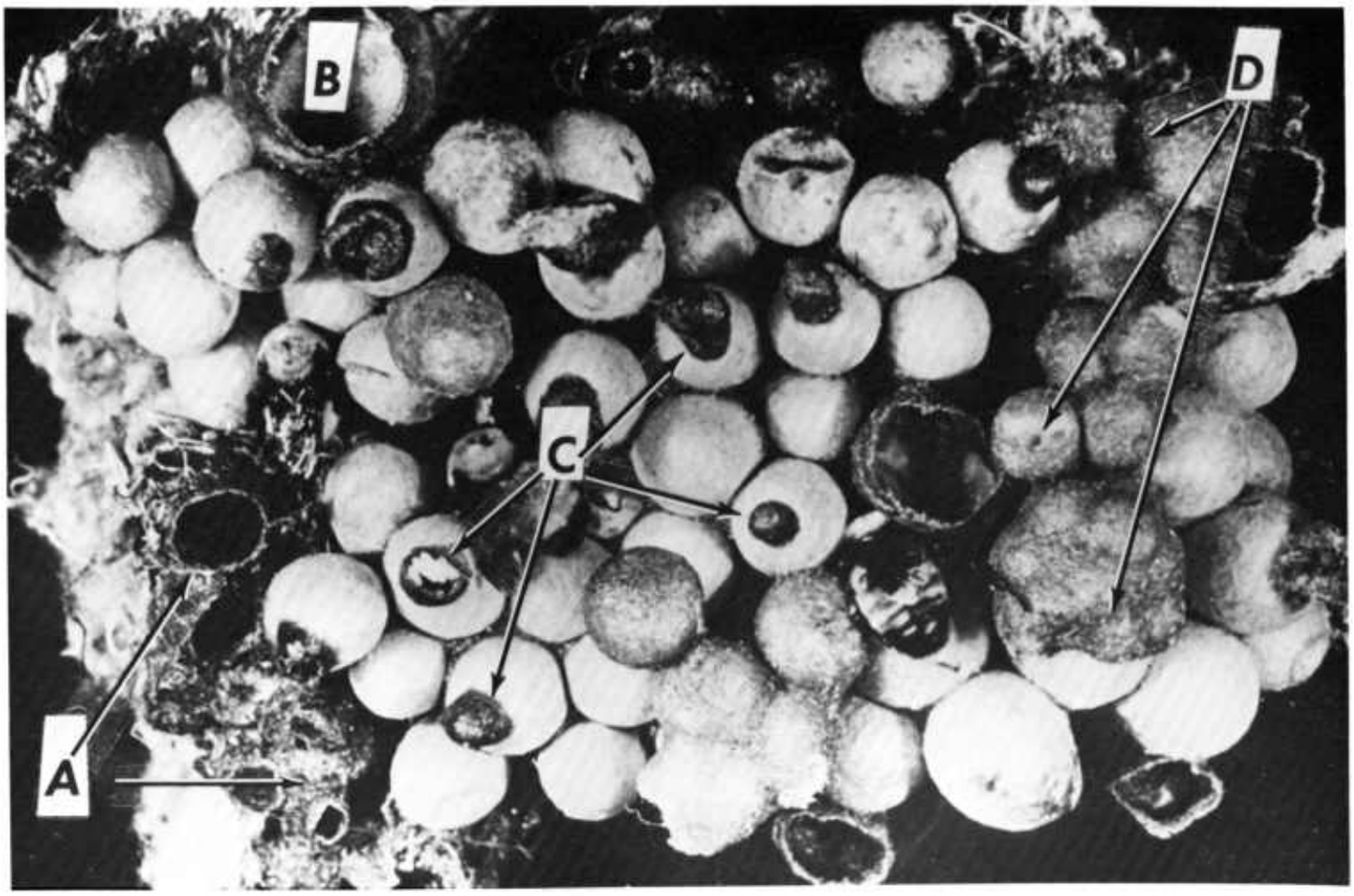

FIGURE 29.—Nest of bumble bee. *A*, Honey pots; *B*, pollen cell; *C*, egg baskets or cocoons; *D*, young brood in wax cells.

Medler (*1954*) and others. They can also be induced to live, mate, nest, and hibernate in greenhouses to a degree that they can be useful as pollinators of small plots (Pedersen and Bohart *1950*). Holm (*1966*) reported that 31 species have been colonized. Unfortunately, their culture is considerably hampered by their nest abandonment each fall. This characteristic prohibits the maintenance of colonies, such as is the case with honey bees or Meliponinae; storage of immature stages as with leafcutter bees, or even maintenance of the immature stages in the area, as with the alkali bees.

Bumble bees are further hampered by diseases and parasites; predators such as mice, skunks, badgers and birds, and man-created problems such as pesticides and the destruction of nesting sites. Their usefulness under natural conditions can be increased by the individual grower or the community where their services are desired. They can be "encouraged" in an area by providing nests and nesting areas for them. Their enemies can be controlled and consideration can be given in the use of herbicides and insecticides. Crops can be planted or wild flowers encouraged on which they can forage during periods when food might otherwise be unavailable.

Carpenter bees.—The carpenter bees (*Xylocopa* spp.) have not been cultured in a true sense although their nesting in certain areas has been encouraged by placement of soft timbers in which they can construct nesting tunnels (see "Passion Fruit"). Because of their large size (almost an inch in length and about half as wide), they resemble large bumble bees but do not have a true pollen basket on the hind leg. They are usually metallic black.

The bees are solitary but numerous ones may be attracted to soft timber in which they can tunnel. This tunnel may be 1 foot long or longer and about one-half inch wide. There may be numerous cells separated by partitions formed by chips of wood cemented together. About 30 to 31 days are required for development from egg to adult.

Because of their lack of gregariousness, these bees are only of limited value where appropriate nesting timbers can be provided. They also have a strong tendency to cut holes in the bases of flowers that have long slender corolla tubes.

Osmia bees.—Bohart (*1972*) reviewed the information on *Osmia* pollination. He stated that *O. cornifrons* (Rad.) has been successfully managed for apple pollination since 1958 in northern and central Honshu, Japan. The bees are captured away from fields or orchards treated with insecticide, taken to the orchard, and released at

the time of apple bloom. The bees nest in bamboo and hollow reeds placed by the growers on shaded platforms in or near the apple orchards. These bees usually begin to fly about 2 weeks before apples come into bloom. They fly at temperatures as low as 45° F., some 20° below that at which honey bees fly.

Levin (*1957*) induced *O. lignaris* Say to nest in specially prepared tubes, 3/8 by 4 by 6 inches, bored in lumber. Levin and Haydak (*1957*) were able to rear the same species on bee-collected pollen but not as efficiently as on *Osmia*-collected pollen.

Free and Williams (*1970*) showed that *O. rufa* (L.) tended to be gregarious and could be induced to nest in drinking (soda) straws. It showed a preference for *Rubus* spp. and other specific plants, indicating that it could be used to advantage.

Introduction of Foreign Pollinators

When a crop is transferred from one area to another, there is always the possibility that the native pollinating agent might be left behind. It might be interesting to ponder over the number of instances a new crop has failed in an area merely because the proper pollinating agent did not accompany the crop. The need for the transfer of bumble bees to New Zealand for pollination of the new crop (to that country) (see "Red Clover") is an example. Also, the effect of the accidentally introduced leafcutter bee into the United States on alfalfa seed production can show the importance of bringing in an improved pollinating agent.

The laborious hand pollination of cacao (see "Cacao") may be due in part to the transfer of this plant without including its pollinating agent or agents. The possibility of increased production or quality of hybrid tomatoes might be considerably enhanced if one of the wild bees of Peru that visit tomato flowers could be successfully brought to this country and cultured. Hurd et al. (*1971*) and Michelbacher (*1968*) pointed out the possibilities for increased yield and quality of cucurbits in many areas if some of the squash bees were introduced.

Bohart (*1962a*) considered the possible value and problems associated with introduction of foreign pollinators and stressed the need for knowing the habits of a pollinator before its importation is made. Some dangers that might and should be avoided are introduction of (1) unwanted arthropod diseases, parasites, and predators; (2) insects with undesirable characteristics, such as stinging or biting people or destroying flowers; or (3) insects that molest or dispossess efficient native pollinators.

There seems to be ample opportunity for reward in exploration of other countries for superior pollinators. For example, if hybrid soybeans materialize through use of male sterility, what might be found in the way of an efficient pollinator in the Orient from whence soybeans came?

The accidental release of the African honey bee in Brazil, with its associated problems, illustrates the need for caution at all stages in the importation of a new species.

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WILD FLOWERS AND CROP POLLINATION

Countless wild flowers are considered of little overall economic significance, even after admitting that the landscape would indeed be drab without them. However, in addition to their beauty they prevent erosion of the soil, and provide seeds, nuts, and fruit for wildlife. For example, Knott (*1950*) stated that 10 of the most heavily used species of noncultivated plants providing food for quail and pheasant were found in the following plant families: Amaranthaceae, Gramineae, Leguminosae, Polygonaceae, and Rosaceae. The first two families are basically anemophilous, but the others are entomophilous. Manning (*1943*) and Yeager (*1937*) also listed numerous forest plants dependent upon or benefited by insect pollination for production of fruits, nuts, or seeds—a goodly percentage of which make up the diets of squirrels, bears, and raccoons (Knott *1950*).

Hassan (*1972*) reported that parasitic hymenoptera utilize pollen and nectar of wild flowers. He stated that the populations of these insects are highest in crops near these food sources, and he inferred that an ample supply of nectar and pollen increased their longevity and productiveness.

Equally significant is another often overlooked part that wild flowers play in the ecological relationship of an area. Their nectar and pollen provide the continual supply of vital food needed by insect pollinators. In turn, the insects serve as pollinating agents for numerous species of these plants (see table 3), and contribute to their survival and genetic prosperity. Darwin (*1889**) recognized the significance of this bee–flower relationship and mentioned bees on at least 87 different pages and pollinating insects even more often. More present day "Darwins" are needed to proclaim the relationship of the whole ecological environment to the pollination of our numerous commercial crops.

Wildflowers are of great importance to the grower of cultivated crops benefited by insect pollination. The abundance of his fruit crop in the spring may be strongly affected by nearby wildflowers of the previous fall that supplied nectar and pollen on which the local bees overwintered. A melon or cranberry crop may be a profit or loss, depending on the volume of previous inconspicuous wildflowers on which wild bee populations might increase.

The major nectar and pollen sources are well known to the beekeeping fraternity. Numerous books and State experiment station bulletins have been written primarily for beekeepers listing plants from which honey bees are known to obtain surplus honey crops or from which the bees collect sufficient nectar and pollen to affect a material increase in the colony population. Regardless of the area that might be considered, if the pollinating insects had at their disposal only the nectar and pollen plants that have been listed in such publications, these insects would be unable to prosper. For them to attain prosperity and contribute to the pollination of commercial crops, there needs to be a daily source of many flowering plants throughout the growing season.

This relationship is revealed in a very dramatic way in the production of almonds in California. Almonds bloom early in the calendar year (January to April) when there are few native insects present to pollinate this crop. The almond growers have come to depend largely upon honey bees for this task. Too often, the honey bee colonies that are used do not have a strong population of bees. One of the primary reasons is that the colonies were deprived of an adequate source of nectar and pollen from fall wildflowers. Unless the colonies can find plants in bloom throughout the fall months from which they can continually collect fresh pollen and nectar, the number of larvae that can be fed is small and the colony is unable to reach adequate strength. Then, even if a food supply becomes available in the early spring, the colony population is inadequate to collect large amounts. Thus, once the colony becomes weak it has difficulty taking advantage of the short flowering period of plants.

Ornamentals are seldom present in sufficient abundance in rural areas to be of material significance to the pollinating insects. Bees are more fortunate near urban or suburban areas where a somewhat continuous although meager supply is usually available. In return for this food supply, pollinators contribute to the beauty of numerous ornamentals by enabling them to set fruit or seed that enhance their attractiveness. The pollinators also service vegetable gardens and nearby farm crops and contribute to the commercial production of ornamental flower seeds, which is a business in excess of $1 million.

Table 3 lists some of the wildflowers and ornamentals dependent upon or benefited by insect pollination. There are doubtless hundreds of others.

Wildflowers that produce pollen and nectar for the pollinating insects need not be, and often are not, eye-catchingly attractive. For example, the flowers of American holly (*Ilex opaca* Ait., family Aquifoliaceae) are scarcely noticeable to us, but they are highly attractive to honey bees. The flowers of numerous grasses are largely unnoticed yet they may be an excellent source of pollen. Puncture vine (*Tribulus terrestris* L.) is a detested prostrate weed of the Southwest, but its tiny, pale-yellow flowers are an excellent source of nectar and pollen for bees. The pollen from flowers of the willow trees (*Salix* spp.) is equally as valuable as that from the more noticeable pestiferous dandelions (*Taraxacum officinale* Weber).

Numerous studies on the nutritional value of pollens have shown they are quite different chemically (Standifer *1966*, Todd and Bretherick *1942*). They influence length of life and development of adult worker honey bees (Standifer *1967*) and also influence hypopharyngeal glands that supply broodfood of developing larvae (Standifer et al. *1970*). Because of these and probably other nutritional differences in pollens, it appears that the pollinating insects benefit from foraging on a variety of plants. This has never been

proven by tests, but beekeepers generally agree that their colonies become most populous in areas where mixed wildflowers are most numerous.

As a practical application, a grower who desires colonies of honey bees of maximum strength for the pollination of his crop would want them to have been foraging previously in an area with the greatest possible mixture of flowers. Usually, cultivated crops do not provide as great a mixture of flowers as can be found in wasteland. The grower who does not arrange for colonies of honey bees to be placed in or near his field for their use as pollinators should be particularly interested in having wildflowers on or near his farm to support the wild bees and other pollinating insects.

Table 3.—Some wild flowers and ornamentals dependent upon insect pollination for seed production

Family	Scientific name	Common name	Source reference
Agavaceae	*Yucca* spp.	Yucca	Baker *1961*
Apocynaceae	*Vinca rosea* L.	Periwinkle	Schnell *1943*
Araceae	*Zantedeschia* spp.	Calla	Coleman *1937a*
Asclepiadaceae	*Asclepias fruticosa* L.	Milkweed	Coleman *1937b*
Cactaceae	*Carnegiea gigantea* (Engelm.) Britt. and Rose	Saguaro or giant cactus	Alcorn et al. *1961*, McGregor et al. *1962*
Do.	*Echinocactus wislizenii* Engelm.	Barrel cactus	McGregor and Alcorn *1959*
Do.	*Lemaireocereus thurberi* (Engelm.) Britt. and Rose	Organpipe cactus	Alcorn et al. *1962*
Campanulaceae	*Campanula carpatica* Jacq.	Tussock bellflower	Darwin *1889**
Caryophyllaceae	*Dianthus caryophyllus* L.	Carnation	Do.
Commelinaceae	*Tradescantia* spp.	Spiderwort	Sinclair *1968*
Compositae	*Tagetes* spp.	Marigold	Edgecombe *1950*
Cruciferae	*Iberis umbellata* L.	Candytuft	Darwin *1889**
Do.	*Matthiola* spp.	Stock	North *1951*
Cyperaceae	*Dichromena ciliata* Vahl	Sedge	Leppik *1955*
Elaeagnaceae	*Shepherdia argentea* Nutt.	Buffaloberry	Hedrick *1938**
Ericaceae	*Kalmia angustifolia* L.	Sheep laurel	Lovell and Lovell *1934*
Do.	*K. latifolia* L.	Mountain laurel	Dowden *1964*
Do.	*Rhododendron canadense* (L.) Torr.	Rhodora	Lovell and Lovell *1932*
Fumariaceae	*Dicentra cucullaria* (L.) Bernh.	Dutchman's breeches	Macior *1970*
Gentianaceae	*Gentiana* spp.	Gentian	Beal *1874*
Iridaceae	*Freesia* spp.	Freesia	Sparnaaij et al. *1968*
Labiatae	*Origanum vulgare* L.	Wild marjaran	Darwin *1889**
Leguminosae	*Cercis* spp.	Redbud	Beilmann *1950*
Do.	*Cytisus scoparius* (L.) Link	Scotch broom	Darwin *1889**
Do.	*Trifolium uniflorum* L.	Solitary clover	Gibson and Chen *1971*
Do.	*Colutea arborescens* L.	Bladder senna	Nye and Bohart *1962*
Lobeliaceae	*Lobelia ramosa* (probably *L. tenuior* R. Br.)	Lobelia	Darwin *1889**
Do.	*L. fulgens* Willd.	- -do- - -	Do.
Loranthaceae	*Phoradendron* spp.	Mistletoe	Bray *1910*
Lythraceae	*Lythrum salicaria* L.	Spiked or purple loosestrife	Stout *1924*
Martyniaceae	*Proboscidea* spp.	Unicorn plant	Hurd and Linsley *1963*
Orchidaceae	Numerous genera and spp.	Orchids	Allen *1954*, Coleman *1929*, Darwin *1877**, Godfrey *1929*
Papaveraceae	*Eschscholizia californica* Cham.	California poppy	Darwin *1889**
Polemoniaceae	Several genera, about 75 spp.	Phlox	Grant and Grant *1965*
Primulaceae	*Primula vulgaris* Hill	Primrose	Marsden-Jones *1926*, Woodell *1960*
Do.	*Cyclamen persicum* Mill.	Cyclamen	Darwin *1889**
Resedaceae	*Reseda lutea* L.	Mignonette	Do.
Do.	*R. odorata* L.	- -do- - -	Do.
Rosaceae	*Amelanchier alnifolia* Nutt. ex. Roem.	Juneberry	Yeager *1937*
Do.	*Prunus besseyi* Bailey	Sandcherry	Do.
Do.	*P. pensylvanica* L.	Pinchberry or pin cherry	Do.
Rubiaceae	*Posoqueria fragrans* Roxb.	([1])	Darwin *1889**
Saxifragaceae	*Ribes aureum* Pursh	Missouri currant	Yeager *1937*
Scrophulariaceae	*Antirrhinum majus* L.	Snapdragon	Mather *1947*
Do.	*Digitalis purpurea* L.	Foxglove	Darwin *1889**
Do.	*Linaria vulgaris* Hill.	Butter-and-eggs	Do.
Do.	*Penstemon gracilis* Nutt.	Penstemon	Crosswhite and Crosswhite *1966*
Solanaceae	*Cestrus nocturnum* L.	Night-blooming jessamine	Overland *1960*
Do.	*Petunia violacea* Lindl.	Petunia	Knuth (*1909**, *3: 158*)
Do.	*P. nyctaginiflora* Juss.	- -do- - -	Do.
Violaceae	*Viola tricolor* L.	Pansy	Veerman and van Zon *1965*

[1] No common name.

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PESTICIDES IN RELATION TO BEEKEEPING AND CROP POLLINATION

The poisoning of bees by pesticides is a major problem affecting the efficiency of bees not only in the production of honey but also in crop pollination (fig. 30). This problem is not limited to the United States but occurs in all other countries that have highly developed agriculture. The problem is complex with many ramifications, frequently interwoven with emotion.

The greater part of the problem is associated with insecticides applied to cultivated crops—cotton, fruits, vegetables, grains, and legumes. Damage also results from treatment of forests and rangelands, and even suburban areas, for the control of pests of man and animals.

PN-3766

FIGURE 30.—Honey bees killed by insecticides.

By nature, honey bees from a colony visit flowers over an area of several square miles. The intensity of visitation in any one part of the area is determined by the relative attractiveness of the flowers. The extent of damage to the colony by a pesticide application is influenced not only by the relative toxicity of the material, the number and methods of application, the time of day, and the weather conditions, but also by the number of bees from the colony visiting the flowers in the treated area, the type of food (nectar or pollen) they are collecting, the type of flowers the food is collected from, the season of the year the damage occurs, and even the influence of forage available to the bees for weeks before and after the application.

Wild bees are also damaged by pesticides. Poisoning may result from contaminated food as well as from florets, leaves, soil, or other material used by the bees in nesting. The toxicity of a specific insecticide to honey bees and wild bees is not always the same, and even among wild bees some materials are more toxic to one species than to another.

The problem of bee poisoning is one of long standing, as pointed out by Shaw (*1941*) and Todd and McGregor (*1952*). It became unusually severe in connection with the use of arsenical sprays on fruit in the early part of this century. This resulted in the enactment of legislation in several States, which prohibited the spraying of the trees while they were in bloom. The legislation was beneficial to both the beekeeper and the grower, because of the need for the bees to pollinate the fruit blossoms as well as for the protection of the bees. The legislation alleviated but did not eliminate the damage because of the flowering habits of fruit trees. Some of them blossom earlier than others or stay in blossom longer. When insecticides are applied to safe trees (those that no longer have open flowers), the material drifts to and contaminates nearby flowers (McIndoo and Demuth *1926*).

There was another surge of damages when ground and air machines began large-scale applications of calcium

arsenate on cotton and other crops (Hawes and Eisenberg *1947*) during the 1920's. These applications increased in volume during the 1930's and into the early 1940's, causing great damage to beekeeping (Bertholf and Pilson *1941*, Butler et al. *1943*, Eckert and Allinger *1935*, *1936*).

This damage subsided during the mid-1940's when growers shifted from the use of arsenicals to DDT (McGregor and Vorhies *1947*, McGregor et al. *1947*). However, with the development of other chlorinated hydrocarbons, phosphates, and carbamates, the problem increased to an even higher intensity, and considerable study was devoted to the problem (Anderson and Tuft *1952*; Anderson and Atkins *1958*, *1967*, *1968*; Anderson et al. *1964*; Palmer-Jones and Forster *1958*; Todd and McGregor *1961*; Weaver *1950*, *1951*).

Severity further increased to the point of disaster for many beekeepers in the late 1960's when usage of DDT and some other chlorinated hydrocarbons was decreased sharply by legislation as a reaction to public concern, and they were replaced in the majority of instances by the more toxic phosphates and carbamates.

The effect of an insecticide application may not be confined to damage to the pollinators of a distant crop or elimination of pollinators for the target crop. Another previously overlooked factor associated with the pesticide may be that it can detract from the plants' productiveness. Beekeepers frequently comment that they believe the pesticide influences the plant itself detrimentally from the bee forage standpoint. This belief has recently received some experimental support. Sedivy (*1970*) reported that only 10.5 percent of pollen grains germinated after they were dusted with Melipax[7] as compared to 62.1 percent in the control pollen. When the pollen grains were treated with 0.3 percent Fribal emulsion, another apparently toxaphenelike compound, only 28.2 percent germinated as compared to 81.5 percent of the control pollen. None of the grains treated with 0.7 percent Fribal emulsion germinated as compared to 79.0 percent of the control.

Gentile et al. (*1971*) reported that the insecticide naled, at only 100 ppm, completely inhibited germination of both tomato and petunia pollen. They also reported that azinphosmethyl, DDT, dichlorvos, dicofol, endosulfan, and Gardona® caused reduction in pollen germination and/or pollen tube elongation. Carbaryl and methomyl had little or no deleterious effect on pollen, and xylene was noninjurious.

The separation of the toxic or repelling effect of the presence of the insecticide on the plant from the possible less attractiveness of affected pollen is difficult, but the idea merits further examination, both from the effect of pesticides on the plants and on the pollinating insects.

Intensity of Damage to Bees by Pesticides

Numerous surveys have been made to determine the extent of the losses of bees from pesticides. Levin (*1970*) stated that some 500,000 colonies were killed or damaged in the United States in 1967, of which 70,000 were in Arizona and 76,000 in California. Swift (*1969*) stated that losses in California in 1968 were even greater—83,000 colonies. Wearne et al. (*1970*) and Barnes (*1972*) concluded that the major problem confronting the beekeeping industry was bee losses due to pesticides—with which there is little disagreement by the beekeeping industry. All indications point to an annual loss by the industry in the neighborhood of 10 percent caused by pesticides alone. Few industries can tolerate such losses and survive. The effect of these losses on the adequacy of crop pollination is unknown.

Crops Involved

Wherever pesticides are applied to plants there is a possibility of damage to bees. Because of the volume of insecticides used on cotton and because of the plant's attractiveness to bees over a long period, this crop doubtless holds first rank in the poisoning of bees. The spraying of fruit, particularly apples, but also apricots, cherries, citrus, nectarines, peaches, pears, plums, and prunes, causes serious losses. After the use of DDT on sweet corn was discontinued, the other materials applied on this crop caused serious damage to bees. Increased use of pesticides on soybeans, a relatively new poisoning hazard, is causing increased damage to bees. The treatment of numerous vegetables also causes severe losses in restricted areas.

Control and eradication programs on specific crops or areas, for example, the cereal leaf beetle or the pink bollworm control program, frequently cause unexpected and large losses because of the concentration of material in the areas involved. Grasshopper control programs on rangelands (Levin et al. *1968*), gypsymoth control programs in forests, nuisance mosquito abatement programs in moist wastelands, or even suburban areas, and specific mosquito or fly eradication programs, as well as certain herbicides and defoliants (Palmer-Jones *1960*), cause the greatest losses (Martin *1970*).

Pesticides Involved—Basic Types and Classes

INSECTICIDES

Insecticides affect bees in one or more ways as stomach poisons, as contact materials, and as fumigants. Arsenicals are typical stomach poisons, pyrethrum is a typical contact insecticide, and hydrogen cyanide, paradichlorobenzene, and carbon disulfide are examples of fumigants.

Botanicals.—Only a small amount of our insecticides are derived from plants. These sources are cube, derris, nicotine, pyrethrins, ryania, sabadilla, and tephrosia. The bulk of this material is used in households and gardens, and, because of its inaccessibility to bees or the relatively minute amount used, it presents no hazards to pollinating insects. Sabadilla dust is sometimes used on citrus where it can create a bee poisoning problem.

Occasionally, bees are poisoned by feeding on nectar or pollen of certain plants, for example, California buckeye (*Aesculus californica* (Spach) Nutt.), locoweed (*Astragalus* spp.), or mountain laurel (*Kalmia latifolia*

[7] According to J. R. Hanson (personal commun., 1972), Melipax is a toxaphenelike chlorinated camphene, which on bioassay shows about 40 percent less activity than U.S.-made toxaphene.

L.). Reaction of the bees to these plant poisons can usually be differentiated from those caused by most pesticides.

Inorganics.—These pesticides include arsenicals, fluorides, mercury compounds, and sulfur. The method and limited use of the mercury compounds precludes their presenting a hazard to bees. Elemental sulfur alone or when used with other insecticides in the field, presents only a slight repelling action, although fumes from burning sulfur are highly toxic to insects. Fluorides are rarely used on a large scale and present no problem. In certain sections of Europe, fluoride compounds from smelters frequently cause bee damage. Whenever arsenicals are used they pose a serious threat to bees.

Organics.—The chlorinated hydrocarbons, organophosphates, and carbamates vary in their toxicity to bees from relatively nonhazardous to highly hazardous, depending upon the individual material or combination of materials.

Pathogens: bacteria, protozoans, and viruses.—None of these that are currently recommended or that have been tested for biological control pose a hazard to bees (Cantwell et al. *1972*).

DEFOLIANTS, DESICCANTS, AND HERBICIDES

Most tests have shown this class of materials to be nonhazardous to bees, except for their removal of the food source from the plant; however, Morton et al. (*1972*) reported that paraquat, MAA, MSMA, DSMA, hexaflurate, and cacodylic acid were extremely toxic when fed to newly emerged worker honey bees at 100 and 1,000 ppm concentrations. Although newly emerged bees do not forage away from the hive, they consume food that others bring in. MSMA, paraquat, and cacodylic acid were also highly toxic when sprayed onto older bees in small cages (Moffett et al. *1972*).

DILUENTS, SYNERGISTS, AND ACTIVATORS

There is little information on the influence of these agents on the toxicity of the primary pesticides on honey bees. Possibly different interpretations of the effects of certain pesticides may have been associated with the materials with which they were applied.

FUNGICIDES

As used, the copper compounds, mercury compounds, pentachlorophenol, sulfur, and zineb have caused no trouble to bees.

SEX LURES, ATTRACTANTS, AND OTHER HORMONES

These usually cause no problems to bees, and their use near bees is generally welcomed. Occasionally, a few honey bees and bumble bees have been found in traps containing Japanese beetle lures (Hamilton et al. *1970*).

BIOLOGICAL CONTROL AGENTS (PARASITIC AND PREDATORY INSECTS)

Beekeepers would welcome biological control of harmful insects on crops because the control agents likely to be used would prey on the specific insects without harming bees. This would permit bees to forage with safety and effectively pollinate the crop.

How Poisoning of Honey Bees Occurs

The majority of poisoning occurs when the bee is in the process of collecting nectar and pollen. In the stomach-poison types of material, the bee is poisoned when the material is ingested with the nectar or pollen. The food may also be transported to the hive where it is fed to and poisons other bees. With some quick-acting poisons, the bee may die in the field. With others, it may return to die in the hive or crawl from the entrance and die nearby. The poisonous material may be obtained from the treated field or it may have drifted from unattractive plants, such as young lettuce or tomatoes, onto attractive plants in bloom such as alfalfa, melons, or flowering weeds.

Bees are also believed to get poison from imbibing water in the form of dew on the plants or from watering places within the treated area, but there is little data to support this.

In the case of nerve-type poisons such as parathion, the bees could easily become poisoned while flying through or over the area while the material in its gaseous form is in the air.

During extremely high temperature, a colony can experience severe loss if the water supply is cut off for only a few hours. If the water supply were so located that the water carriers became poisoned in flight, the colony could suffer both directly in the loss of the water carriers and indirectly from lack of water, even though the pesticide were applied to a totally unattractive crop.

Pesticides applied to plants may get into the nectar directly or reach it indirectly by moving from the treated parts through the plant system (Jaycox *1964*, King *1964*). The likelihood of bees being killed in economic numbers by the latter method (Johansen et al. *1957*) with currently recommended materials is extremely small, and the likelihood of such materials reaching the public in marketable honey is indeed remote.

The various materials can and frequently do reach the hive in pollen that can cause serious poisoning when fed to the developing brood. Pollen gathering is also reduced when the plants are treated (Todd and Reed *1969*). This reduction in turn reduces brood production and colony strength.

SYMPTOMS OF BEE POISONING

The individual bee.—Bees react differently to the effect of different insecticides. The symptoms of arsenic poisoning are very pronounced. In the early stages, adult bees become sluggish and soon neglect their duties, so the brood apparently dies of starvation; later, their abdomens become greatly swollen, being filled with a yellowish watery liquid, still later, the legs and wings become paralyzed; and, finally, the bees die in a state of coma. By contrast, the symptoms of bees affected by DDT were described by McGregor and Vorhies (*1947*): "They acted as if cold, lighting on leaves, twigs, or lumps of soil, selecting warm spots, and generally sitting motionless unless disturbed. Sometimes they fell from these perches, then revived and departed slowly, as a cold bee does, or in rapid erratic flight to alight again a

few yards away. In crawling they were much slower than arsenic poisoned bees. After becoming unable to crawl they would be helpless, sometimes for hours if protected from direct sun. They often lay on their backs or sides making feeble movement with legs or antennae."

Other materials affect bees other ways. When bees are exposed to the insecticide BHC, for example, they are much more inclined to sting.

The cluster.—Usually, the first noticeable effect of insecticide poisoning on the colony is recently dead or dying bees on the ground near the hive entrance, although this is not always the case. If poisoning is severe, the affected or dead bees will accumulate on the floor of the hive faster than the normal bees can remove them.

Flight from the entrance decreases and fresh nectar can no longer be shaken from the brood combs. As the cluster population decreases, its size and the concentration of bees within it also decreases. The brood is gradually abandoned, the smaller larvae begin to die, and many of the larger larvae crawl from their cells and fall to the floor of the hive before they die. The sealed brood begins to die and as it does so the color of the capped cells becomes darker.

As the cluster continues to diminish and become disorganized, the combs in colonies exposed to the hot sun begin to melt. Soon the liquid honey begins to ooze from the hive entrance and spreads among the dead bees on the ground. Frequently, the last individual to die is the queen. Wax moths quickly discover the deserted colony, lay their eggs within it, and the developing larvae soon riddle and destroy the remaining combs.

Bees frequently store contaminated pollen in the combs, for example, pollen collected from corn sprayed with carbaryl. This contaminated pollen remains toxic for months, even in combs removed from weakened or destroyed colonies. If such pollen-filled combs are placed on nonpoisoned colonies, the pollen may cause serious poisoning to the young larvae to which it is fed.

Poisoning may result in complete destruction or the colony may be weakened to varying degrees. If it is exposed to a single application that does not destroy it, the field force may be lost, but if it has a large amount of brood emerging its apparent recovery is rapid. More severe poisoning may prevent rapid buildup, and the colony may go into winter without adequate reserves of food or young bees. Such colonies may die or survive the winter in such a weakened condition as to be of no value for much of the following year.

The grower is sometimes confused when he is told that colonies have been damaged by pesticides yet he sees apparently normal bees entering and leaving the hive entrance. He may be influenced by the fact that young bees take their orientation or "play" flight near the entrance before they reach the foraging age. This can give an impression of great activity when no food is being stored. Also, the difference between colony survival and a surplus honey crop may be the loss of only a few thousand bees, which only an experienced beekeeper can detect.

DIFFICULTY IN ESTABLISHING DEGREE OR PROOF OF DAMAGE

Beekeepers sometimes want to establish that the bees have been damaged by a pesticide, or establish the degree of such damage. To do so is extremely difficult, even if the colony is completely destroyed.

If destruction occurs just before a honey flow no honey is stored, and all the labor and expense of care and maintenance of the colony at its appropriate strength in anticipation of the flow is lost. Destruction a few weeks later might leave the hive with considerable stores of honey that could be salvaged.

If the colony is not completely destroyed, again the time of damage influences the degree of loss. Removal of a few thousand field bees from a strong colony cannot usually be detected by the average beekeeper, yet this loss just before a honey flow may result in no surplus honey storage for the beekeeper. The same loss a few weeks later might have no economic significance on current production. It could, however, affect the overwintering ability of the colony.

Honey bees, like range cattle, need not be under daily surveillance by the owner. In both cases, the owner knows the critical periods in the life and growth of each, and observations and management are timed accordingly. Manipulating honey bee colonies daily is detrimental. The beekeeper knows through experience when honey flows are expected. He manipulates the colony to its major strength at the appropriate time, gives it the anticipated storage area needed, then leaves it undisturbed, sometimes for a few days, at other times for several weeks.

For these reasons, the beekeeper may not know when the bees are damaged. If only the predominant field force is destroyed, and there is no accumulation of dead bees at the entrance, the number of house bees remains relatively constant. An examination of the colony by an expert beekeeper might fail to detect the loss of bees. Only if he knows the normal rate of honey storage for this particular time and location, and recognizes that normal storage has ceased, can the effect be recognized.

Determining the source of the pesticide is even more difficult. If more than one field is treated on the known day of damage, or if numerous fields in the area are receiving periodic treatments, the beekeeper frequently has no way of determining in which area the bees are foraging and the source of damaging material.

If there is only one major source of nectar in the area (and only the experienced beekeeper can determine this), and if only one field from which this nectar is derived is treated on the day the bees show serious poisoning symptoms, the deduction can be drawn that the particular field is the source of damage.

CHEMICAL ANALYSIS

The bees, themselves, are more frequently affected than are either the nectar or the pollen. An identification of the material on or in the bees, if identical with the material known to be applied to the field, is a strong inference as to the source of the material. However, many pesticides break down rapidly

when exposed to the elements or the samples taken by the beekeeper for analysis are otherwise not properly handled.

For chemical identification, the sample for analysis should be collected immediately after exposure and kept frozen until analyzed. Even with these precautions, the analysis may not reveal the identity of the material.

There is no Federal laboratory equipped for routine analysis of bee samples for all pesticide residues. Some State experiment stations are equipped to determine certain residues. Some commercial laboratories analyze for residues for a fee. If analysis of the bees is desired, the analyst should be consulted before the sample is submitted to determine if the analysis can be conducted, and the best method for taking the samples.

SUGGESTIONS FOR REDUCING BEE LOSSES

Grower action.—Because of the value of bees to agriculture as pollinators, the grower should become well informed about them and about the relative damage of different pesticides to them. This will help him to take practical steps to avoid damage to bees. The grower can take numerous steps to prevent or alleviate this damage. It is in his interest that this be done.

The grower can prevent the treatment of many plants when they are in bloom, or he can arrange for the treatment to be made at the time of day or period in the plant's growth when the bees are not visiting it. He can also have the material applied in the form or manner that would cause the least damage. He can choose between materials that vary in toxicity to bees and use the one least toxic.

Control methods other than the use of harmful chemicals can also be considered by the grower. These methods include biological, cultural, and integrated control as well as the use of field sanitation, crop rotation, and resistant varieties. These offer the greatest safety to bees. Their use, as compared to the broad spectrum insecticides, would permit maximum use of bees as pollinators.

Finally, the grower can become acquainted with the beekeepers and the apiary locations in his area. Then when the use of materials highly toxic to bees is anticipated, he can notify the beekeeper so that protective steps may be considered.

Beekeeper action.—If the apiary is a permanent one, the beekeeper should let nearby growers know where it is located. If this is impractical, the beekeeper's name, address, and telephone number should be prominently posted in the apiary so that it can be obtained without danger of bee stings. Registered brands on the hives is another way of establishing ownership. This is useful only if the brand is known locally by officials who can release such information.

Beekeepers frequently state that the only solution to the bee poison problem is to go out of business. Usually, moving colonies to escape damage from pesticides is equally unsatisfactory. The reluctance of beekeepers to move an apiary is frequently not understood and treated as recalcitrance on his part. With the best knowledge and care, the colonies at times are likely to be completely destroyed if certain insecticide material is to be applied to a nearby crop. When such is the case and removal of the colonies is the only recourse, why is the beekeeper hesitant to move or why does he sometimes leave the colonies in the area? A considerable amount of beekeeping knowledge is involved in his decision.

The colonies may contain new combs filled with honey that will break under vibration by the truck that hauls them over rough roads. Should this occur, the bees in the cluster will be drowned by the honey and the combs lost.

Dependable safe alternate locations are difficult to find. Furthermore, maintaining such locations, including a road to them, rental, shade, and other factors make them expensive insurance.

No beekeeper can determine the value of a bee location merely by looking at it. Each must be proven by test as to its productiveness, safety, and dependability. When a beekeeper moves an apiary to a new location, he must become acquainted with a new ecological environment, including flora, fauna, soil, geography, water, rainfall, wind directions, velocity, and scores of other interrelated factors. When the bees are moved to the new location, therefore, they may suffer from lack of water or from flooding, they may become overgrown with weeds or shrubs, or suffer from lack of shade. The plants may not yield an adequate source of food and the colonies starve, or they may yield at an unsuspected time and cause excessive swarming and the colonies deteriorate.

If the beekeeper does not move, he should become acquainted with the crops in the area, the pesticides recommended, and the period of the year when the pests are likely to require control measures. He should also be acquainted with the relative toxicity of the pesticide materials so that if he is notified of a pending treatment he can anticipate the outcome.

The colonies should be kept in the best condition practical, because a *strong broodnest* will provide rapid replacement of field bees. *Shade* for colonies under hot weather conditions has proven quite beneficial (Owens *1959*). An ample supply of *clean water* should be nearby so the colony will not suffer for lack of it if many of the field bees are destroyed. There should be *ample space* within the hive for normal growth and expansion. The colony should be headed by a *young, vigorous queen* so that maximum broodrearing will be maintained, with the food supply and colony strength permitting.

When the beekeeper knows in advance that a short-residual but highly toxic insecticide is to be applied shortly after dawn on a nearby crop, the colonies may be confined until the danger of the pesticide is past (Jaycox *1963*). One method of confinement when the temperature is high is to cover the colonies before dawn with a blanket of burlap. This should be kept moist (Owens and Benson *1962*) as long as the bees are confined. If the temperature is not high, the bee colony entrance may be blocked before flight begins, then opened as soon as danger of the insecticide is past.

Even when the colonies are not moved, something may occur that alleviates or prevents insecticide damage. The grower may decide that treatment is unnecessary or at the last minute he may be prevented by weather or other factors from applying the material. The bees may fail to visit the field, or the damage suffered may be less severe than anticipated. Subsequent honey production may counteract the damage. Frequently, a beekeeper moves, only to have the colonies destroyed by pesticides in the new location.

Because of all of these factors, many beekeepers realize that moving is as much a gamble as remaining near the pesticide-treated area.

State or Federal action.—The 91st Congress enacted provisions for indemnification payments to beekeepers for losses sustained from pesticides (U.S. Congress *1970*). A major problem in carrying out the purposes of this bill concerned the just and adequate compensation for losses sustained and the establishment of acceptable proof of degree of such loss. Because there is little reciprocal benefit from indemnification payments, this would not appear to be a long-term satisfactory solution to the bee poison problem.

Research on bees and their relationship to pollination is beneficial to both the beekeeper and the grower. The new knowledge may concern the bee itself, including its behavior, breeding, management, or nutrition, or it may concern the value of the bee to the crops. In either instance, the new information is permanent and beneficial to both groups.

The information on the relative danger of pesticides to bees and on the value of the bees to the crops can be released to growers and beekeepers at opportune moments when it is of most usefulness. In addition, grower-beekeeper meetings can be sponsored in which each learns of the problems of the other and the need for cooperation.

Relative Poisoning Hazard of Pesticides to Bees

Hundreds of pesticides have been tested as dusts or sprays for their relative degree of hazard to bees. These tests have been summarized on numerous occasions but recently by Anderson and Atkins (*1968*), Anderson et al. (*1971*), Atkins et al. (*1970*), and Johansen (*1969*). Table 4,[8] taken from Anderson et al. (*1971*), shows the relative toxicity of numerous materials determined by laboratory and field studies. The hazards to wild bees through poisoning of the leaves used for nest building (Waller *1969*) as well as through their food or contact was summarized by Johansen (*1969*) and is presented in table 5.

Additional studies on effect of herbicides by Moffett et al. (*1972*) showed that cacodylic acid, MSMA, and paraquat were highly toxic when sprayed on honey bees in small cages. When fed to newly emerged worker bees, the following materials were relatively nontoxic: 2-chloroethyl-phosphonic acid; 2,3,6-TBA; 2,4-D; 2,4-DB; 2,4,5-T; chloramben; dalapon; dicamba; EPTC; Ethrel®; picloram; and silvex. The following were extremely toxic at concentrations of 100 parts per million by weight: cacodylic acid, DSMA, hexaflurate, MAA, MSMA, and paraquat.

These herbicide tests have shown that some materials considered safe by the previously mentioned short-term cage tests with dust were indeed highly toxic when tested by other methods. They also indicate that the toxicity of materials cannot be predicted and that the toxicity may vary according to methods of application and other factors.

[8] Tables 4 and 5 are reprinted essentially as they appeared in their original form.

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TABLE 4.—Relative toxicity of pesticides to honey bees as determined by laboratory and field tests in California, 1950-71 (Source: Anderson et al. 1971).

GROUP 1—HIGHLY TOXIC: Severe losses may be expected if the following materials are used when bees are present at treatment time or within a day thereafter, except as indicated by footnotes.

aldrin[2]
arsenicals[1 2]
Azodrin® (crotonamide)[1 2]
Baygon®
Baytex® (fenthion)
BHC[2]
Bidrin®[1 2]
Bux® (RE-5353)
Chlorthion®
Cygon®, DE-FEND® (dimethoate)[2]
Dasanit® (fensulfothion)
DDVP (dichlorvos)
diazinon[2]
Dibrom® (naled)[2 3]
dieldrin[1 2]
Dimecron® (phosphamidon)[2]
Dursban®[2]
EPN[1 2]
Ethyl Guthion® (azinphosethyl)[2]
Famophos® (famphur)
Furadan®[2]
Gardona®[2]
Guthion® (azinphosmethyl)[1 2]
heptachlor[1 2]
Imidan®
Lannate® (methomyl)[2]
lindane[2]
malathion[2 4]
Matacil®
Mesurol®
Metacide®[1]
methyl parathion[1 2]
Methyl Trithion®
Mobam®
Monitor®[2]
parathion[1 2]
Phosdrin® (mevinphos)[1 2 3]
Sevin® (carbaryl.)[2]
Sumithion®
Temik® (aldacarb)[1 2 7]
TEPP[1 2 3]
Zectran®[2]
Zinophos®

GROUP 2—MODERATELY TOXIC: These can be used around bees if dosage, timing, and method of application are correct, but should not be applied directly to exposed bees in the field or at the colonies.

Abate®,[2] Biothion®
Agritox®
Banol®
Carzol® (formetanate)[2]
chlordane[2]
Ciodrin®
Co-Ral® (coumaphos)
DDT[1 2]
Di-Syston® (disulfoton)[1 6]
endothion
endrin[1 2]
Korlan® (ronnel)
Meta Systox® (methyl demeton)
Meta-Systox R® (oxydemeton-methyl)
mirex
Perthane®[2]
Phosalone®
Phosvel®, Abor®[2]
Pyramat®
Systox® (demeton)[1 2]
tartar emetic
Thimet® (phorate)[1 2 6]
Thiodan® (endosulfan)[2]
Trithion® (carbophenothion)[2]

GROUP 3—RELATIVELY NONTOXIC: These can be used around bees with a minimum of injury.

INSECTICIDES

Acaraben® (chlorobenzilate)
Allethrin
Aramite®
Bacillus thuringiensis
cryolite[2]
Delnav® (dioxathion)[2]
Dessin®
Dilan®[2]
Dimite® (DMC)
DNOCHP (dinitrocyclo-hexyphenol)
Dylox® (trichlorfon)[2]
Eradex®
Ethodan® (ethion)[1 2]
Fundal®, Galecron® (chlorophenamidine)
Heliothis virus
Kelthane® (dicofol)[2]
Kepone®
methoxychlor[2]
Mitox® (chlorbenside)
Morestan®
Morocide® (binapacryl)
Murvesco® (fenson)
Nemagon®[2]
Neotran®[2]
nicotine[2]
Omite®
OMPA (schradan)[1]
Ovotran® (ovex)[2]
Phostex®
pyrethrin
rotenone[2]
Rhothane® (TDE)[1 2]
ryania[2]
sabadilla[2 5]
Saphos® (menazon)
Strobane®
Sulphenone®
Tedion® (tetradifon)
toxaphene[1 2]

See footnotes at end of table.

TABLE 4.—Relative toxicity of pesticides to honey bees as determined by laboratory and field tests in California, 1950-71 (Source: Anderson et al. 1971)—Continued

FUNGICIDES

Arasan® (thiram)	Cyprex® (dodine)	Glyoxide® (glyodin)	Phaltan® (folpet)
bordeaux mixture[2]	Dexon®	Karathane® (dinocap)	Polyram®
captan	dichlone	Manzate® (maneb)	sulfur[2]
copper oxychloride sulfate	Difolatan®	Mylone®	Thynon® (dithianon)
copper 8-quinolinolate	Dithane® M-45 (folcid)	Parzate® (nabam)	Zerlate® (ziram)
copper sulfate (monohydrated)[2]	Du-TER® (TPTH)		
cuprous oxide	Dyrene®		

HERBICIDES

AAtrex® (atrazine)	dalapon	Kerb® (RH-315)	Randox® (CDAA)
amitrol	DEF®[8]	Lasso® (alachlor)	Sinbar® (terbacil)
Ammate® X (ammonium sulfamate)	diquat	Lorox® (linuron)	Stam® F-34 (propanil)[1]
Banvel® (dicamba)[1]	Eptam® (EPTC)	MCPA[1]	TOK® (nitrofen)
Benlate® (benomyl)	Folex®[8] (merphos)	Milogard® (propazine)	Trysben® (2, 3, 6-TBA)[1]
Betanal® (phenmedipham)	Herbisan® (EXD)	monuron	VCS-438
Caparol® (prometryne)	Hyvar® (bromacil)	NPA	Vegedex® (CDEC)
Casoron® (dichlobenil)	Igran® (terbutryne)	paraquat	2, 4-D[1 2]
	IPC	picloram[1]	2, 4-DB[1]
	Karmex® (diuron)	Planavin®	2, 4, 5-T[1 2]
		Princep® (simazine)	

[1] California State regulation requires permits for most uses of these materials; also for 2,4-D and 2,4,5-T as weed treatments but not as hormone sprays on citrus.

[2] These materials have been laboratory tested and field tested mainly on alfalfa, cotton, citrus, ladino clover, and sweet corn; all others are laboratory tested only.

[3] Dibrom®, Phosdrin®, and TEPP have such short residual activity that they kill only bees contacted at treatment time or shortly thereafter. These materials usually are safe to use when bees are not in flight; they are not safe to use around colonies.

[4] Malathion has been used on thousands of acres of blooming alfalfa without serious loss of bees. However, occasional heavy losses have occurred, particularly under high temperature conditions. If applied to alfalfa in bloom, it should be only as a spray, and treatment should be made during the night or early in the morning when bees are not foraging in the field. Undiluted technical malathion spray should not be used around bees.

[5] Sabadilla as a 20-percent dust, as it is sometimes used for stink bug control, may cause bee losses.

[6] Di-Syston® and other systemics used as a seed treatment have not caused bee losses.

[7] Temik®, although highly toxic to bees as a contact poison, is used only in granular form and extensive field usage has not resulted in bee losses.

[8] Defoliants.

Note: For references to chemical and other names of pesticides listed in table, see Atkins et al. (*1970*).

TABLE 5.—Wild bee poisoning hazard of insecticides on blooming crops (Source: After Johanson 1969)

ALFALFA LEAFCUTTER BEE

Hazardous at any time:

Abate® + Systox	Ethion	Methyl parathion[1]	Sevin®	Toxaphene + Meta-Systox-R®
Bidrin®	Gardona®	Parathion	TEPP[1]	Toxaphene + Systox®
Cygon®	Guthion®	Phosdrin®[1]	Thiodan®	Trithion®
DDT	Lannate®	Phosphamidon	Toxaphene	
Endrin	Malathion	Ronnel	Toxaphene + DDT	

Not hazardous IF applied in late evening after bees have quit foraging:

Abate®	Dibrom® EC (emulsifiable concentrate)	Gardona® EC

Not hazardous IF applied in either late evening or early morning when bees are not foraging:

Delnay®	Dylox® + Systox®	Isopropyl Parathion	Phostex®	Systox®
Dylox®	Galecron + Fundal® D (dust)	Meta-Systox-R®	Schradan	Thimet® G (granules)
				Zolone

Not hazardous at any time:

Baygon®	Furadan® G	Kelthane®	Menazon	Temik® G
Di-Syston® G	Galecron® + Fundal® S (spray)			

ALKALI BEE

Hazardous at any time:

Bidrin®	Dieldrin	Lannate®	Methyl parathion[1]	Phosphamidon
Cygon®	EPN	Malathion ULV (ultra low volume)	Parathion	Sevin®
Diazinon	Gardona® D		Phosdrin®[1]	Thiodan®

Not hazardous IF applied in late evening after bees have quit foraging:

Abate® + Systox®	Endrin	Malathion EC	Toxaphene + DDT	Trithion®

Not hazardous IF applied in either late evening or early morning when bees are not foraging:

Abate®	Dylox® + Systox ®	Meta-Systox-R®	TEPP[1]	Toxaphene + Meta-Systox-R®
DDT	Galecron® + Fundal® D	Methoxychlor	Thimet G	Toxaphene + Systox®
Dibrom® EC	Gardona® EC	Schradan	Toxaphene	Zolone
Dylox®	Isopropyl parathion	Systox®		

Not hazardous at any time:

Aramite®	Di-Syston® G	Galecron® + Fundal® SP	Tedion®	Temik® G
Baygon® G	Furadan® G	Kelthane®		

BUMBLE BEES

Hazardous at any time:

Bidrin®	Diazinon	Malathion ULV	Parathion	Sevin®
Cygon®	Guthion®			

Not hazardous IF applied in late evening after bees have quit foraging:

Dibrom® EC	Malathion EC	TEPP[1]

Not hazardous IF applied in either evening or early morning when bees are not foraging:

DDT	Dylox®	Dylox® + Systox®	Systox®	Toxaphene
DDT + Toxaphene				

Not hazardous at any time:

Aramite®	Di-Syston® G	Kelthane®	Tedion®	Temik® G
Baygon® G	Furadan® G			

[1] TEPP, methyl parathion, and Phosdrin® should not be used where there is a possible fumigation hazard to alfalfa leafcutter bees, alkali bees, or bumble bees.

POLLINATION AGREEMENTS AND SERVICES

Various kinds of agreements have been used in renting bees for pollination. Some have been verbal, others written. The written ones have varied in length from a brief paragraph to several pages. Too frequently, a pollination agreement ends in dissatisfaction, to the detriment of both the grower and beekeeper, because of some condition not clearly agreed upon in advance. One reason for such misunderstandings may be that conditions peculiar to the use of bees in a pollination program are not usually encountered by either grower or beekeeper in other agricultural or apicultural practices.

Because of these and numerous other reasons that may arise, involving legal considerations as well as good-neighbor policy, an explicit agreement should be insisted upon by the participants when bees are rented to pollinate a crop. The agreement is more likely to be satisfactory if it is drawn from the experience and knowledge of numerous growers and beekeepers who have used bees to pollinate crops. Legal experts with knowledge of the value and limitation of specific items proposed for the agreement should also be consulted.

Sometimes a written agreement is no stronger than the party's word, because no penalty for breaking the agreement is included. For example, one agreement that has been used merely stated:

> "I, (*beekeeper's name*), agree to supply _ colonies of bees to (*grower's name*) to pollinate _ acres of (*crop*) for the year _____. I (*grower's name*), agree to pay (*beekeeper's name*) $ _ per colony for ___ colonies of honey bees to pollinate my (*crop*) for the year _____." (*Date*), (*Beekeeper's signature*), (*Grower's signature*).

In this agreement, neither the grower nor the beekeeper is adequately protected. There is no penalty if the beekeeper fails to deliver the colonies, delivers inadequate colonies, fails to take adequate care of the colonies while they are being used in the pollination program, or fails to remove them at the time desired by the grower. There is no indication as to what steps the beekeeper might take in caring for the colonies or even if he has the rights of entry upon the premises to care for them. There is no indication that the grower is obligated in any way to take steps to protect the colonies from pesticides or other harmful farm practices. Nor is there a penalty for delay in payment or nonpayment of fees, and no agreed-upon recourse for the beekeeper in case of default by the grower.

Such an agreement usually leads to later misunderstanding between the parties involved. More lengthy agreements have been used that covered many obligations of both parties, including changes of plans because of environmental conditions and acts of God.

Regardless of the type or the length of agreement used, unless it protects both parties and includes enforceable penalties for breach of contract, it is unlikely to be satisfactory.

Factors That Should Be Covered for a Satisfactory Pollination Agreement

IDENTIFICATION OF PARTICIPANTS

The general terms of the agreement should be indicated in a preamble, including the date, the landowner or grower and his address, the owner or operator of the bees or their agent and his address, and the crop involved and its location. If special beekeeping or farming terms are used, which are not clearly understood by all parties involved, a glossary should be included. Some agreements require signatures in the presence of a notary public or witness.

RENTAL PRICE

The rental price for the colonies should be specified. If the rental payment is to be made by cash or check, the time, place, and method of delivery of the payment should be stipulated. If payment consists of a portion of the pollinated crop, the amount and quality of the product should be clearly stated. In addition, the responsibility for delivery of the portion of the pollinated crop to the beekeeper or designated place of storage should be specified. If costs of containers, transportation, storage, or special treatment of the crop is involved, the agreement should specify who pays such costs.

TIME OF DELIVERY OF THE COLONIES

The date of delivery of the bees should be specified or a mutually satisfactory arrangement made for notifying the beekeeper when they are desired. (For some crops a delay of a few days may result in complete failure of the bees to pollinate the crop. For other crops a staggered rate of delivery, as growth and flowering progresses, may be desired.) The exact method of notification should be specified. The penalty for late delivery should also be specified.

Enough time after notification to permit orderly scheduling of colony delivery should be required. Weekends and periods requiring overtime pay of employees should be considered. The parties should remember that if weather is the predominant factor in the initiation of flowering, it is likely to affect all fields under pollination agreement of the beekeeper. The beekeeper should therefore schedule no more colonies than he can deliver in an anticipated alloted time.

NUMBER OF COLONIES

The number of colonies to be used per acre of a specific crop and the acreage should be stated. The contract may designate "colony equivalents," if the bees are rented on the basis of size of cluster or area of the broodnest. By this method, 90 populous or 110 weaker colonies may be equivalent to 100 colonies of a specified strength. Payment on the basis of colony equivalents should encourage the delivery of colonies of adequate strength. This method of payment would

require rather close examination of the colonies by a qualified person. If this method of determining the numbers of colonies is to be used, the details should be expressed in the agreement.

STRENGTH OF COLONIES

Honey bee colony populations can vary from a few hundred to about 100,000 bees, the cluster size from a few cubic inches to a cubic foot or more, and the brood area from none to about 2,000 in^2. For these reasons, the agreement should specify the colony strength. This might be in square inches of sealed brood, square inches of total brood (eggs, larvae, and pupae), or cluster size at certain approximate outdoor temperatures. The cluster size might be described as covering a specified number of combs or filling of specific size chambers or "supers" of the hive.

The grower should require permission to examine the colonies or have them examined to determine if they qualify for the standards agreed upon.

The beekeeper should attempt to deliver only colonies that meet these standards. He should require incentive payments for colonies that exceed the requirements if penalties are imposed for those that fail to reach the requirements.

If the grower examines the colonies to determine their strength, the beekeeper should require that such examination be made in a way that is not detrimental to the hives or their contents. The method of examining the colonies should be agreed upon in advance. The tolerance permitted on standards for colony strength should be specified.

PLACEMENT OF THE COLONIES

The locations for the colonies should be specified precisely, so that no confusion will arise when the laden vehicle arrives at the location during the night. If the colonies are to be distributed in the field or orchard, the distance between locations and the approximate number of colonies per location should be stated. The colonies should be placed as nearly as possible where the grower desires them, but so that they can be maintained and operated normally. If only a portion of the colonies are to be delivered at a time, the number and rate of delivery should be specified. Locations should be designated where they are accessible to the beekeeper or his vehicles from time of placement until removal. The locations should be so designated that farm employees, the public, and domestic animals are unlikely to be stung by the bees.

OPERATION AND MAINTENANCE OF COLONIES

The grower should allow access to the colonies by the beekeeper so that they can be maintained in optimum condition for pollination of the crop. The beekeeper should make every effort to keep them in this condition. This may require feeding of the colonies if stores are low, or removing excess honey so there is storage space for nectar and pollen. The beekeeper may need to add extra space as the colony expands. This requires expert care of the colonies by the beekeeper.

If the colonies are more than about half a mile from a water supply, the beekeeper should arrange with the grower in advance to provide water. He might explain to the grower that considerable time is required by the bees in collecting water; therefore, the nearer the supply, the more time the bees have to pollinate the crop.

The beekeeper should be prudent in entering upon the property of the grower to service the bees. He should also manage them prudently to minimize the danger of stings.

PROTECTION OF COLONIES FROM PESTICIDE APPLICATIONS AND OTHER FARM PRACTICES

The agreement should explicitly state the pesticide program likely to be in effect at the time the crop is to be pollinated, on the grower's property and, to the best of his ability, on nearby property. The grower should determine in advance if a pesticide application is likely to be needed, its probable effect on the bees and their pollinating efficiency, and the liability if damage to the bees occurs.

The time and method of notifying the beekeeper before application of the pesticide and the penalty for damage to the colonies should also be specified.

In the event of bee kill and the two parties cannot agree as to its extent, the agreement should specify that each shall select an arbiter and that these two shall select a third party. This three-man team will then examine the colonies and determine the extent of loss within a specified time.

REMOVAL OF THE COLONIES

The failure of the beekeeper to remove the colonies after the crop has been sufficiently pollinated is often frustrating to the grower who wants to spray, cultivate, or harvest the crop. For a few crops, an excessive set of fruit can create a thinning problem. The agreement should therefore specify the time and conditions of removal of the colonies, the time and method of notification of the beekeeper, and the penalties for the failure to remove the colonies within a specified time.

The agreement should also specify under what conditions the colonies may be removed for protection from pesticides. If the colonies are to be returned to the field after such removal, the cost of removal and return should be specified, along with the time and method of paying this cost.

Frequent misunderstandings arise over the need for the bees to be returned to the crop after their premature removal. This removal date, in relation to the progress of the crop, can seldom be predetermined. The agreement should, therefore, indicate who makes the final decision in this situation.

PROTECTION FROM STINGS AND ASSOCIATED LIABILITIES

Although the colonies should be so placed that stings are unlikely to occur to the innocent, the agreement should specify who is liable in the event trouble arises over stings. Such incidents can arise as a result of the manipulating of the colonies by the beekeeper, the disturbance of the colonies by certain farm operations, or by the molesting of the colonies by outsiders.

PAYMENT OF POLLINATION FEES

Most of the problems with pollination agreements arise over the payments. The agreement should, therefore, be explicit in stating how, when, where, and under what conditions payment is made. If the colonies, when delivered, failed to comply with a specified standard and deductions influence the payments, the agreement should specify when and how such deductions are calculated and how they influence the payments.

The agreement should also specify penalties for defaulting on payments, including such costs of collection as legal fees, interest, and damages.

PENALTIES AND REWARDS

Both the grower and the beekeeper should strive to adhere to the terms of the agreement; however, no agreement is likely to be binding without penalties and rewards. The agreement should specify the rewards, such as discounts, if any, for prompt payment of fees, credit for colonies that exceed the standards set, or bonuses for crop production that exceeds specified amounts.

Penalties should also be specified. Those against the beekeeper might cover late delivery or early removal of the colonies, failure to remove the colonies within specified dates, inadequate colony strength, inadequate colony care, or lack of prudence in relation to activities on the grower's premises. Penalties against the grower might include interest on delayed payment of pollination fees and expenses for collecting the fees, including legal action, cost of collection agencies, or other expenses, or damage to the colonies or hives by imprudent action of the grower or his employees while the colonies are on his premises.

Availability and Open Lines of Communication

The beekeeper should be available by phone in the event the grower needs to contact him about the bees, their services, protection, delivery, or removal. Likewise, the grower should be available in the event something occurs concerning delivery, removal, or protection of the bees while on the grower's premises.

The grower and the beekeeper or agent should agree on the bee sites or locations when the agreement is signed. These sites must be accessible when the bees arrive. Frequently, the truck loaded with the bees arrives late at night. If a gate is locked, a road or driveway changed, a field plowed or irrigated so that the site is inaccessible, and the driver is unacquainted with the farm layout, valuable time is lost and the beekeeper's schedule is disrupted. Disturbing the grower or learning that he is unavailable for deciding upon an alternate site may cause delay and ill will.

Colony Strength and Price Rates

Colonies are sometimes rented on a flat-rate basis with little regard to their condition, although populous colonies supply more bees to the field, and their bees also tend to fly at lower temperatures than bees in weaker colonies (Todd and Reed *1970*).

Farrar (*1929*) proposed a price adjustment based on the number of frames covered by the cluster when the temperature was in the range of 60° to 65° F. He proposed that with the then current price of $5 for a cluster that covered five- to six-frames, there should be a reduction of $1.25 for each frame less than five, and $1 additional for each frame above six that was covered with bees.

By this method, a cluster covering only four frames would rent for $3.75 and three frames, for only $2.50. Those with seven frames would rent for $6, eight frames for $7, 10 frames for $9, and 13 or more for $12.

The defect in this proposal was that the incentive to have stronger colonies was not sufficiently great. A more realistic stimulus for supplying stronger colonies might be based on one of the following equivalent scales:

Cluster size[1]	Frames with brood	Sealed brood	Proposed comparative price
		Square inches	*Dollars*
2	1	100	0.50
4	2	200	3.00
6	3	300	5.50
8	4	400	8.00
10	5	500	10.50
12	6	600	13.00
14	7	700	15.50
16	8	800	18.00
18	9	900	20.50
20	10	1,000	23.00

[1] Frames of bees.

By using such a scale, the beekeeper would have an incentive to unite his weak colonies or otherwise provide stronger ones. Such a scale is supported by data of Sheesley and Poduska (*1970*). They showed (table 6) that colonies with eight or more frames covered on both sides with bees collected more than two and one-half times as much almond pollen (and presumably pollinated the almond flowers in the process) as colonies with only four or five frames covered with bees, and more than four times as much pollen as colonies with only three frames covered with bees.

In this way, a standard for colony strength may be used, but the price of the unit should fluctuate. The beekeeper should consider costs and other expenses when considering and establishing the price for his colonies. Factors that will enter into this price cost will include the length of time the crop will be in bloom, the distance that the bees must be hauled to the crop, the relative danger of pesticide damage while the bees are on the crop, and the time of flowering in relation to the major honey flows in his area.

Instead, the beekeeper is frequently more inclined to set the price for the colonies below the expense of supplying them. Too frequently, he fears that better pollination fees will attract competition into the area, and the locations will be lost or decreased in value. The price is set with "his eye on the honey can" rather than

TABLE 6.—Average weight of pollen collected by colonies of 5 population strength groups, expressed as percentage of group 3 (Sheesley and Poduska, 1970)

Experimental colony group	Group 1 (0-2 frames[1])	Group 2 (3 frames)	Group 3 (4-5 frames)	Group 4 (6-7 frames)	Group 5 (8 or more frames)
	Percent	*Percent*	*Percent*	*Percent*	*Percent*
1969[2]	6.2	63.9	100	199.1	286.9
1970[3]	5.2	42.4	100	164.7	292.4
1970[4]	16.0	54.1	100	148.8	305.9

[1] The equivalent number of frames covered on both sides with bees.
[2] 6-day collection from 113 colonies.
[3] 7-day collection from 143 colonies.
[4] 10-day collection from 99 colonies.

his consideration of maximum pollination service to the grower.

Both the beekeeper and the grower would benefit if cutrate prices were not used. If the beekeeper is to stay in business and provide optimum service, he must be adequately reimbursed. Failing to do this, he eventually must abandon the pollination business, whereupon the grower suffers. Probably the best way this can be achieved is through independent contractors who can determine adequate fees and appropriate strength and numbers of colonies for the crop then enforce these requirements for the betterment of both groups.

Qualifications of a Stable Pollination Service

INDUSTRY REPRESENTATION

A pollination service that expects to continue on a large scale over a long period must be equally interested in the welfare of the grower and the beekeeper. It should be directed by both crop and bee specialists. Unless both industries are represented and have equal status in directing the program, it is doomed to failure.

The crop specialist should strive to obtain the pollination service that will result in maximum economic crop production.

The bee specialist should strive to obtain fees for the beekeeper who supplies the pollination service sufficient to profitably maintain the colonies, equipment, and help in providing the grower service.

Each specialist should have equal expression in determining the services the grower needs and the fees that the beekeeper receives. Each should see that the contracts are so written that both parties are legally protected and that the responsibilities of each party is clearly and explicitly delineated.

SCOPE

A pollination service organization that includes a large number of growers and beekeepers should be more stable and likely to continue to function, if managed properly, than one with a smaller number of members. Like a large insurance company, it should survive individual or local failures or adversities that affect the crops, the bees, or both.

Because of the costs and other logistic problems associated with moving honey bee colonies long distances, the contracts and services would, from the economy standpoint, tend to be regional in scope. For example, the area of operation of an individual beekeeper is based largely on the distance he can move a truckload of bees during the night, with a possible extension into the cooler part of the next morning—some 300 to 600 miles.

Some States have regulations prohibiting transportation of colonies into the State, entry fee for the transported colonies, or control of the location of the colonies after they enter the State. Most States require a certificate of inspection indicating that the colonies are apparently free of contagious or infectious diseases (Michael *1967*). From the crop pollination standpoint, these regulations, important in the control of bee diseases, can hamper but will not prevent large-scale use of colonies in a pollination program.

METHOD OF OPERATION

A large-scale pollination program would lend itself well to computerization, although field men would be required to "sell" the service by making the contracts with the growers, mapping the locations for the bees, insuring colony quality control, and providing other grower and beekeeper protective measures. For example, the various grower and beekeeper locations could be fed into the computer, along with dates bees might be needed and when they are available. Then the computer could, without bias, determine the nearest or most logical beekeeper available for pollination of a specific crop. If the beekeeper could not comply, the computer could immediately indicate the most logical second choice. Such a program might be national or even international in scope, subject to existing laws and regulations, with regional and local headquarters for the field men who make personal contact with the growers and beekeepers. Its size would permit greatest flexibility in the use of bees on different crops in the different areas. This could benefit both parties.

In summary, the pollination agreement should be as complete as possible so that both the grower and the beekeeper are protected. Agreements between individual growers and beekeepers can be satisfactory. A pollination service encompassing numerous growers and beekeepers, and administered by agents equally concerned with the welfare of both groups, offers the possibility of greater and continual stability.

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CROPS DEPENDENT UPON OR BENEFITED BY INSECT POLLINATION

ACEROLA

Malpighia glabra L., family Malpighiaceae

Acerola, also known as Barbados cherry or West Indian cherry, is grown to a minor extent in the frost-free regions of Florida and in Hawaii, primarily in home gardens (Miller et al. *1965*). This plant is most noted for the extremely high ascorbic acid (vitamin C) content of its fruit, with 10 to 40 mg/g of edible fruit, far more than any other known fruit. By comparison, the other rich sources of vitamin C are rose hips (*Rosa rugosa* Thunb.) with 17 mg/g of edible matter, mirobalan (*Phyllanthus emblica* L.) with 8 mg/g, and guava (*Psidium guajava* L.) with 3 mg/g of edible matter (Asenjo and Freire de Guzman *1946*, Moscoso *1956*). One fruit the size of a large sweet cherry can furnish a man's daily requirement of this vitamin (Ledin *1958*). The fruit, which is also rich in iron, is used in sherbet, ice cream, and jelly (Mortensen and Bullard *1968*) and baby foods, fruit nectars, and soft drinks (Arostegui and Pennock *1956*). The juice retains its cherry-red color and flavor if it is processed and frozen immediately. The development of a chemical method of producing vitamin C has reduced the need for acerola.

Plant

Acerola is a shrub or small tree to 15 feet tall, with thick spreading branches and conspicuous raised white lenticels or "breathing pores" in its bark. The plants are set 6 to 15 feet apart and bear when about 2 years old. The fruit is light orange to dark red, three lobed, soft, thin skinned, and juicy and looks somewhat like a small, rather flat tomato. It ripens 3 to 4 weeks after flowering. Some fruits are sweet, wheras others may be tart. They may be borne singly or in clusters of two or three. The fruit usually has three rather large seeds. If the fruit is picked daily, yields of up to 26 tons/acre may be obtained (Ledin *1958*). Most plants are harvested three or four times a year but some may bear six or seven crops a year (Arostegui and Pennock *1956*).

Inflorescence

The ¾- to 1-inch red, pink rose, or white flowers are produced in great abundance. They occur in a forked cluster in the leaf axil, appearing in 25-day cycles from April or May to late fall. There are five petals, one of which is fan-shaped and larger than the others. The 10 erect stamens are shorter than the petals and slightly shorter than the style. Two of the stamens are thicker and have longer filaments than the others. Three styles point outward with the stigmatic area on the inner angle. Nectar is secreted at the base of the anthers. Ledin (*1958*) stated that the flowers were attractive to honey bees, although Yamane and Nakasone (*1961a*) considered them relatively unattractive. Whether the attractive factor was for nectar or pollen or both was not determined.

Pollination Requirements

When Yamane and Nakasone (*1961a*) excluded pollinators, they obtained 1.3 to 11.5 percent fruit set. When they hand self-pollinated flowers, they obtained 6.7 to 55.1 percent set. When they hand cross-pollinated flowers, they obtained 6.7 to 74.1 percent set. Their overall average set of fruit from the selfed flowers was 2.3 percent; open pollination, 26.3 percent and hand cross-pollinated flowers, 51.7 percent. They concluded that the basic cause of low fruit set was lack of adequate pollination. Miyashita et al. (*1964*) also concluded that although anther dehiscence is affected by weather, the absence of cross-pollination, but not pollen failure, contributed to poor fruit set. Plants propagated from seed generally produce a variable population.

The pollination requirements of acerola are, therefore, not too well understood, but apparently cross-pollination is essential for the highest percentage of fruit set.

Pollinators

Yamane and Nakasone (*1961a,b*) concluded that wind is not an effective pollinating agent of acerola, but that insects are effective. Mortensen and Bullard (*1968**) stated that inadequate pollination by specific insects or wind was the primary cause of poor fruit set in Hawaii. Ledin (*1958*) stated that acerola is attractive to bees. Yamane and Nakasone (*1961a*) stated that honey bees and syrphid flies (*Eristalis agrorum* (F.)) were the only insects readily visible, but when plantings of 30 to 40 trees were in full bloom they attracted fewer than a dozen of each of the two insects. Honey bee colonies were moved to within 50 feet of the plants, but the number of floral visitors or fruit set was not increased "to any great degree." Chapman (*1964**), probably referring to the test by Yamane and Nakasone (*1961a*), also stated that placement of beehives near the plants was of little value. The relative attractiveness of other plants to bees in the area was not mentioned. There has reportedly been no particular pollination problem on the small acreage of acerola in Florida

where honey bees as well as other pollinating insects are quite abundant.

The meager data indicate that insects are the effective pollinating agents of acerola, but the most effective species remain undetermined.

Pollination Recommendations and Practices

There are no recommendations on the pollination of this crop, and no steps are taken by growers to use the services of pollinating insects. If the acreage is increased or concentrated where few pollinating insects are available, a problem of low fruit setting could develop unless growers arrange for honey bee colonies to be placed nearby.

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ALFALFA

Medicago sativa L., family Leguminosae

Alfalfa, also known as lucerne in many other countries, is the most important forage crop in the United States, accounting for about half of all the hay produced. More than 27 million acres, mostly in the north central States, produced 3 tons of hay per acre with a farm value approaching $2 billion in 1969. One-half million acres were also devoted to the production of over 100 millions pounds of alfalfa seed. The seed crop, valued at $40 million, was produced in many States but about three-fourths of it came from 11 Western States. California led in seed production with 96,000 acres and 33 million pounds of seed. Washington and Idaho each produced about 14 million pounds.

Because of the worldwide importance of alfalfa and the unique relationship of its flower structure to its pollination requirements, hundreds of papers have been written that deal with its pollination, probably more than for any other crop. Citing all of these papers here is both unnecessary and impractical. For that reason, the majority of the citations in this publication are written in English, although excellent research on alfalfa has been conducted in many foreign countries, and the results have been published in German, Japanese, Russian, Swedish, and other languages. Some of the key papers that deal with the history, culture, and development of alfalfa, listed chronologically, include: Brand and Westgate (*1909*), Oakley and Westover (*1922*), Stewart (*1926*), Carlson (*1932*), Westover (*1946*), Tysdal and Westover (*1949*), Graber (*1950*), Pedersen et al. (*1959*), Taylor et al. (*1959*), Bolton (*1962*), and Jones and Pomeroy (*1962*).

Plant

Alfalfa is a perennial herbaceous legume that grows from a semiwoody base or crown. The crown sends up many thin, but succulent, leafy multibranched stems 2 to 4 feet high; each stem terminates in a raceme or cluster of 10 to 100 purple, white, or greenish-yellow florets.

When alfalfa is grown for hay the seed is usually drilled or broadcast at the rate of about 10 to 20 lb/acre, and the plants are clipped when the field is in about one-tenth bloom. When grown for seed it is usually planted in rows at the rate of only about 1 lb/acre. Jones and Pomeroy (*1962*) stated that highest seed yields are obtained from alfalfa planted in 36-inch rows, the plants 12 inches apart in the row. This spacing would require only a few ounces of seed per acre. Frequently, the crop is planted for hay, then climatic, agronomic, or economic conditions cause the grower to leave the crop uncut to develop seed, which usually results in low seed yield. Stands thicker than 100,000 plants per acre are excessive for seed production (Pedersen et al. *1959*). The highest yields can be expected from sparse stands that flower during the warmest part of the season, but other factors also affect seed production. Proper agronomic care, sufficient pollination, freedom from harmful insects and diseases, and proper seed-harvesting methods are equally important.

The great demand for alfalfa and other legume seed in the early 1940's, encouraged by a Congressional subsidy

for such seed (Enlow *1944*), stimulated interest in both increased production of seed and in new cultivars adapted to particular areas and conditions. This interest led to studies on insect pollination and plant breeding and culminated in the development of improved cultivars (Kehr *1959*, Hanson et al. *1964b*) and stabilized methods of seed production. Search continues for early high-yielding (hay) cultivars resistant to the alfalfa weevil and other pests and diseases.

There are many hardy, semihardy, and nonhardy cultivars of alfalfa; some are certified (by State agencies), others are proprietary (owned exclusively by private firms), and still others are uncertified. The major cultivars, their history and qualities, were reviewed in detail by Hanson et al. (*1960*). The breeding that goes into a synthetic cultivar (typical of many crops) is illustrated in the sketch of the wilt-resistant cultivar A-136 by Kehr (*1959*) shown in figure 31.

Inflorescence

The ½-inch-long florets begin opening at the base of the 1-to 4-inch-long alfalfa raceme. A week is usually required for the opening to proceed from the base to the tip of a raceme. A floret may open at any time of day and remains open for about a week if not pollinated, but wilts within a few hours after pollination.

The corolla consists of the standard petal, sometimes considered to be the landing support for bees, two smaller wing petals, and two fused petals called the keel (fig. 32). The keel encloses, under considerable tension, the sexual column, which terminates in the stigma and 10 anthers. The details of the floral characteristics and their modifications were discussed by Graumann and Hanson (*1954*), Larkin and Graumann (*1954*), Nielsen (*1962*), and Pankiw and Bolton (*1965*).

The color of the corolla varies from purple or violet through various shades of blue, green, yellow, or cream, to white. A scale for visually classifying alfalfa flower color was proposed by Barnes (*1972*).

The sexual column is normally nonfunctional, unless it is released from the keel. Once released ("tripped"), it does not return to its former position within the keel like the column in most other legumes. After release, if successful fertilization occurs, the ovules in the ovary begin to develop, and a tightly curled pod results. The number of curls, varying from one to five, is determined by the number of ovules that develop into mature seeds. A pod may have a dozen seeds but usually it has fewer, the number depending at least partly on the degree of pollen compatibility. The pod matures and is ready for harvest about a month after pollination.

TRIPPING

The release of the sexual column is a phenomenon that has been known for many years. Henslow (*1867*) described the tripping process, but Cockerell (*1899*) was apparently the first to use the term "tripping." After much study and observation (Piper et al. *1914*, Brink and Cooper *1936*), and also much controversy (Carlson *1928*, Coffman *1922*, Whornham *1936*, Pengelly *1953*), tripping was proven necessary for profitable seed production (Armstrong and White *1935*; Tysdal *1940*, *1946*; Zaleski *1956*).

The column is released when the bee, in searching for nectar or pollen, inserts its proboscis into the flower throat and exerts pressure upon the keel petal, causing it

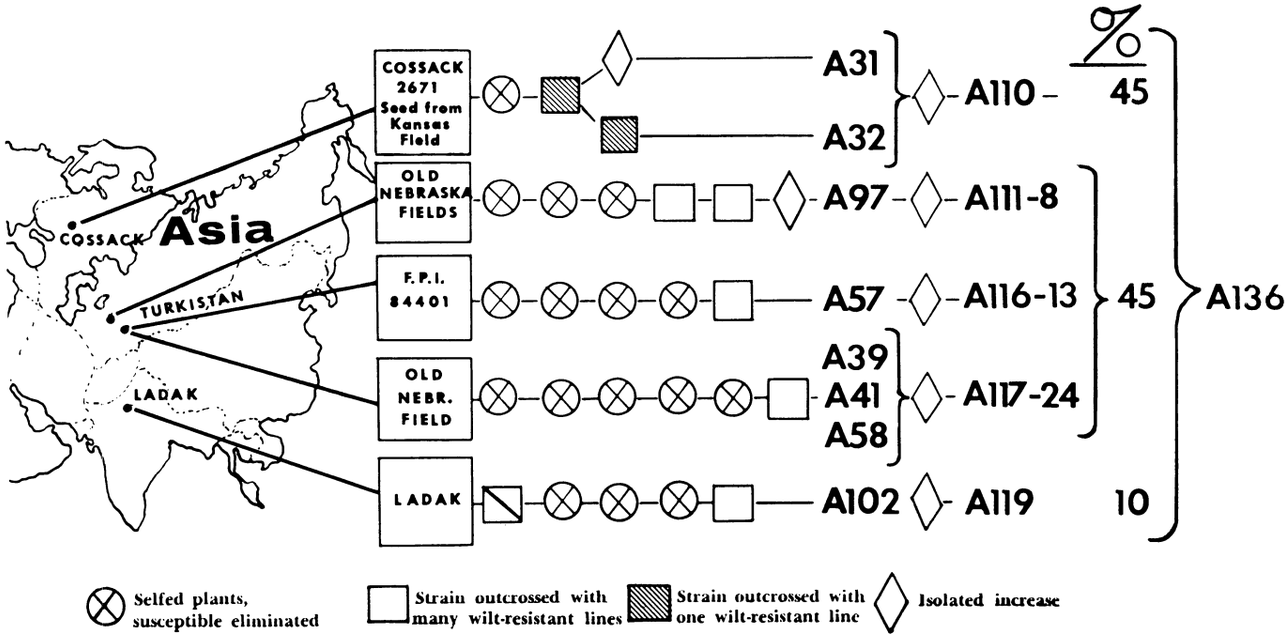

FIGURE 31.—Origin, history, and breeding methods used in developing Ranger (A 136), a wilt-resistant alfalfa cultivar. (Reproduced from Kehr *1959*.)

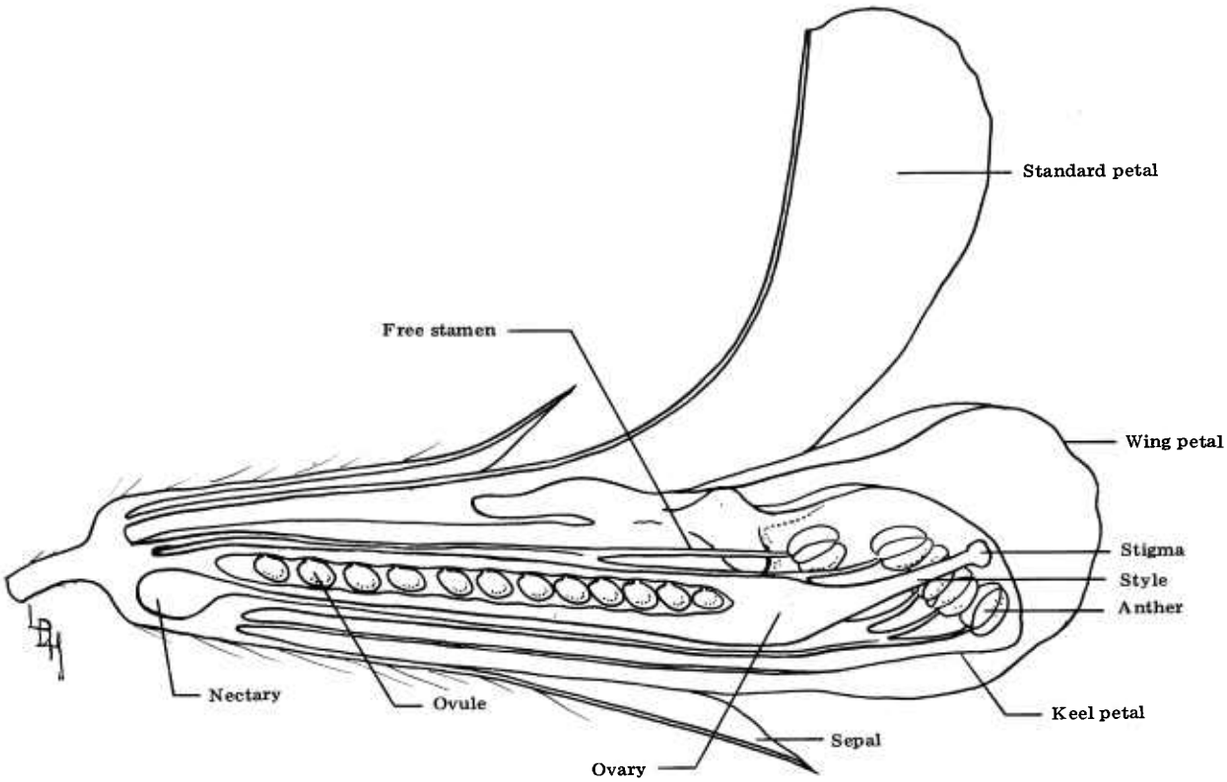

FIGURE 32.—Alfalfa flower longitudinal section, × 20.

to separate (fig. 33). Upon release, the column strikes the standard petal, sometimes striking the underside of the head of the bee first, at times with such force that the bee can extricate its head only after a struggle. When the flower is tripped, the pollen is dusted upon the bee and is then carried to another alfalfa flower. At the same time, pollen brought from another flower is accidentally rubbed upon the stigma and cross-pollination results. In the field, less than 1 percent of the self-tripped flowers produce seed, and most nontripped flowers fail to do so (Cooper and Brink *1940*, Tysdal *1946*), although from time to time workers—for example, Carlson (*1930*)—have reported seed set from nontripped flowers.

FIGURE 33.—Tripped alfalfa floret and pollen-laden honey bee.

FIELD APPEARANCE AND SEED SET

When the flowers are tripped as rapidly as they open, racemes can be found with developing seed pods on the lower part, a circlet of one to four open florets in the middle and unopen buds toward the tip. Growers sometimes refer to this as the crop going "from bud to curl," and associate it with the likelihood of a big seed crop. This condition was incorrectly interpreted by Whornham (*1936*) who believed that the flowers were self-pollinated without coming into flower. Such a field has a brownish cast, in contrast to fields with a "flower-garden" appearance, where each raceme has a large number of open florets but few if any seed pods.

HONEY YIELD, NECTAR SECRETION, AND POLLEN PRODUCTION

Vansell (*1941*) showed that some alfalfa cultivars yield more honey than others. Loper and Waller (*1970*) showed that when several clonal lines of alfalfa were presented in bouquets to honey bees, the bees consistently showed preference for certain ones. Several terpenoid compounds have been identified in alfalfa varieties (Loper et al. *1971*, Loper *1972*). The significance of these compounds in honey bee behavior

is under investigation. Loper et al. (*1971*) identified one of the aromatic compounds as ocimene. Its true significance in bee attractiveness has not been determined. If an attractant factor can be isolated, its use in the breeding and selection for cultivars with greater attractiveness to pollinators could become quite important.

Alfalfa produces a large amount of nectar, which is highly attractive to many species of bees, and from which honey bees produce excellent crops of high quality honey. Kropacova (*1963*) estimated that alfalfa produces 416 to 1,933 pounds of nectar per acre. McGregor and Todd (*1952**) estimated that 54 to 238 pounds of nectar per acre were produced during a peak flowering day.

When alfalfa is cut for hay just as flowering starts, as is normally practiced, the beekeeper gets little or no alfalfa honey. If the crop is left to produce seed, the amount of nectar available to a colony depends upon the plant density, the competition from other bees, and other environmental and agronomic factors. As a general rule, one strong colony per acre of seed alfalfa should store 50 to 100 pounds honey. When the colonies are in the area at the rate of three per acre they may store little or no surplus honey.

Alfalfa is a poor source of pollen for honey bees. Usually they will collect it only when no other source is available. When honey bees have only alfalfa upon which to forage, the colony strength diminishes rapidly. Alfalfa pollen is relished by many other species of bees including the genera of *Bombus*, *Halictus*, *Megachile*, *Melissodes*, and *Nomia*. Numerous observers have reported that honey bees collect alfalfa pollen more freely in the Southwestern and Western States than in the Northeastern States. But whether the higher visitation rate is due to condition of the alfalfa plants, lack of pollen producing competing plants, or both conditions has never been resolved.

Tysdal (*1946*) estimated that 2 billion flowers per acre of alfalfa were produced in Nebraska. Lesins (*1950*) calculated that about 200 million flowers per acre were capable of setting pods. At five seeds per pod and 220,000 seeds per pound, this indicates a potential of 5,000 pounds of seed per acre. Pedersen et al. (*1956*) showed that 46.7 percent of the flowers can produce pods, indicating that a ton of seed per acre is possible.

Pollination Requirements

As previously stated, the alfalfa flower must be tripped if seed is produced. Furthermore, if cross-pollination occurs, the stigma must come into contact with pollen from another plant during the fraction of a second after the stigma is released from the keel, and before it imbeds itself against the standard petal. Tysdal et al. (*1942*) and Jones and Olson (*1943*) showed that cross-pollinated flowers not only set more pods than selfed flowers, but they also set more seeds per pod. Moriya et al. (*1956*) showed that the highest percentage of pods developed from flowers that were pollinated the first day after they opened.

When the rays of the sun are focused through a magnifying glass into a flower, it will trip almost instantly. Also, rough treatment of the flower, for example by a strong wind, will cause some flowers to trip during the warmer part of the day. Knowing this, various growers and researchers have tried heat and other mechanical devices including the dragging of a rope, wire, chain, brush, or roller across the plants to increase the number of flowers tripped (Carlson *1930*, Goff *1953*, Koperzinskii *1949*, Pharis and Unrau *1953*). One grower employed a helicopter to fly a few feet above the plants each afternoon, dragging a broad cloth behind. He hoped the downdraft would cause the flowers to trip and the cloth would hold the pollen in the air around the plants so that when tripping occurred the stigma would come in contact with the pollen. None of these methods proved to be of practical value in increasing seed production, even though Lejeune and Olson (*1940*) had shown that artificially tripped flowers set a few more seed than nontripped ones.

Of particular significance pertaining to selfed plants was the test by Tysdal et al. (*1942*) that showed that production of forage from self-pollinated plants decreased rapidly in a few generations to about a third of the former capability. This was further verified by Wilsie (*1958*). This information means that even if self-pollinated seed could be produced in large amounts, such seed is undesirable for planting use, either for forage or seed production.

Busbice and Wilsie (*1966*) and numerous others have looked for self-tripping or easily tripped strains, but because of the rapid degeneration of such lines none have been or are likely to become acceptable cultivars. Stevenson and Bolton (*1947*) left little doubt that self-tripping or self-fertile alfalfa plants are undesirable as a source of breeding material for improving the yield of alfalfa seed. The grower should, therefore, always obtain his planting seed from fields in which every effort possible was made to produce only cross-pollinated seed. Then Lovell (*1924*) prophetically stated: "They can be disproven only by statistical investigations in which it shall be shown that the honey bee trips a large number of flowers . . . in regions where alfalfa produces a large seed crop, and is freely visited by bees for nectar." This test was conducted more than two decades later (Utah Agr. Expt. Sta. *1950*).

Even with the need for tripping and cross-pollination established, lack of agreement continues as to the best pollinating agent. Hunter (*1899*) covered blossoms with cheesecloth and found that no seed were produced. He examined pods one-half mile from an apiary and found 5.6 plump seeds per pod as compared to 3.3 shriveled seeds per pod in a field 25 miles away where there were no honey bees. Cockerell (*1899*) stated that an alfalfa field in Kansas, supplied with honey bees, produced twice as much seed as a similar field without bees, and the pods were larger. Aicher (*1917*) gave some credit to wind and various bees, but Hay (*1925*) concluded that the honey bee was of no practical value in alfalfa seed production. Carlson (*1935*, *1946*) and Carlson and Stewart (*1931*) associated good seed crops only with low populations of harmful insects. Gray (*1925*), Engelbert (*1931*), and Sladen (*1918*) considered the leafcutter bee or bumble bee beneficial but honey bees of no value in tripping alfalfa flowers.

Lovell (*1924*) agreed with Sladen (*1918*), stating: "These facts [that honey bees are ineffective] cannot be controverted by hasty assertions of over-ardent defenders of the honey bee who think that because they are often numerous in alfalfa fields they must be valuable pollinators."

Gray (*1925*) was apparently the first to study the effect of caging flowering alfalfa plants to exclude pollinating insects, and he showed that doing so reduced seed yields. In a limited way, Megee and Kelty (*1932*) and Dwyer and Allman (*1933*), also using cages, showed that honey bees are effective pollinators. An editorial note (Bowman *1934*) stated, without supporting data, that good seed crops usually result when honey bees work alfalfa freely. Vansell (*1928*) stated: "The matter of pollination of alfalfa seed crop [in California] does not bother the alfalfa grower, particularly because bee men are anxious to concentrate their bees about alfalfa fields. The set of seed seems satisfactory generally." Jackman (*1940*) discounted the honey bee, but Pellett (*1941*) suggested that five colonies of honey bees per acre might produce a full crop of alfalfa seed. Stephens (*1942*) also indicated that honey bees were of value, and Rudnev (*1941*) showed that stimulative feeding of colonies caused some increase in storage of pollen by colonies in the vicinity of alfalfa. Stimulative feeding has since been largely abandoned as impractical. Knowles (*1943*) discounted the value of honey bees but gave credit to leafcutter bees; however, the same year, Hollowell (*1943*) concluded that increasing honey bees in the alfalfa field "may be of considerable value."

Eventually, wind, self-tripping, or the setting of seed without tripping were less frequently mentioned as pollinating agents of alfalfa, and the controversy settled down to the relative merits of honey bees and wild bees.

Pollinators

HONEY BEES

Before 1946, honey bees were attributed a minor role in the production of alfalfa seed; however, studies by means of pollen traps (Hare and Vansell *1946*) established that under certain conditions honey bees collect large quantities of alfalfa pollen. Vansell and Todd (*1946, 1947*) showed that honey bees have an essential role in seed production. The flowers on plants they caged to exclude bees failed to trip or set seed, wheras flowers in cages with bees or in the open set seed abundantly. These men concluded that in Utah the most important alfalfa pollinating bees were honey bees, alkali bees (*Nomia* spp.), and leafcutter bees (*Megachile* spp.). Honey bees collecting pollen from alfalfa were differentiated from nectar-collecting bees, which frequently take nectar from the flower without tripping it. Tucker (*1956*) showed that bees "learn" to avoid tripping flowers but trip 7 to 85 percent of them during the learning process. This points up the importance of having a preponderance of new foragers in the colonies used for alfalfa pollination.

Bohart et al. (Utah Agr. Expt. Sta. *1950*) stated: "Alfalfa under most conditions is an attractive source of nectar and suffers little from competition with other plants for visits from nectar collectors. It is not an attractive source of pollen, however, and pollen collectors are apt to neglect it in favor of better sources. Consequently in alfalfa fields nectar collectors nearly always outnumber pollen collectors, in some areas by more than 100 to 1." Pedersen (*1953a, b; 1958*) showed that nectar secretion of alfalfa influenced its seed production. When large numbers of honey bees are concentrated on alfalfa fields, however, the competing pollen in the area may be exhausted so the bees resort to alfalfa pollen from lack of choice. This was proven in a seed production test on alfalfa grown in replicated open plots and cages of the type designed by Pedersen et al. (*1950*). In some of the cages, bees were excluded; in others, a colony of honey bees was present (Utah Agr. Expt. Sta. *1950*). In this test, with harmful insects controlled by use of DDT, the cages without bees produced only 14 lb/acre, whereas similar cages with bees produced a maximum of 1,018 lb/acre. This, incidentally, was the experiment to prove the value of honey bees that was specifically called for decades earlier by Lovell (*1924*) after his review of the literature failed to support claims of ardent beekeepers that honey bees increase production of alfalfa seed.

This experiment (Utah Agr. Expt. Sta. *1950*) also presented data showing that colonies transported from California to Utah alfalfa fields for honey production affected Utah seed production. A correlation (that was highly significant statistically) was calculated between the number of colonies of honey bees transported into Utah and the alfalfa seed yields per acre in that State. It showed that high seed yields occurred in years when large numbers of colonies were moved in and low seed yields when few colonies arrived.

Before 1947, the beekeeper placed colonies near alfalfa fields to obtain honey crops. Reports on the value of such honey bees to alfalfa were generally unfavorable. Pellett (*1941*) hinted that there was a difference in operating colonies for honey production and for seed production and that probably more seed could be obtained if as many as five colonies per acre were used, but no data were given to support the statement. He also recognized that such a colony concentration would produce no surplus honey for the beekeeper.

Vansell (*1951*) showed the value of a high concentration of honey bees in fields. In 1947, a 95-acre field at Knights Landing, Calif., had 275 colonies distributed in small groups within the field (2.9 colonies per acre), and the grower harvested 560 pounds of recleaned seed. A 200-acre field at Ryer Island, Calif., had three colonies of honey bees per acre placed around the field, and the yield of seed was 550 pounds per acre. In 1949, six colonies per acre were distributed throughout a 132-acre field at Davis, Calif., and the grower harvested 1,120 pounds per acre of thresher-run seed.

According to Whitcombe (*1955*), in 1948 an alfalfa seed grower at Hemet, Calif., paid a beekeeper $1.40 per colony to place 275 colonies in small groups on three roadways across a 95-acre field. The grower harvested 540 pounds of recleaned seed per acre. The colonies showed no gain in weight while in the alfalfa fields. Previously, beekeepers had paid alfalfa growers (usually

with a 60-pound can of honey) for the privilege of setting an apiary near the alfalfa field. The grower at Hemet paid the beekeeper to place the colonies in the field, a gamble that made history in legume seed production although it caused a financial loss to the beekeeper.

These and other convincing data presented by Vansell (*1951*) proved that alfalfa seed production could be stabilized by using honey bees distributed within the field. He stated, "An especially heavy set was obtained from plants within 100 yards of the colonies." With the grower obtaining 150 or more pounds of alfalfa seed per acre from the service of each bee colony and with the colonies producing little honey for the beekeeper under such conditions, Vansell (*1951*) concluded: "For pollination service requiring a large number of colonies the seed grower should pay the beekeeper [an amount] at least equal to that [obtainable] from a good honey crop." Todd (*1951*) urged similar compensation for the services of the bees.

With this basic information, growers and beekeepers cooperated in the rental and use of bees for alfalfa seed production, and the seed industry was stabilized to the benefit of both. Also, dependable use of honey bees made possible the production of various selections and cultivars, which were confined to the breeder's shelf before the insect pollination requirements of alfalfa were understood. It also opened the door to the development of hybrid alfalfa, and in this regard it shows the importance of attempts to find cultivars attractive to bees or special alfalfa-pollinating strains of bees (Boren et al. *1962*; Cale *1970*, *1971*; Clement *1965*; Hanson et al. *1964a*, Pedersen and Todd *1949*; Nye and Mackensen *1965*, *1968a*, *b*; *1970*; Mackensen and Nye *1966*, *1969*).

The rental and placing of many thousands of colonies of honey bees in alfalfa fields became an accepted practice in the early 1950's (Townsend et al. *1956*) and has continued to the present. This practice is responsible for producing the bulk of the alfalfa seed (Doull *1967*).

Jones (*1958*) reported that about 75,000 colonies were used per year on legumes in California from 1942 to 1947, but by 1956 the number had risen to 400,000 colonies. Experience and experiments proved that large numbers of colonies distributed uniformly throughout the field produced satisfactory seed crops even though only nectar collecting bees were active in the field (Akerberg and Lesins *1947*, *1949*; Bieberdorf *1949*; Bohart *1957*; Linsley and MacSwain *1947*; McMahon *1954*; Pedersen *1962*; and many others). The maximum economic number of bees was never established.

That nectar-collecting bees were contributing to pollination was attested to by the fact that alfalfa pollen was found in the proboscis fossae of such honey bees (Vansell *1955*, Grinfeld *1956*, Furgala et al. *1960*, Kropacova *1964*). Levin and Glowska-Konopacka (*1963*) showed that increasing the numbers of colonies in the groups in the field caused the bees to forage closer to their own hives. Todd (*1957**) urged that this type of behavior be exploited by uniformly distributing groups of colonies at $^1/_{10}$-mile intervals in the field and creating the competition necessary to force the bees to "shop around" within their foraging area (fig. 34).

PN-3767

FIGURE 34.—One of many groups of honey bee colonies placed in large fields of alfalfa grown for seed.

The alfalfa pollination fees established by beekeepers in the early 1950's and carried over into the 1970's were not too different from fees for pollination of other crops paid almost half a century ago. At that time, the beekeeper expected his colonies to improve in population or stores while pollinating the crop. Under present agricultural conditions, colonies frequently deteriorate to such an extent that no surplus honey is stored, the population of the colonies is reduced, and some colonies fail to survive the winter.

Unless beekeepers establish fees commensurate with their operating costs, or unless the use of pesticides on or near alfalfa seed fields is replaced by some form of biological control, the prospects of a continued supply of an adequate number of strong honey bee colonies for maximum alfalfa seed set are gloomy to say the least. See "Pesticides and Beekeeping."

WILD BEES

The value of wild bees—numerous species in numerous locations—as pollinators of alfalfa has also been reported by scores of researchers (Bohart *1947*, *1952**, *1958b*; Bohart and Knowlton *1952a*, *b*; Burton et al. *1964*; Crandall and Tate *1947*; Hobbs *1956*; Hobbs and Lilly *1954*; Medler *1957*; Menke *1952a*, *b*, *1954*; Pengelly *1958*; Stephen *1955*, *1959*; Tysdal and Westover *1937*; Utah Agr. Expt. Sta. *1950*; Wilson *1968*). (Also see "Wild Bees and Wild Bee Culture.") An advantage suggested for honey bees over the various wild bees, so far as planned pollination was concerned, was that honey bee colonies could be transported when desired, and in appropriate numbers, to the alfalfa fields. Recent studies, however (Bohart *1958a*, *1962b*), have shown that at least two species of wild bees, the alkali bee and the leafcutter bee, can also be transported and manipulated for the pollination of alfalfa on a commercial scale, and they do an excellent pollination job in some areas. Much credit for our knowledge of these two bees must be attributed to Bohart (*1947*, *1950*, *1952**, *1958b*, *1962b*, *1967*, *1970*), Bohart et al. (*1955*), Hobbs (*1956*, *1962*, *1964*, *1965*, *1967*), Hobbs and Lilly (*1954*), Menke (*1952a*, *b*, *1954*), Stephen

(*1955*, *1961*, *1962*, *1965*), and Utah Agricultural Experiment Station (*1950*). Bohart (*1962a*) stated that there might also be other pollinating insects, in foreign countries, superior to any indigeneous species and that they might warrant our importing.

Both alkali bees and leafcutter bees are far more efficient, on a bee for bee basis, than honey bees in pollinating alfalfa. Their primary motive in visiting the flowers is to collect pollen to provision the nest for their young, and they show a preference for alfalfa pollen. By contrast, the honey bee, if given a choice, visits the alfalfa flower to collect nectar, which it must have in great abundance to survive, but will visit some other flowers for pollen.

The alkali bee will nest in highly alkaline areas on which little or no plant growth occurs. Growers can prepare such areas for nesting sites (Frick et al. *1960*). Once established, a favorable site may produce enormous populations—as many as 200,000 nests. Although each female builds her own nest in which she may rear about 5 to 20 offspring, the bees are instinctively gregarious; that is, they nest close together, sometimes with as many as 100 nest entrances per square foot. The foraging range of the alkali bee is similar to that of the honey bee. This bee is much less likely to sting people or domestic animals than is the honey bee. It overwinters in the immature stage.

The disadvantage of the alkali bee is that the nesting sites require a year or so to become established, and they cannot be transported from field to field. A special area must be maintained for them (Bohart *1958a*). Also, because they are affected by the elements, they may not emerge at the right time to pollinate a desired crop. They may be destroyed by flooding, cultivation, pesticides, parasites, predators, or diseases.

The leafcutter bee is also gregarious, but prefers to nest above ground in holes about three-sixteenths inch wide by 2 to 4 inches deep. To utilize this bee, the grower prepares such holes in boards (Stephen *1961*, *1962*) and places the boards where these bees are abundant and active. The holes are soon filled with nests. The immature bees can then be transported in the boards to other areas as desired. The leafcutter bees do not forage as far afield as honey bees, so the boards must be distributed at close intervals in the alfalfa field. The bees are not aggressive and can be handled without protection from stings.

Leafcutter bees, like honey bees, can be transported and established wherever desired and are quite effective as pollinators of alfalfa as long as the weather conditions are favorable during their active period. After this short active period, the adults die. The immature stages can be stored under refrigeration, then placed in incubation to permit the adults to emerge when desired. Leafcutter bees, like alkali bees, forage freely on alfalfa pollen, with which they provision their nests. They require nesting holes of a rather specific size and depth and, because these insects are gregarious, many hundreds of nesting holes are more conducive than a few to their nesting in an area. Current methods utilize "nesting boards," timbers about 4 inches by 4 inches by 4 feet, with about 2,000 holes, ¼ inch by 3½ inches deep, although some boards are fabricated with grooves (Nye and Bohart *1964*) that, properly placed, form holes. When these boards are disassembled, the individual leafcutter bee nests can be removed, handled in bulk, and placed in containers in the field where the adults can emerge at the nesting site when desired. Leafcutter bees forage primarily within a few hundred feet of the nest, therefore, are more likely to be of service not only in the field but in the part of the field where they emerge. Their use is quite likely to increase because of their ease of handling, safety from the standpoint of stings, and efficiency as pollinators of alfalfa.

In the pollination of alfalfa, honey bees, leafcutter bees, and alkali bees, alone or in any combination, are of great value. The grower who desires maximum seed production should utilize the best combination of these bees and the best information available concerning them. He should keep in mind, however, that the location of his particular field and general area may determine the proper bee or combination of bees most suitable for him. This decision can only be made if he has a thorough knowledge of the bees, the crop, and the environment.

Pollination Recommendations and Practices

The alfalfa flower must be tripped and cross-pollinated by insects for maximum production of high-quality seed. The majority of the western alfalfa seed producers now use either honey bees, leafcutter bees, alkali bees, or some combination of the three. Honey bees are usually rented from beekeepers. Leafcutter bees are usually purchased in the pupal stage, either in bulk (1 U.S. gallon contains about 10,000 pupae in cells) or with the cells intact in the prepared holes in boards. The grower usually prepares his own alkali bee bed and cares for it as a perennial holding.

Recommended rates for usage of honey bees vary from 1 to 10 colonies per acre. Jones[9] recommended two colonies per acre, plus one colony for each additional 100 pounds of seed expected in excess of 250 to 500 pounds. Later, Jones (*1958*) recommended a colony concentration that would provide two to seven nectar collectors per square yard. Todd and Crawford (*1962*) recommended that they be distributed about 0.1 mile apart in the field. Most growers use two to four colonies. From 2,000 to 3,000 leafcutter bee nests, or 10,000 individual leafcutter bees have been recommended, with a bee shelter and nests on each 4 acres. A well-populated alkali bee bed, 30 by 50 feet for each 40 acres of alfalfa, or 2,000 female alkali bee visitors per acre is recommended. The data supporting these recommendations are surprisingly meager.

Many factors influence the degree to which the grower follows these recommendations. Also, many variables influence the effectiveness of the pollinators in the field. As a result, one field may be adequately pollinated while another, in which the grower tried to follow the same recommended treatment, may suffer from lack of adequate pollinator activity. Such factors as competing plants, pesticides, adverse weather, bee

[9] JONES, L. G. FACTORS IN ALFALFA SEED PRODUCTION, INCLUDING WEED CONTROL. Div. Agron., Univ. Calif., Davis. File 3.21, 3.061, 5 pp. 1949. [Processed.]

diseases, strength of colony (of honey bees), and agronomic manipulations can alter effectiveness of the pollinators.

When the grower elects to use honey bees, each colony should have a minimum of 800 in^2 of healthy brood in all stages and sufficient bees to blanket 15 to 20 combs (Todd and Reed *1970*). There should be three to six honey bees per square yard of flowering alfalfa during the more active part of the day, to provide maximum pollination to every bloom. This may mean some colonies should be moved into the field at the beginning of flowering and augment their numbers as flowering progresses. Water for the bees should be within one-quarter mile of any colony, and shade should be provided in warmer areas.

When alkali bees are used, an equivalent of about 40 ft^2 of a well-populated nesting site should be provided per acre of alfalfa. The nesting site should be protected from flooding, exposure to pesticides, trampling by livestock, or damage by predators and parasites. In the field, there should be about one bee for each square yard of blooming alfalfa.

When leafcutter bees are used, from one to five boards, bearing about 2,000 nest-filled holes, or 1 to 5 gallons of pupae should be placed for emergence, and nesting holes should be supplied on each 4 acrea of alfalfa. The nesting areas should be protected from hot sun, rain or irrigation water, parasites, and predators. There should be one female leafcutter per 5 yd^2 of alfalfa flowers (Bohart *1967*).

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ALMOND

Prunus amygdalus Batsch, family Rosaceae

Almond production in the United States is limited almost exclusively to California, which produces more than one-third of the world supply of almonds (Anonymous *1969b*). In 1971, 169,000 acres of bearing trees were reported.

The average annual production in the United States for 1958-68 was 740 pounds of meat (the edible portion of the fruit) per acre, ranging from 568.5 to 944.4 lb/acre (Anonymous *1969a*). The 1970 farm value of the crop was $80.1 million.

Plant

The deciduous almond resembles the peach in its general size, manner of growth, blossoms, and leaves. The blossoms, however, appear earlier in the spring than peach blossoms, usually before the leaves develop. The fruit also resembles the peach in structure, the thin leathery inedible hull (mesocarp) corresponding to the flesh of the peach (Kester *1969*). This hull splits at maturity, revealing the usually thin shell with its edible

kernel (meat) inside. Thus, we eat the flesh of the peach and discard the pit and enclosed kernel, while the hull of the almond is discarded and the kernel of the nut is eaten. This may be consumed raw, roasted, or toasted, whole or sliced, alone, or in candy, confections, or prepared dishes.

An almond tree may remain in production 50 years or more. The trees are usually planted 20 to 30 feet apart. Because of the self-incompatibility of commercial cultivars, the orchards are usually planted with two rows of the main cultivar and one of the pollenizer cultivars. Almonds prosper where summer temperatures are hot and dry, but they require chilling during dormancy, with a minimum of freezing weather after mid-February. Immature fruit may be killed at 31° F. During flowering, fair weather with daytime temperatures above 57° is essential to permit flight of pollinating insects. For these reasons, the area in the United States where almonds can be successfully grown is limited primarily to the Sacramento and San Joaquin Valleys of California.

'Nonpareil' is planted more than any other cultivar and accounts for more than half of the almond production. The 'Kapareil', developed and deriving its name from the 'Eure*ka*' and the 'Non*pareil*', is a good pollenizer for the 'Nonpareil' (Kester et al. *1963*). The 'Nonpareil' shell is thin (shelling 60 to 70 percent meat), and the nuts ripen in late August or early September. The 'Texas' or 'Texas Prolific' is the second most important cultivar. It shells only 40 to 45 percent meat, blooms several days to 1 week after 'Nonpareil,' and ripens in late September or October. Other cultivars include the following (Griggs *1970*, p. 186*):

Early

'I.X.L.',[10] 'Jordanolo', 'Ne Plus Ultra', 'Peerless'.

Midseason

'Cressey', 'Davey', 'Drake', 'Kapareil', 'Merced', 'Nonpareil', 'Norman', 'Paxman', 'Price Cluster', 'Profuse', 'Vesta'.

Late

'Ballico', 'Butte', 'Emerald', 'Empire', 'Mission' ('Texas'), 'Ripon', 'Ruby', 'Thompson', 'Tioga', 'Wawonal', 'Yosemite'.

Very Late

'Tardy Nonpareil.'

Inflorescence

The 1- to 1½-inch almond flower has a single pistil with two ovules (fig. 35). One or both of the ovules may develop into fruits; however, a "double" is not desired in commercial production. The ovary is in a floral cup formed by the green bracts, the five pinkish petals, and the 10 to 30 stamens. Nectar is secreted within the cup. The pollen, which is not windblown, is produced on the anthers that loosely surround the stigma. The abundant flowers open from late January to late March (Vansell and Griggs *1952**, Vansell and DeOng *1925*), but primarily from mid-February to mid-March. The crop is harvested in the fall.

Honey bees visit the flowers eagerly for both nectar and pollen. Honey produced from almonds is of poor quality and when harvested from the hive is used in the bakery trade. It is usually left in the hive as feed for the bees. The nectar and pollen stimulate honey bee brood-rearing. Nectar foragers are active on almonds throughout the day if weather permits, but pollen foragers are most active during midday. The honey bee is the primary insect visitor to almond flowers.

Pollination Requirements

The almond flower is self-incompatible. A pollen tube of a flower of the same tree, the same cultivar, and sometimes of certain other cultivars, will not grow down the style (Kester *1969*). Hatch (*1886*) noted that trees of the 'Languedoc' cultivar near seedling trees of other parentages always produced heavier crops than when in solid blocks. According to Griggs and Iwakiri (*1964*), all almond cultivars grown in California require cross-pollination to produce a crop. These authors also stated that under weather conditions favorable for honey bee flight the individual flower is most receptive to cross-pollination the day following opening and remains decreasingly receptive the next 3 or 4 days. Flowers not cross-pollinated shed in about a month (Kester and Griggs *1959a*). A few pairs of almond cultivars are interincompatible. If a grower wants to grow these, he should plant at least one other cultivar as a pollenizer (Griggs *1970**).

A profitable almond crop depends upon the cross-pollination of practically all flowers. The grower wants the heaviest possible set of almonds, because there is no fruit-thinning problem and nuts with small kernels are in greatest demand (Griggs *1953**). (By comparison, 5 percent of the blossoms on an apple tree can produce an economic yield.) The failure of any almond flowers to be cross-pollinated reduces yield by just that much. Only the bees that carry pollen from a flower of one cultivar to another receptive flower contribute to fruit set. Not all flowers set, and several must be cross-pollinated for every almond expected (Kester *1958*). To obtain a maximum crop of almonds, essentially 100 percent of the flowers must be cross-pollinated (Kester and Griggs *1959b*). The bee population should therefore be sufficiently heavy that repeated visits to every flower occur and the bees must "shop around;" that is, they should not only visit many flowers on one tree but also must visit between cultivars to obtain their loads of nectar and pollen. In this way, the pollen is spread from one tree to another to the maximum extent.

Pollinators

The honey bee is practically the only pollinating insect of economic importance on almonds, and growers throughout the world have been urged to use it (Ferreres in Mexico, *1947*; Gagnard in Algeria, *1954*; Griggs in California, *1970**; Muttoo in India, *1950*; Purdie and Winn in Australia, *1964*, *1965*). The importance of a heavy honey bee population cannot be

[10] 'Jordanolo', 'I.X.L.', and 'Drake' are no longer being planted, but there are significant acreages of bearing trees of these cultivars.

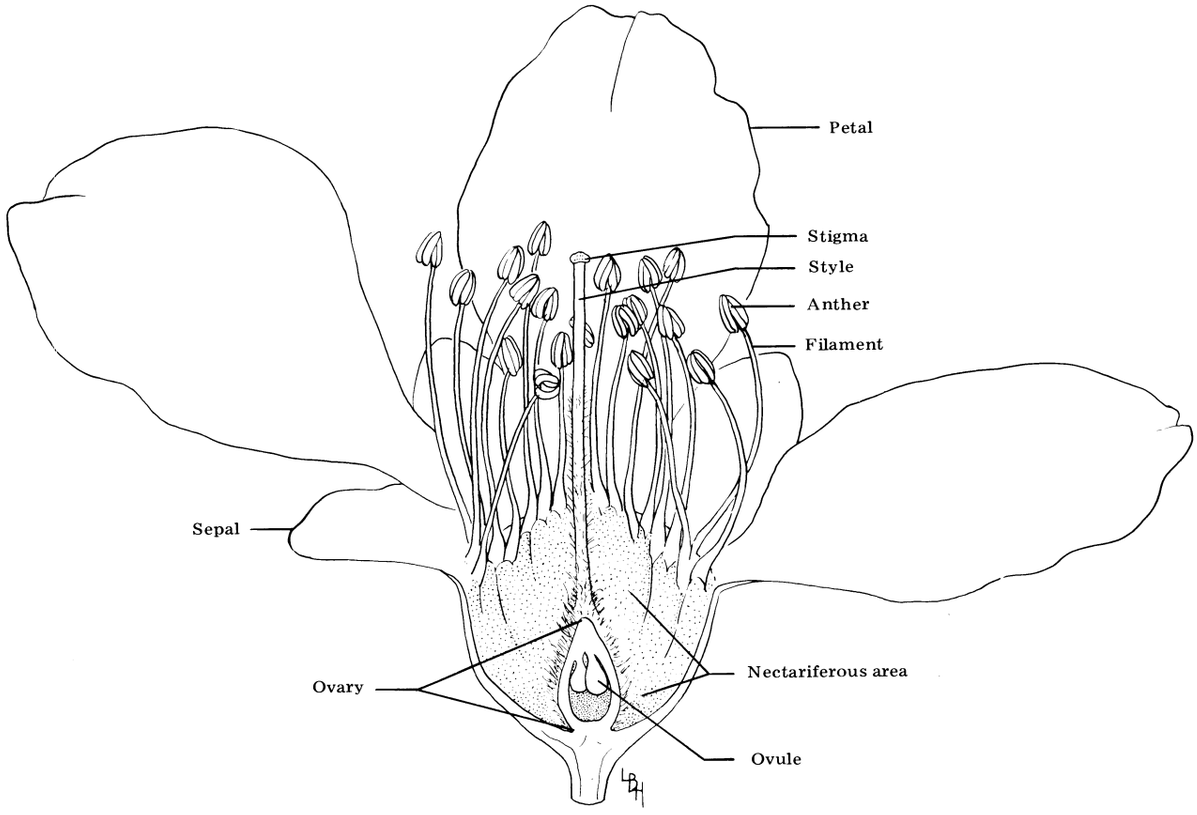

FIGURE 35.—Longitudinal section of 'Mission' ('Texas') almond flower, × 6.

overemphasized. Almond blossoming occurs when days are short and cool, other pollinators are absent, and the honey bee colonies are frequently in their weakest condition of the year. The weather is most likely to be unsettled, and temperatures often restrict bee activity to 1 to 3 hours at midday.

Although only 1 grain of pollen is theoretically necessary to set an almond fruit (Tufts *1919*), the pollen must come from another compatible cultivar at just the right time. Bees often visit scores of blossoms on a tree before moving to another if nectar or pollen is plentiful, yet maximum transfer of the pollen between appropriate trees is necessary. This calls for a heavy bee concentration on the trees. An orchard with a bee population that permits the colonies to store surplus almond honey would be questionably low for maximum pollination and maximum almond production. The more a bee is forced to "shop around" between trees to acquire a load of food, the more effective it becomes as a pollinizer of almonds.

As pointed out by Brittain (*1933*), the adjoining acreages can influence forager effectiveness, so that the area within one-half mile or so, and not only the orchard alone, must be considered the unit when calculating the pollinator force necessary for the orchard.

Most almond growers recognize that cross-pollination by bees is essential, and they make some effort to provide this service to the flowers. Frequently, too few colonies are obtained, they are not sufficiently populous in field bees, they are not properly distributed for maximum efficiency in visiting all flowers, or the bees become damaged by pesticides before their services on the crop are completed. Sometimes, only a few weak colonies near the orchard are depended upon to set the almond crop rather than the adequate number of populous colonies distributed uniformly throughout the orchard. Frequently, "bargain prices" are paid for truck loads of 100 or more colonies unloaded in one easily accessible place (for the beekeeper), and where the bees have a choice of other than almond flowers to visit.

Sometimes, the grower is unable to locate an uncommitted beekeeper or one who wants to supply bees. Such a situation was recognized in 1970 when growers were told (Anonymous *1970*) that bees were scarce due to pesticide losses and the reluctance of beekeepers to supply bees for pollination. The growers were further told that the situation was likely to continue; therefore, they should consider contracts for 1971 and even future years to assure themselves of bees.

The most serious problems appear to be (1) the low rental fee which is established largely by the beekeeping industry itself, (2) colonies of inadequate strength, and (3) colonies not strategically placed or properly serviced to provide adequate pollination. The beekeeper tends to feel that higher pollination fees would only invite competition by other beekeepers. He therefore charges little if any more than the $5 to $10 recommended 40 years ago (Phillips *1930*). The statistics indicate that there are not sufficient mobile colonies in California or in nearby adjoining states to satisfactorily pollinate the current almond orchards.

Pollination Recommendations and Practices

The literature on almond pollination leaves no doubt about the need for an ample supply of bees to pollinate the flowers. There is no other choice than to have honey bees perform this task. The question is one of quantification—how many bees?

Vansell and Griggs (*1952**) recommended that there be either one pollinizer row of trees for every three rows of the main variety, or two rows of pollinizer trees for each two of the main variety. Then they recommended that two to three strong colonies of honey bees be used per acre. Woodrow (*1932*), Purdie and Winn (*1964*), and Sheesley and Poduska (*1970a, b, c*) showed that strong colonies were much more effective than weak ones, particularly at lower temperatures, such as those likely to occur during almond blossom time.

Griggs et al. (*1952**) counted 20 to 30 bees on each of two almond trees caged with a colony of honey bees. The weather was favorable for bee activity at the time the counts were made. Griggs and Iwakiri (*1960*) counted 150 to 200 bees per tree in the open, which they considered fair to good bee activity. There were seven colonies per acre (half of them were weak, half were strong) supplied to the orchard in which the counts were made.

The studies indicate that at least two to three strong colonies per acre may be required for maximum production of almonds. The colonies should be distributed within the orchard in small groups one-tenth mile apart. Each colony should have at least 800 in^2 of brood and a cluster of bees that covers most of the frames in a two-story deep-frame hive. The colonies should be in the orchard at the beginning of flowering and should remain until flowering on the main cultivar has ended.

Whether more colonies per acre or closer placement of the groups of colonies within the field will result in greater net increase to the grower has not been determined. In the San Joaquin Valley of California, a commonly held idea is that almond production at bloom time can be increased more with less investment by having adequate bees than with any other expenditure, all other factors being equal. In general, this would indicate that not enough colonies are being used for maximum production of almonds.

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ALSIKE CLOVER[11]

Trifolium hybridum L., family Leguminosae

Alsike clover has been an important summer legume in north central and northeastern United States; however, it is being replaced by alfalfa. A small amount of seed is produced in the Pacific Northwest. Most of the seed that we use comes from Canada. In 1969, we imported 3,715,000 pounds, most of which was probably used in mixed pasture planting.

Plant

Alsike clover is a perennial but usually grows as a biennial, and in some situations it behaves as an annual. It is intermediate in size between white and red clover. Many smooth stems, bearing smooth trifoliate leaves, arise from its crown. The noncreeping stems may grow to a height of 5 feet but usually reach about 2 feet. They bear flower heads along their entire length, the youngest always toward the top. It is a good hay, pasture, and green manure crop, and like other legumes, it improves the soil and contributes to reduced soil erosion.

Inflorescence

The flower head of alsike clover is made up of many florets and is similar to the more common white clover, although there may be four times as many heads per square yard as are normally found on white clover. The florets on some heads are pink, on others they are white, and on some they are both pink and white. This variation in flower color led to an earlier belief that alsike was a cross between red and white clover, hence the scientific name hybridum.

A floret will produce two to three seeds. Flower heads with 100 seeds indicate a good seed crop. The flowers are quite attractive to bees, especially honey bees, for the nectar and pollen. Pellett (*1923*) stated that some beekeepers estimated that alsike clover might produce 500 pounds of honey per acre in good seasons. This seems abnormally high but indicates the importance beekeepers attach to this crop as a source of honey. Holmes (*1960*) noted that boron favorably influenced nectar secretion in alsike clover, but apparently this information has not been used to increase seed production.

Pollination Requirements

The florets are largely self-incompatible so they must receive pollen from another plant to produce seed (Pieters and Hollowell *1937*). In Ohio, Dunham (*1939*) showed that three cultivars set only 0.4 to 5.5 seeds per head when selfed, 3.4 seeds per head when wind pollinated, and 120 to 125 seeds per head in a cage with bees. Open plots had 2.6 to 90.4 seeds per head. He calculated that the seed yielding capacity of a field with 1,000 heads per square yard, averaging 50 seeds per head, would be 350 pounds per acre, 90 seeds per head would produce 625 lb/acre and with 120 seeds per head the yield would be 825 lb/acre.

In Oregon, Scullen (*1956**) reported 5.1 seeds per head where bees were excluded but 69.2 seeds per head where bees had access to them. (About 500 lb/acre, according to Dunham's (*1939*) method of calculation.) Oregon averages 300 to 415 lb/acre, but occasional phenomenal yields of 1,000 lb/acre are obtained. The overall United States average is about 140 lb/acre (Wheeler and Hill *1957**). Evidently, seed production in most areas could be significantly increased with adequate pollination.

Pollinators

Few detailed studies have been made on the insect pollinators of alsike clover. Megee and Kelty (*1932*) concluded that the honey bee was an effective pollinator on alsike clover in Michigan. Dunham (*1957*) studied alsike clover seed setting for a number of years in an area of Ohio where intensive farming was practiced. He found that native bees set only 1.5 to 3 percent of the seeds. Valle (*1960*) reported that in Finland the honey bee was a much more important pollinator of alsike clover than bumble bees. According to Pankiw and Elliott (*1959*), the honey bee is the primary pollinator of alsike clover in western Canada. They found that fields with higher populations of pollinators matured earlier as well as produced more seed. Harrison et al. (*1945*) concluded that honey bees were essential to alsike clover in Michigan. Tucker et al. (*1958*) reported that honey bees comprised 93 to 99 percent of the pollinating insects on alsike clover in Minnesota. Smith (*1960*) stated that honey bees represent 83 percent of the total pollinator population on alsike fields in southern Ontario.

Pankiw and Elliott (*1959*) stated that honey bees are excellent pollinators of alsike clover and that they visited the florets at the rate of 18.7 per minute, as compared to 20.0 per minute for leafcutter bees, and 28.6 per minute for bumble bees. Fischer (*1954*) reported that honey bees will leave alsike for sweetclover. Wahlin (*1962*) observed that when widespread cultivation of oil plants occurred in the red and alsike clover seed growing area of Sweden, the bees visited these crops, which resulted in a reduced clover seed harvest.

Holdaway et al. (*1957*) in three observations over 2

[11] See "Clovers, General," p. 158.

years obtained yields of 15, 20, and 20 pounds of seed per acre without insect pollination; 102, 207, and 368 lb/acre with insect pollination, no harmful insect control and no fertilizer added; and 685, 691, and 808 pounds of seed per acre with pollination, harmful insect control, and the addition of phosphorus and potash fertilizers. They recommended at least two colonies per acre, the colonies placed at the edge of the field.

Studies have established that the honey bee is the primary insect pollinator of alsike clover and its activity accounts for the bulk of the seed produced. Evidently, seed production of this crop can be significantly increased over current commercial averages if honey bees are present in adequate numbers.

Pollination Recommendations and Practices

Pankiw and Elliott (*1959*) recommended one colony of honey bees per acre of alsike clover for fields of 50 acres or more but up to three colonies per acre for smaller fields. They obtained about 375 pounds of seed per acre with a bee population of about three-quarters of a bee per square yard. Smith (*1960*) recommended two to three colonies per acre with the colonies placed in or close to the field. Holdaway et al. (*1957*) recommended at least two colonies per acre. Tucker et al. (*1958*) concluded that seed yields were increased about 260 lb/acre for each colony per acre. They calculated that one bee per 3 yd^2 set 175 pounds of seed per acre, but one bee per square yard set 800 pounds of seed per acre. The number of colonies per acre necessary to provide the one bee per square yard was not indicated.

Dunham (*1938*) thought that the number of colonies necessary to provide maximum pollination of alsike might be so great it would make the renting of bees prohibitive. No study has been made to determine this factor. The data indicate, however, that the alsike seed grower can afford to and should obtain several colonies per acre at current colony rental prices (see "Pollination Agreements and Services").

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ANISE

Pimpinella anisum L., family Umbelliferae

Anise is a minor crop cultivated for its seeds or the oil pressed from them which are used in condiments, beverages, medicines, soaps, and perfumery. Probably no more than a few hundred acres are grown in the United States.

Plant

Anise is a pubescent annual about 2 feet high (fig. 36). It is usually planted in 15- to 30-inch rows, the plants thinned to 6-inch intervals. Planting is usually in the

FIGURE 36.—Anise plant in full bloom.

springtime in temperate climates, although Griffiths et al. (*1946**) recommended that it be planted in September in Arizona.

Inflorescence

The small but copious yellowish-white flowers are in large loose umbels and appear in late summer, about 3 months after planting if the seeds were planted in the spring. Pellett (*1947**) reported that the blossoms, which are attractive to honey bees, yield a light-colored honey with a mild elusive flavor. Sievers (*1948*) stated that 400 to 600 pounds of seed per acre was an annual yield, Rosengarten (*1969**) mentioned 500 to 800 pounds. Griffiths et al. (*1946**) stated that 600 pounds per acre could be expected in Arizona. The influence of insect pollination on seed production was apparently not considered in relation to these yields.

Pollination Requirements

No reference could be found on the relation of pollinating agents to production of anise, although its flower structure and family relationship would indicate that it benefits from, if it is not entirely dependent upon, insect pollination. Hawthorn and Pollard (*1954**) support this by stating that insufficient insect pollination frequently results in reduced yields of some crops, including anise. Growers interested in obtaining the highest possible yields of anise should, therefore, give consideration to its insect pollination.

Pollinators

Although there seems to be little information on the insect pollination of anise, the honey bee could probably pollinate it adequately, considering the flower's structure and its reported attraction to honey bees.

Pollination Recommendations and Practices

None.

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APPLE

Malus sylvestris Mill., family Rosaceae

In 1969, about 6.7 billion pounds of apples, valued at $274.4 million, were produced in the United States. In the six States where almost two-thirds of the entire crop was produced, the volume, in million pounds, was: Washington, 1,675; New York, 855; Michigan, 720; California, 540; Pennsylvania, 525; and Virginia, 472.

Hedrick (*1938**) stated that 4,000 to 5,000 cultivars of apples were described, but Henderson et al. (*1969*) showed that fewer than two dozen cultivars account for 95 percent of the total crop. The leading cultivar is 'Delicious', which accounts for 30 percent of the total production. 'Golden Delicious' ranks second and accounts for 13 percent. Other leading cultivars and their percentages of the total crop are: 'McIntosh', 10 percent; 'Rome Beauty', 8 percent; 'Jonathan', 6 percent; and 'York Imperial', 5 percent.

Plant

The apple tree may reach a height of 40 feet or more; however, for various cultural reasons, commercial apple growers keep their trees of standard rootstock less than half that high. Trees on the recently developed dwarf (fig. 37) and semidwarf rootstock (Tydeman *1955*) in the newer orchards and replants may be less than 10 feet. This development of dwarf apples is so changing apple production that much of the older information on culture, pollination, and harvest of this crop may no longer be applicable. An example of the difference in the size and planting rate of apple trees is given in table 7.

Many of the older trees were spaced 40 by 40 feet (27 per acre) and took 25 years to reach their maximum

FIGURE 37.—Dwarf apple tree in bloom.

TABLE 7.—Difference in the size and planting rate of apple trees[1]

Tree type	Height	Breadth	Spacing	Trees per acre
	Feet	*Feet*	*Feet*	
Standard[2]	15.5	29	24 × 36 or 30 × 38	50
Vigorous on M-II[3]	14	26	20 × 32 or 22 × 30	68
Semidwarf on M-VII	13	19	16 × 24 or 18 × 22	113
Dwarf on M-IX	9	12	8 × 15 or 10 × 12	363

[1] Source: Hutchinson (*1964*).
[2] A 20-year-old McIntosh.
[3] M = rootstock originally developed at East Malling (England) Research Station; Roman numeral = designation of a particular type.

production of 500 bushels (a bushel weighs about 44 pounds) per acre (Anonymous *1969*). Snyder (*1968*) reported production of 113 to 377 bu/acre on 21 farms observed in western New York, where the number of trees ranged from 70 to 182 and averaged 91 per acre. Kelly (*n.d.*) reported 313 bu/acre on 18 farms in Pennsylvania, where over 50 percent of the trees were standard cultivars. Henderson et al. (*1969*) reported an average of 592 bu/acre for California.

By using dwarf apple trees, the growers can have as many as 1,000 trees per acre, and expect a maximum production of 900 bushels in 6 years on 'Jonathan' trees, or as much as 1,300 bu/acre on 'Golden Delicious' (Anonymous *1971*). The smaller trees yield more per acre, reach maximum production at a much earlier age, are more easily pruned and sprayed, and the fruit is much more accessible for thinning and harvesting (Shoemaker and Teskey *1959*, Gaylord *1965*).

Norton (*1971*) considered the density of the trees per acre as follows: Low, 75 to 150 trees; medium, 200 to 300 trees; high, 400 to 800 trees; ultra-high, 1,000 or more trees.

Inflorescence

The apple flower cluster, made up of about six flowers, is produced on a 1- to 3-year-old woody shoot, ½ inch to 2 inches long, called a spur. The clusters are usually found at the tip of the spur in the axils of leaves, and are formed the previous summer (Bradford *1915*, Latimer *1933*). The primary or "king" bud opens first, and usually produces the choicest fruit. If the king bloom fails, the lateral blooms, which open a day or more later, can also produce fruit. Howlett (*1926a*) showed, however, that the lateral flowers are much more likely to shed, making the preservation of the king bud still more important.

The five pinkish-white petals of the 1- to 1½-inch broad and pleasantly scented blossom (fig. 38) shed a few days after they open, but the five green sepals persist in a dried shriveled state in the blossom end of the mature fruit. The five stigmas, which unite into a common style that leads to the ovary, are surrounded by 20 to 25 erect pollen-bearing stamens. Nectar is secreted between the bases of the stamens and the style.

The ovary is divided into five compartments, each containing two ovules (four in the case of the cultivar 'Northern Spy') so that 10 (or 20 in 'Northern Spy') seeds may develop (Goff *1899*, *1901*).

The apple flower produces both nectar and pollen in abundance, more nectar than most of our other deciduous fruit trees produce (Smith and Bradt *1967**). Apple pollen and nectar are eagerly collected by honey bees, and are important contributors to spring buildup in honey bee colonies. Colonies usually arrive in the orchard low on stores and relatively weak, the period of bloom is short, and frequently the weather is unfavorable for bee activity. This prevents the storage of surplus honey, so that apple honey on the market is rare. The amount that the bees are able to collect is left in the hive for food reserves.

The average blossoming period for apples is about 9 days. Cool weather lengthens and warm or dry windy weather shortens this period (Morris *1921*). Bee activity on apples during the day is usually greatest about 9 a.m. (Brittain *1933*). Although numerous blossoms appear on the apple tree, a set of only 5 percent will produce a fair apple crop (McDaniels and Heinicke *1929*, Brittain *1935*).

Pollination Requirements

The pollination of apples has been of interest since Cooke (*1745*) stated that the "farina" (pollen) of one apple tree influenced the fruit of another. Eventually, Wicks (*1918*) showed that foreign pollen does not bestow a benefit to the fruit in either size, shape, color, or quality. The pollen stimulates development of the seed, which in turn produces an auxin that stimulates adjoining tissue to develop. Of course, the pollen influences the offspring that develops from the seed.

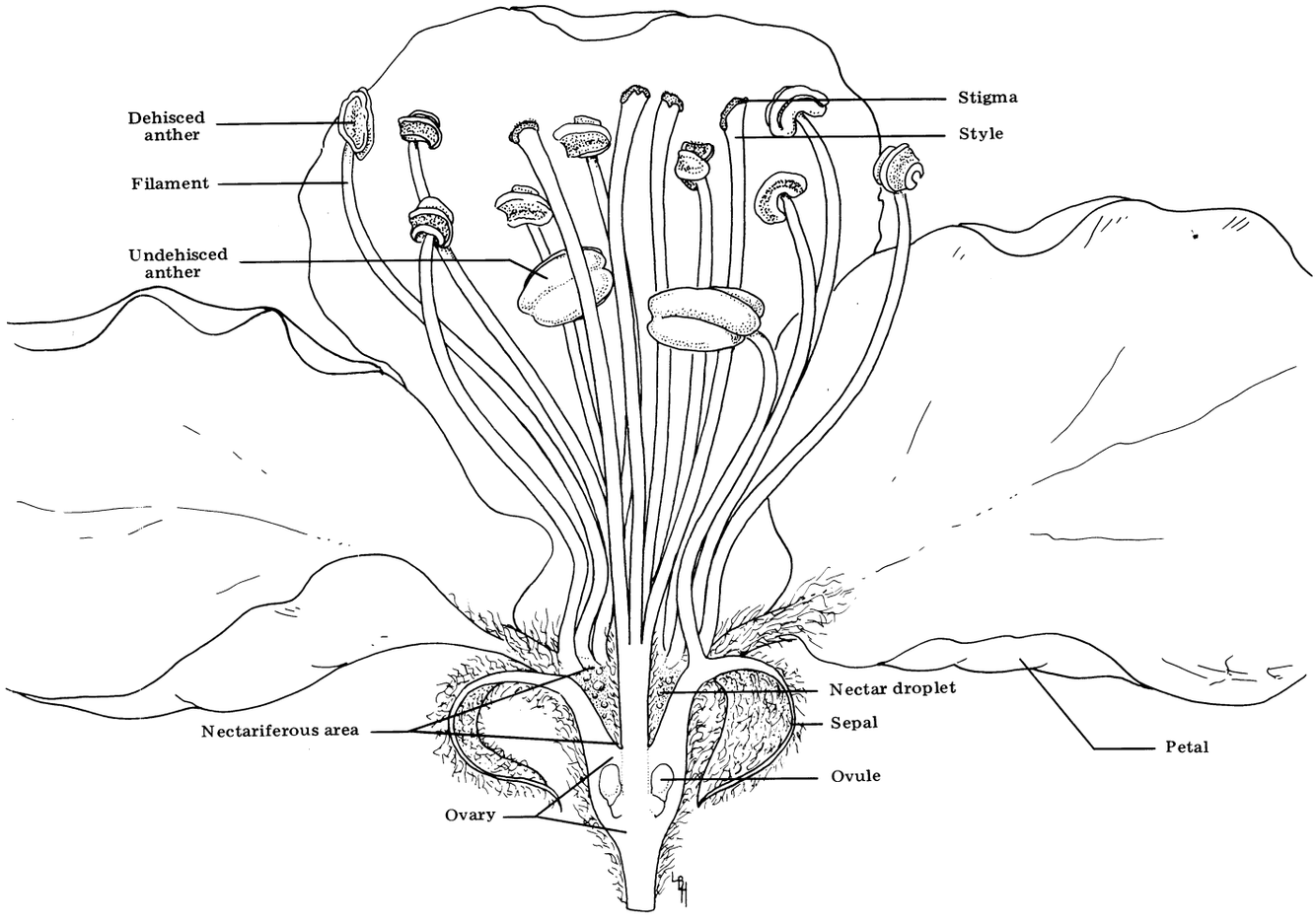

FIGURE 38.—Longitudinal section of 'Delicious' apple blossom, ×6.

The fertilization of every ovule in the ovary is not essential to fruit development, but the larger the number fertilized the greater the likelihood that the fruit will succeed in the competition for the plant's nutrients and remain on the tree until harvest (Brittain *1933*, Tydeman *1943*). Usually, the more seeds that develop in the apple, the larger it is (Murneek and Schowengert *1935*). About six or seven seeds are necessary for good fruit set (Hartman and Howlett *1954*). Some apple selections set seedless fruit without pollination, but no commercial cultivar has this characteristic (Chan and Cain *1967*).

The research by Waite (*1895*, *1899*) produced the first concrete evidence that apples and other pomaceous fruits benefit from the interplanting of and cross-pollination between cultivars, and that pollinating insects are essential for transferring the pollen between compatible cultivars. This research led scores of other scientists to study the pollination requirements of apples, both in the United States and abroad. These studies have been reviewed by Hutson (*1926*), Brittain (*1933*), and Free (*1960*, *1970**), who also conducted research on the subject.

Griggs (*1970**) stated that all apple cultivars are self-incompatible to some degree. Some set no fruit at all when self-pollinated; others set various proportions of a commercial crop under favorable conditions. He also stated that the self-fruitfulness of an individual cultivar may vary in different parts of the country, but apple specialists generally agree that no apple cultivar is sufficiently self-fertile to be dependably productive when planted alone. The grower, then, has no choice except to interplant. His problem is to find the most satisfactory and profitable combination of cultivars to produce his crop.

Studies, in particular by Brittain (*1933*), Burrell and Parker (*1931*), Latimer (*1931*), MacDaniels and Heinecke (*1929*), and Overholser (*1927*), proved that interplanting of cultivars was necessary, but that all cultivars were not equally compatible. The best pollinizer cultivar is one that has the most compatible pollen, and it blooms at the same time as the main cultivar. Although numerous studies have been made on the pollination of apples, we may not have full information on these points for all major cultivars in all apple-growing regions.

In selecting appropriate cultivars for interplanting, the grower should choose those that flower at the same time. Way (*1971*) showed that, at least in New York, flowering of early, midseason, and late cultivars

generally overlaps sufficiently for their use as pollinators of any commercial cultivar. In the southern section of the apple-growing regions, this difference between cultivars increases, and an overlapping of flowering dates is less likely to occur. This increases the importance of selecting cultivars that flower at the appropriate time. Compatible cultivars should, of course, also be chosen.

The importance of compatibility of cultivars, even when they flower at the right time, was shown by Overholser (*1927*). The cultivar 'Newtown' set 51.5 percent of its blossoms when cross-pollinated with 'Bellflower' (under a tent enclosing a colony of honey bees, which, presumably, provided maximum cross-pollination), but 'Bellflower' set only 4.3 percent of its flowers that were cross-pollinated with 'Newtown'.

FROST

The damaging effect of frost is sometimes blamed for poor yields, when, actually, the problem is inadequate cross-pollination. However, blossoms that have been pollinated are believed to be less susceptible to frost damage than nonpollinated ones. The grower should strive, therefore, to get the flowers pollinated as soon as possible after they open. This increased effort to get the flowers pollinated may result in excessive set of fruit some seasons, but excess fruit can be thinned. There is no way to put fruit on the tree after flowering has ceased. As Rom (*1970*) stated, "Pollination is without question the most critical event in the yearly production cycle [of apples]."

PROBLEMS WITH INTERPLANTING FOR CROSS-POLLINATION

In one planting pattern that has been used, every third tree in every third row is a pollinizer. This places every tree of the main cultivar next to a pollinizer. This plan was satisfactory, from both the pollination and the harvesting standpoint, with standard cultivars and separated trees.

In high-density orchards, the trees within the row frequently form a hedge. If pollinizers are planted within the row, the pickers or picking machines fail to separate the fruit from the two cultivars, which may be necessary for the packaging of uniform fruit. If the pollinizer trees are planted on separate rows, the bees, being inclined to forage only within the row rather than to cross the intervening space between rows, become ineffective.

In an attempt to solve this problem, some growers are seeking a small pyramidal crabapple selection that might serve within the row as a pollinizer, occupying little space, furnishing compatible pollen for the main cultivar, yet producing fruit unlikely to be harvested with that of the main cultivar. This should be a satisfactory solution, if the flowers are equally attractive, so that the bees will forage indiscriminately between flowers.

BEEKEEPER PROBLEMS WITH DWARF TREES

Beekeepers who provide colonies for the pollination of apples claim that the narrow spacing between rows of dwarf apple trees creates a maneuvering problem for large vehicles used in transporting bee colonies. Some beekeepers deliver the colonies to the edge of the orchard; then the grower, using a forklift or other small vehicle, distributes the colonies within the orchard.

Pollinators

The need for an appropriate agent to transfer pollen from one self-incompatible cultivar to another was established by Waite (*1895*, *1899*), although growers had associated insect pollination with increased production for years.

Wind has been suggested and disproved at various times as a possible agent in the transfer of apple pollen (Lewis and Vincent *1909*, Free *1966*). It is no longer considered of significance for this task.

Various wild bees have been mentioned as important pollinators of apples, including the genera *Andrena*, *Bombus*, *Halictus*, and *Osmia* (Brittain *1933*, *1935*; Free *1964*; Glukhov *1955*; Hutson *1926*; Kitamura and Maeta *1969*; Löken *1958*; Phillips *1933*; Horticultural Education Association *1967*). Some wild bees, for example *Osmia*, visit flowers at lower temperatures than do honey bees. At times and in some areas, wild bees are sufficiently abundant to set an apple crop. In general, however, wild bees cannot be depended upon to adequately pollinate the blossoms of a commercial apple orchard in the United States.

Honey bees are easily handled, and they can be concentrated within the orchard to the degree desired. As a result, commercial apple growers have come to depend upon the honey bee as their apple pollinating agent.

The precise method of utilizing honey bees on apples for maximum economic production is less well defined than the appropriate agent. Free and Spencer-Booth (*1963*) showed that bees were consistently fewer between groups of nine colonies in the center of 9-acre blocks but not when they were in groups of four or singly at one colony per acre. The strength, placement, and manipulation of colonies, the effects of competing plants, soil, and weather, and other factors both within the colony and in the environment contribute to the effectiveness of honey bees.

Smith and Bradt (*1967**) mentioned, as had various others before them, that when the honey bee visits an apple blossom for nectar its proboscis is sometimes inserted at the base of the stamens, leaving the anthers and stigma untouched (fig. 39). When this is done, little pollination occurs. By contrast, the larger bumble bee clambers over the anthers and stigma when foraging and cannot help but transfer pollen from flower to flower. Preston (*1949*) found that bees visited one cultivar four times as frequently as another. He associated this difference in visitation to the accessibility of nectar in the flowers. The filaments of the 'Delicious' apple are in a narrow upright cluster, more so, according to Roberts (*1945*), than other cultivars. This permits the bee to alight on the petal, insert its proboscis between the upright filaments, and collect nectar without touching the stigma. For this reason, he recommended that more colonies be used to pollinate 'Delicious' than would be needed on other cultivars. When honey bees are collecting apple pollen, their pollinating efficiency on apples is much greater than when they are collecting nectar.

Beekeepers also mention that dwarf trees have more blooms per acre than trees on standard rootstock; therefore, more bees are needed on the dwarf plantings.

Griggs (*1970**) stated that growers who previously worried about overpollination now favor it, knowing that no adequate set can be otherwise obtained. Then, when there is too much fruit set, they thin with chemical sprays to the desired set of fruit, which prevents alternate bearing.

Viable, compatible pollen has been distributed by hand, airplane, or other mechanical means, even by pollen dispensers attached to the entrance of beehives (Bullock and Snyder *1946*, Corner et al. *1964*, Jaycox *1971*, Snyder *1946*). When pollen is applied by any of these methods, the grower expects the pollinating insect to pick up the pollen and redistribute it to flowers that were not directly applied with the pollen. Since insects are thus required, the grower would generally get more satisfactory pollination if he would utilize more pollinating insects. A study of pollen tube growth in relation to marginal temperatures (which frequently stimulate growers to use artificial means of pollination) would be of interest. If the tube does not grow at such temperatures, the grower would be wasting his investment in these methods.

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FIGURE 39.—Honey bee on apple blossom. *A*, Collecting nectar; *B*, collecting pollen.

Pollination Recommendations and Practices

There are no recommendations for use of wild bees on apples in the United States, but scores of papers have recommended the use of honey bees. These recommendations have changed considerably since Doolittle (*1893*) first suggested that apiaries of 100 colonies should be placed every few miles. The recommended placement of the colonies now is near or distributed within the orchard (fig. 40), and the recommended number of colonies has increased. These have varied from (1) one colony per 2 to 4 acres (Hooper *1913*, Howlett *1926b*, Kelty *1929*, Kurrenoi *1969*, Luce and Morris *1928*, West *1912*); to (2) one colony per acre (Brittain *1933*, Griggs *1953**, Hutson *1926*, Jaycox *1968*, Lundie *1927*, Phillips *1930*, Philp and Vansell *1932*); to (3) two or more colonies per acre (Benton *1896*, Burrell and MacDaniel *1930*, Rom *1970*).

Many of the recommendations are based more on grower experience with use of bees than precise experimental results. The recommendations stress "strong" colonies, but the growers often leave colony strength to the discretion of the beekeeper.

Woodrow (*1933*, *1934*) and Gooderham (*1950*) showed that populous colonies of honey bees were much more effective in apple pollination than weaker ones, and overwintered colonies superior to packages of bees. MacDaniels (*1929*) supported the value of strong colonies, particularly in the ability of such colonies to

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FIGURE 40.—Honey bee colonies in apple orchard.

effectively pollinate an orchard when only a few hours of weather were favorable for bee flight.

Even the appropriate number of bees per blossom has not been established with certainty; however, Palmer-Jones and Clinch (*1968*) indicated that there should be one bee for each 1,000 blossoms. Petkov and Panov (*1967*) reported that the percentage of 'Jonathan' flowers that set increased with bee visits up to six visits per flower. They also associated larger fruit with increased numbers of bee visits.

The effectiveness of the bee is determined by the cross-visits it makes between compatible varieties. If the visits are confined to one variety they are not effective. Repeated cross-pollination of the flowers must occur to produce the optimum set. If a sufficiently large bee population is created, it superimposes over the fixed population a number of wandering bees. These wanderers consist of a few old bees driven on by competition and a larger number of young bees that have not yet become fixed to any particular area of the crop. These wanderers, which are forced to "shop around" from tree to tree to obtain their load of food, are the most valuable to the grower.

When temperatures are marginal for bee flight, bees tend to visit only the blossoms that are near the hive, and also those blossoms on the warm or leeward side of the tree. This preferential visitation can be substantially overcome by the use of strong healthy colonies and by thorough distribution of the colonies in the orchard. If the weather is fair and calm and the temperatures range into the seventies or above, a single group of colonies might adequately pollinate an orchard of many acres in a single day. With cold, cloudy, or windy days, the bees are likely to visit only trees within a few hundred feet of the hives.

The grower should expect the best but prepare for the worst. This includes providing plenty of strong colonies, appropriately distributed for getting ample pollination and a maximum harvest of highest quality fruit even under unfavorable conditions.

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APRICOT

Prunus armenica L., family Rosaceae

Apricots are produced primarily in California. In 1969, 223,000 tons were produced as compared with 3,050 tons in Washington and 4,500 tons in Utah. The estimated value of the total 1969 apricot crop was $33.5 million.

Plant

In appearance, the apricot tree, fruit, and flower seem to be somewhat intermediate between the plum and the peach. The tree may be larger than a plum tree but spreads like the peach. The flowers are usually white like plum flowers, but they are not borne in clusters. The pit is smooth, somewhat like that of the plum but broader, flatter, and more winged, and intermediate in size between that of the peach and plum (fig. 41). The fruit is peach shaped (Cullinan *1937*).

Inflorescence

The white flower is borne either singly or doubly at a node on very short stems. There are about 30 stamens with one pistil, again like both the plum and the peach (fig. 42). The flowers are attractive to bees for both pollen and nectar. The cultivars of apricots were discussed by Coe (*1934*) and Hesse (*1952*).

Pollination Requirements

The literature on pollination of apricots is meager and not in complete agreement. Cook and Green (*1894*) reported that the best set of fruit was obtained from

FIGURE 41.—Harvesting apricots from fruit-laden tree.

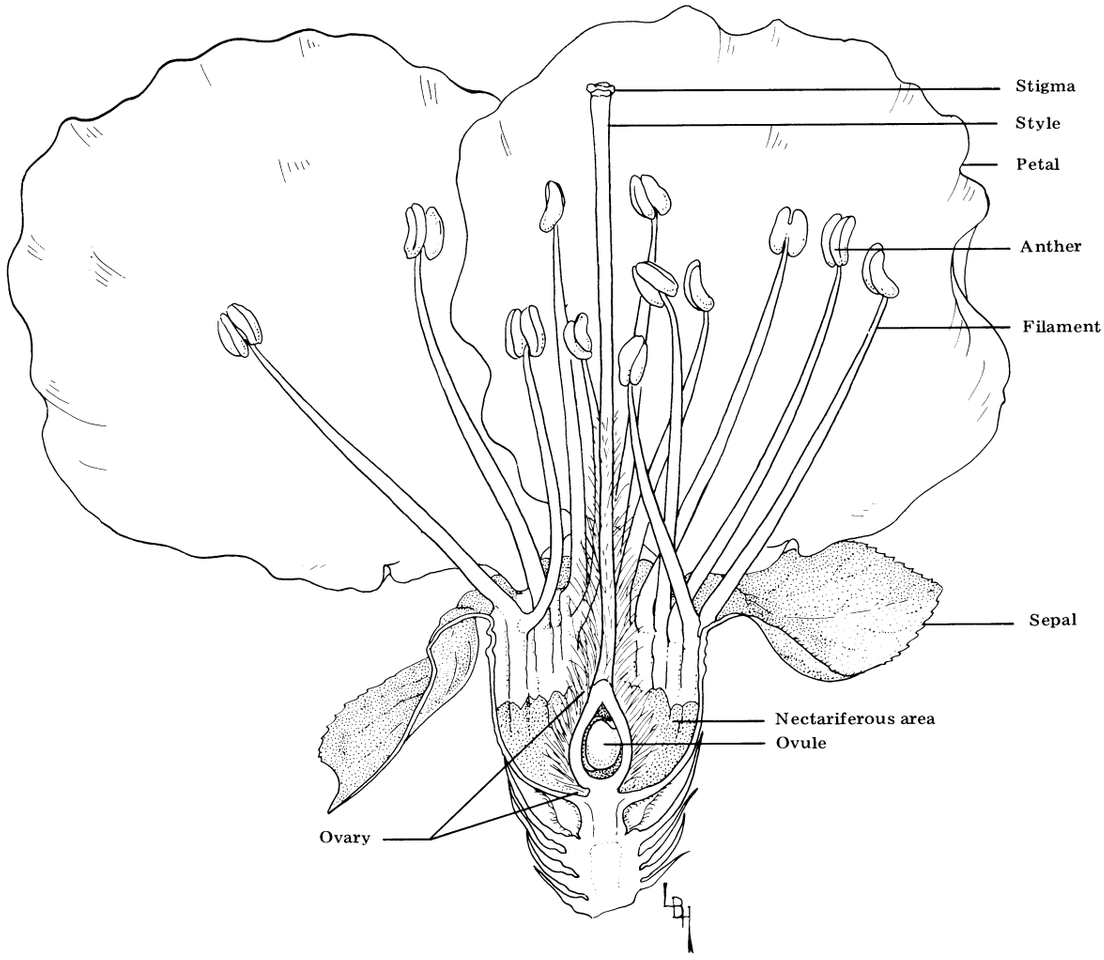

FIGURE 42.—Longitudinal section of 'Royal' apricot flower, ×6.

bagged flowers, with the next best from flowers in bags with honey bees, and the lowest set in the open. They did not comment on the activity of the bees either in the bags or on the open flowers. Cullinan (*1937*) stated that the apricot is self-fruitful. He did not indicate whether he meant the flowers would pollinate themselves or that they would set only if pollinated with their own pollen. Jusubov (*1957*) reported that some cultivars were self-fertile and some were completely self-sterile. Kostina (*1966*) also found variation in degrees of fertility between cultivars. When Schultz (*1948*) bagged flowers on different cultivars, he reported good sets on 'Blenheim', 'Royal', 'Tilton', and 'Wenatchee Moorpark'. Schultz (*1948*) and Griggs (*1970**) identified two self-incompatible cvs., 'Perfection' and 'Riland'. Slate (*1970*) stated that some cultivars are self-unfruitful. Luce and Morris (*1928*) stated that visits to blossoms by insects "seem to increase the set of fruit even in larger blocks of a single variety." Corner et al. (*1964*) reported that half of the Canadian cultivars were self-sterile. Hootman (*1935*) stated ". . . even self-fertile varieties produce better crops when interplanting is practiced."

The rather meager data indicate that some apricot cultivars must be cross-pollinated and other cultivars are benefited by cross-pollination.

Pollinators

There seems to be little question as to which pollination agents are effective on apricots. Jorgensen and Drage (*1953*) stated that wind is not an effective pollinating agent. Instead, they said that the sticky pollen needs the help of insects to carry it from the stamens to the stigma. Murneek (*1937*) also concluded that, whether a cultivar is self-sterile or self-fertile, insects are equally necessary for proper pollination and setting of fruit.

The chief pollinators are bees. Stark (*1944*) stated: "Other insects may be responsible for the pollination of an occasional flower but would not begin to do the job for a commercial crop of fruit."

These observations and statements show that insect pollination is required on self-sterile cultivars and is at least beneficial to the self-fertile cultivars. Honey bees are the primary pollinating agents.

Pollination Recommendations and Practices

The available literature indicates that the apricot, like the peach and nectarine, depends upon pollinating insects to set a commercial crop on all cultivars. A heavy population of bees may be unnecessary, but they should

be distributed throughout the orchard. Thus, since the bees are required but not in large numbers, the recommendation by Corner et al. (*1964*) of a colony of honey bees per acre would seem adequate, providing the colonies were distributed in small groups in the orchard.

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ARROWLEAF CLOVER[12]

Trifolium vesiculosum Savi, family Leguminosae

Arrowleaf clover is a winter annual clover adapted to well-drained soils in most areas of coastal Georgia to Mississippi where it is grown on a limited scale.

Plant

Arrowleaf clover may grow 20 to 28 inches tall with stems to 40 inches long. Although it is later in maturity and produces less during the winter and early spring, it exceeds crimson clover in annual forage yield. There are several cultivars including 'Amclo' (Beaty et al. *1963*), 'Yuchi' (Hoveland *1967*), and 'Meechee' (Knight et al. *1969*). The 'Yuchi' cv. is productive for 2 months longer in the spring than crimson clover, tolerant to drought, and resistant to the alfalfa weevil and the cloverhead weevil (Hoveland et al. *1969*). It is not adapted to alkaline soils.

Inflorescence

The white flower head, which turns to pink and then purple, is conical, 2 inches or more long by 1 ¼ inches across, and consists of 50 to 170 florets. Each floret is capable of producing two to three seeds. The 'Yuchi' cv. flowers from May to July (Hoveland et al. *1969*). Seed yields of 100 to 500 lb/acre have been reported.

Pollination Requirements

Hoveland et al. (*1969*) stated that bees are essential for pollinating arrowleaf clover.

Pollinators

Apparently, honey bees are good pollinators of arrowleaf clover, just as they are for many other clovers.

Pollination Recommendations

According to Hoveland et al. (*1969*), one colony of honey bees is recommended per acre, but no data are given to support this recommendation.

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[12] See "Clovers, General," p. 158.

ARTICHOKE OR GLOBE ARTICHOKE AND CARDOON

Cynara scolymus L.,[13] family Compositae

The artichoke is grown almost entirely in California where there were about 11,000 acres in 1969 with a farm value of about $7 million.

Plant

The artichoke is a herbaceous perennial, the plant being renewed from year to year by lateral offshoots that arise just below the surface of the ground. Each offshoot forms a rosette of leaves, in the center of which the flower stalk later appears. The plant will grow indefinitely, but is usually replaced every 4 to 7 years. It grows to a height of 3 or 4 feet but as much as 6 feet across.

The marketable portion is the 1- to 4-inch immature flower head (fig. 43), including the tender bases and inner portion of the numerous fleshy bracts, the enclosed immature staminal column, and the receptacle or base.

If seed heads are allowed to mature, the flower stalk withers. Propagation is usually vegetative by use of the lateral offshoots or "suckers" (Wellington *1917*, Tavernetti *1947*). Propagation by planting seed has been considered impractical (Wellington *1917*) because of the variation in the offspring. With improved breeding techniques and development of pure lines, however, the use of planting seed is more practical.

Inflorescence

The unremoved buds develop centripetally into purple-centered globular flower heads 6 to 8 inches in diameter, resembling those of a gigantic thistle (fig. 44). The numerous 1- to 2-inch long florets, with their slender corolla tubes, are set closely together on the receptacle. The pistil is elongated and conspicuous and appears to be receptive throughout its upper portion (Jones and Rosa *1928**). The anthers discharge their pollen near the stigmatic area of the style, and, according to Foury (*1967*), the elongating style and stigma take with them a considerable quantity of pollen ready to germinate, but the stigma is not receptive until 5 to 7 days later. By then, the pollen is no longer viable.

Pollination Requirements

The pollen must be transferred from anthers of one floret to the stigma of another. According to Harwood and Markarian (*1968*), pollination is brought about by insects or mechanical agitation of each flower. This indicates that the flower is incapable of self-fertilization, although it is self-compatible. Harwood and Markarian (*1968*) stated that seed production problems in Russia were reported by Panov (*1949*).

[13] Cardoon (*Cynara cardunculus* L.) is similar to artichoke except that it is spiny and more robust. It is cultivated, on a much smaller scale than artichoke, for its edible root and thickened leafstalk. The inflorescence and pollination relationships are similar to artichoke (Bailey *1949**).

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FIGURE 43.— Artichoke at the proper bud-harvesting stage.

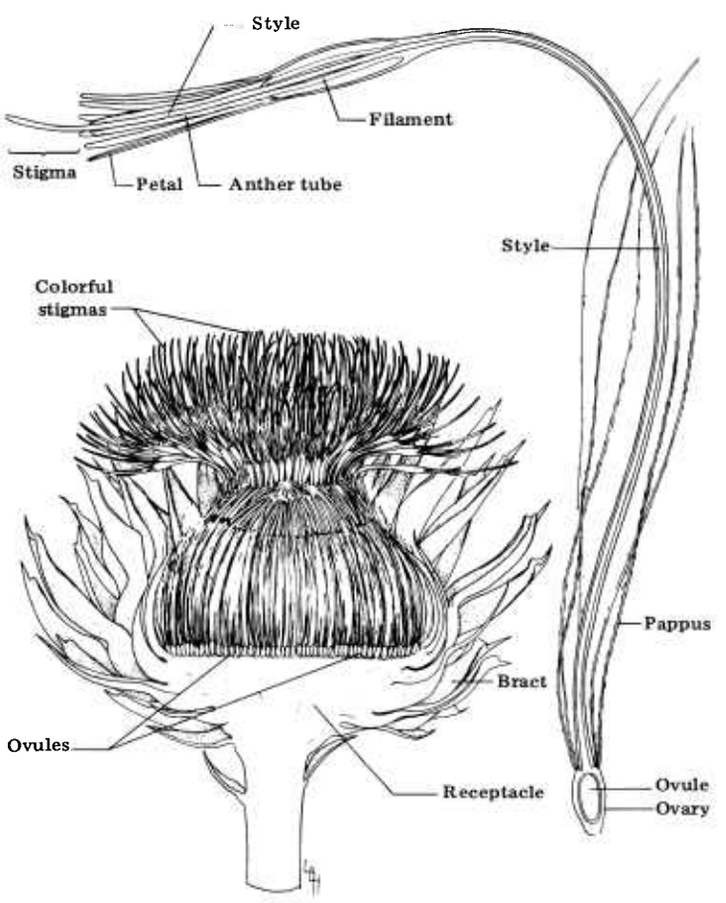

FIGURE 44.—Longitudinal section of artichoke flower, × 1/3, and floret, × 2.

Pollinators

Foury (*1967*) stated that insects are the exclusive pollinators of artichoke. The flowers are freely visited by honey bees and other pollinating insects. Harwood and Markarian (*1968*) stated that seed yields are uncertain, which they associate with vernalization and weak floral development. The relation of increased pollinating insect population to seed production is not mentioned. The fragmentary information indicates that where maximum seed production is desired, the use of an adequate concentration of pollinating insects would be necessary.

Pollination Recommendations and Practices

There have been no recommendations for the use of pollinating insects on artichoke, and there is no indication that growers take steps to use such insects.

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ASPARAGUS

Asparagus officinalis L., family Liliaceae

In 1969, asparagus was grown on 123,830 acres in the United States. Almost half, 44,700 acres, was in California; 22,700, in New Jersey; 17,400, in Washington; and 13,900, in Michigan. The crop was valued at $57 million.

Plant

The underground portion of the perennial, herbaceous asparagus plant is a massive collection of rhizomes and fleshy and fibrous roots. The rhizome sends up a shoot or spear that is harvested when a few inches above ground, otherwise it will continue to develop as an upright flowering stalk or "fern" 4 to 6 feet tall. The stalk develops either female or male flowers, rarely both. If the flower is female, it produces a small round, reddish, 3/8-inch berry that may have a total of two seeds in each of its three locules or six seeds per berry. Frost kills the upright portion of the plant, but the underground portion may live 10 years or more (Hanna *1952*).

Reproduction is by seeds or by rhizomes called "crowns."

Inflorescence

The asparagus inflorescence has been variously referred to as pseudohermaphrodite male and pseudohermaphrodite female (Kerner *1897**, *p. 299*); dioecious, rarely hermaphrodite (Knuth *1909**, *p. 464*); dioecious, sometimes changing to monoecious (Hexamer *1908*); normally dioecious (Jones and Rosa *1928**); and dioecious (Hawthorn and Pollard *1954**). Intergrades from strongly pistillate to strongly staminate have been observed (Jones and Robbins *1928*). In their early stages, the flowers are similar, with both sets of sexual organs present. Later, however, one set usually aborts, leaving a "male" flower with an outer and inner whorl of three stamens each, or a "female" flower with a three-lobed pistil and three-locule ovary, and the other parts rudimentary (fig. 45). Both kinds of flowers have nectaries at the base of the corolla. The individual, whitish-green flowers, from one to four in each axil, are pendulous, bell-shaped, about one-quarter inch long (the male is slightly larger than the female flower) with a characteristic odor (Knuth, *1909**, *p. 464*). They are freely visited by honey bees and other bees (Norton *1913*, Jones and Robbins *1928*, Eckert *1956*, Pellett *1947**, Jones and Rosa *1928**).

The flowers produce nectar and pollen copiously (Norton *1913*), and beekeepers sometimes get good honey crops from asparagus when the plants are allowed to flower (Pellett *1947**).

Pollination Requirements

If asparagus seed is to be produced, the pollen must be transferred from the male or staminate flowers to the female or pistillate ones. This transfer must be made between early morning, when the pollen first becomes available, and about noon, when it begins to dry. There should be at least one male plant within 5 feet of each female (Huyskes *1959*), about one male for each six female plants.

Pollinators

Wind is not a factor in asparagus pollination. Bees and primarily honey bees are responsible for the seed crop

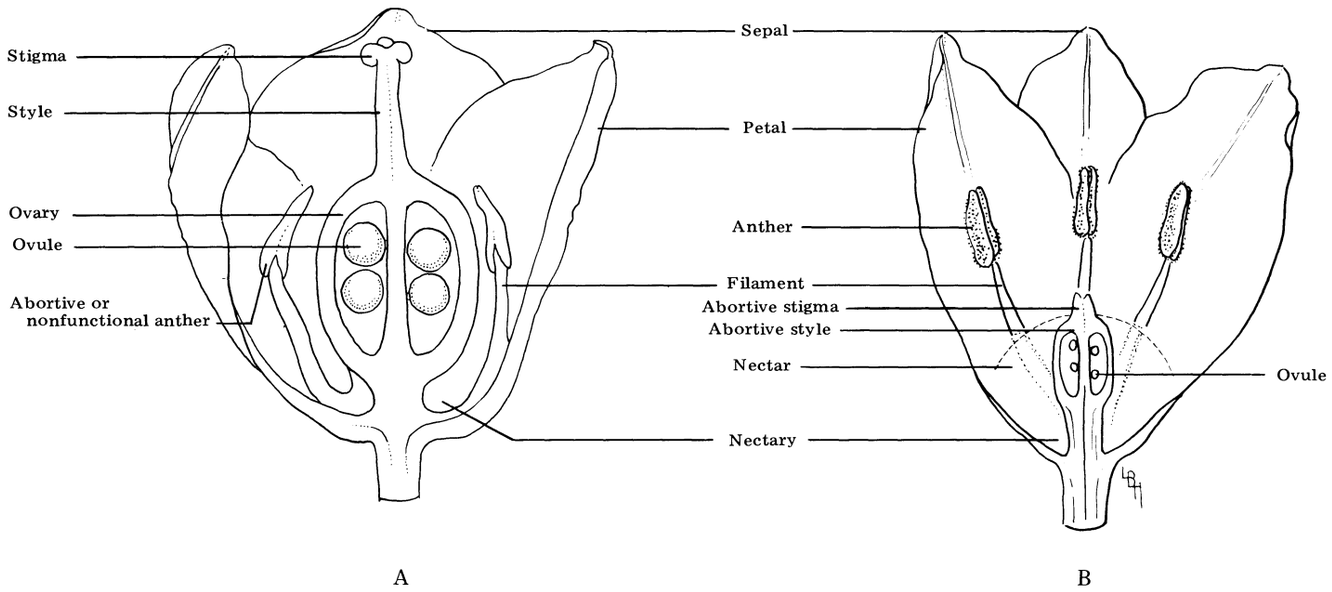

FIGURE 45.—Longitudinal section of asparagus flower, ×17. *A*, Female; *B*, male.

(Norton *1913*, Jones and Robbins *1928*, Jones and Rosa *1928**). Eckert (*1956*) caged one female and two male crowns to exclude all except tiny insects. He harvested only 6.2 g of seed, but an open plant near the cage produced 775 g of seed. He concluded that insect pollination was essential to commercial seed production and that growers should provide one to two colonies per acre to their seed fields for pollination purposes.

Pollination Recommendations and Practices

There have been no specific recommendations for the use of bees in asparagus seed production except the previously mentioned work by Eckert (*1956*). Later, he (*1959**) made a general recommendation of two colonies per acre for vegetable seed production. There are no reports to indicate that growers take steps to provide insect pollination.

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AVOCADO

Persea americana Mill., family Lauraceae

The avocado is grown primarily in California, to a lesser extent in Florida, and on only a few acres in Hawaii, Puerto Rico, and southern Texas. Crop production in 1970 amounted to 83,400 tons valued at $30 million. California produced 64,600 tons and Florida produced 18,800 tons.

On mature trees, about 2 tons of fruit per acre are harvested, although productive orchards will yield 3 to 6 tons. Year-to-year production varies, depending upon many factors, but a year of high production is frequently followed by a year of low production. Weather has a strong impact upon production. Prolonged cool weather, subfreezing weather, low humidity, strong winds at flowering time, or tornadoes can all result in low set of fruit and low production. The most critical effect of temperature occurs during flowering.

Plant

The avocado is a tropical evergreen, upright shrub or tree that grows to 60 feet high, but usually between 15 and 30 feet in height (fig. 46). Its dark green leaves are 4 to 10 inches long and 2 to 3 inches wide. The plant may

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FIGURE 46.—Avocado orchard in bloom.

exhibit two or more growth flushes during the year in contrast to the single growth period of most deciduous plants. It may flower in summer or in winter, and may have a flowering period lasting 6 months. It is less tolerant of cold than lemons or navel oranges and prefers high humidity and calm weather. The fruit, which can remain on the tree for several months after maturity, is a nutritious, fresh food rich in oil and high in calories and vitamin E. A few seedling dooryard trees are estimated to be 100 years old, but commercial trees last about 35 years (Goodall et al. *1970*).

Hundreds of cultivars have been tried in the United States, but about two dozen are of commercial importance (Rowland *1970*).

The cv. 'Fuerte' has for years provided the bulk of the avocado crop (Bergh et al. *1966*, Rock and Platt *1968*, Rowland *1970*). Its fruit weighs 8 to 16 ounces and contains 18 to 28 percent oil. It is cold resistant and ripens over a long period—December to May. By comparison, the Florida cv., 'Pollock', weighs 30 to 50 ounces and contains only 3 to 5 percent oil. The 'Haas' cv. is second in importance to 'Fuerte.' Its fruit weighs only 6 to 12 ounces. Other important California cvs. include the 'Bacon', 'Zutano', 'Rincon', 'Nabal', 'McArthur', 'Anaheim', 'Carlsbad', 'Dickinson', and 'Puebla'. In Florida, the most important cultivars include 'Booth 8', 'Lula', 'Booth 7', 'Waldin', 'Pollock', and 'Hickson' (Rowland *1970*).

Avocados can be grown from seed, but the plants are usually propagated by grafting. They are set in the grove 20 to 40 feet apart depending upon whether the type of growth is spreading or upright. Sometimes they are set at 15 to 20 feet with the alternate plants removed after a few years. Older orchards with spreading trees may have as few as 40 trees per acre. Orchards with upright trees may have 150 trees per acre. About 90 trees per acre is average (Lee and Burns *1967*). Fruit bearing begins at 3 to 6 years of age and may continue for 50 or more years.

The honey bee is attracted to the plant for both the nectar and the pollen, although citrus, mustard, and many other plants that flower at the same time as avocado are much more attractive to bees than are avocado flowers. Pellett (*1926*, *1947**) reported that bees collect only a small amount of avocado honey. Vansell (*1931*) stated that avocados are visited moderately by bees for nectar and pollen. In general, beekeepers consider the plant as a source of buildup for their bees rather than as a source of surplus honey.

Inflorescence

A full-grown avocado tree may bear a million flowers in a season, the flowers occurring in panicles of several dozen to several hundred on the ends of the numerous branches (Robinson and Savage *1926*) (fig. 47).

The relatively inconspicuous blossom is about one-half inch in both width and depth. Three sepals and three similar-appearing green petals make up the perianth. The single pistil has a simple, bulbous, smooth ovary and a somewhat elongated style terminated by a slightly enlarged stigma. There are nine stamens inserted in two whorls. The inner whorl consists of three stamens, with three prominent, orange, nectar-producing staminodes (sterile or aborted stamens) alternating between them. Opposite each stamen and staminode of the inner whorl is one of the six stamens of the outer whorl. There is an orange nectary, slightly smaller than the staminode, on each side of each outer stamen.

The flower opens twice on subsequent days or in two stages (fig. 48). In stage 1, the first day, the petals separate and bend outward. The stigma is whitish, fresh, and receptive to pollination (Hodgson *1930*), but the stamens, bent out at right angles to the pistil, release no pollen. Some nectar appears on the staminodes. After a few hours, the flower closes.

In stage 2, the second day, the flower opens again. This time, nectar on the six true nectaries is secreted more profusely than occurred on the staminodes. The pistil is shriveled and dark and no longer receptive. The stamens are longer and larger, the inner three overtopping the stigma but facing away from it, and the outer stamens at about a 45° angle from the style and facing it, and both sets releasing sticky clumps of pollen. Each stamen has four pollen sacs, the valves of which hinge at the top.

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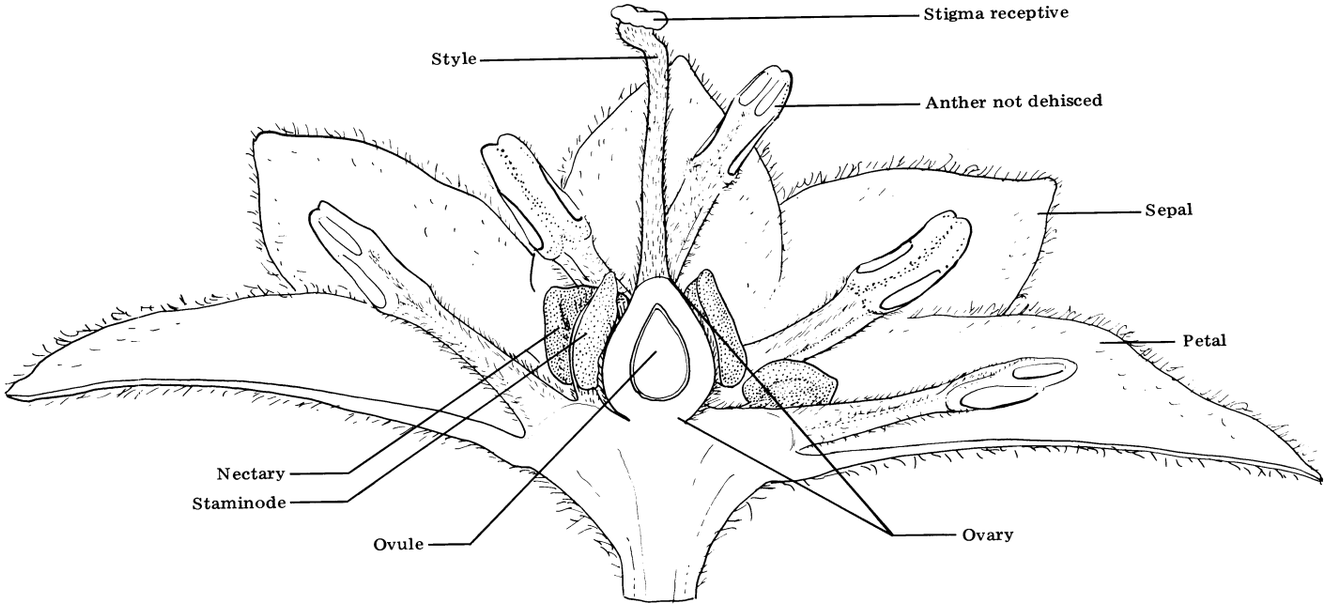
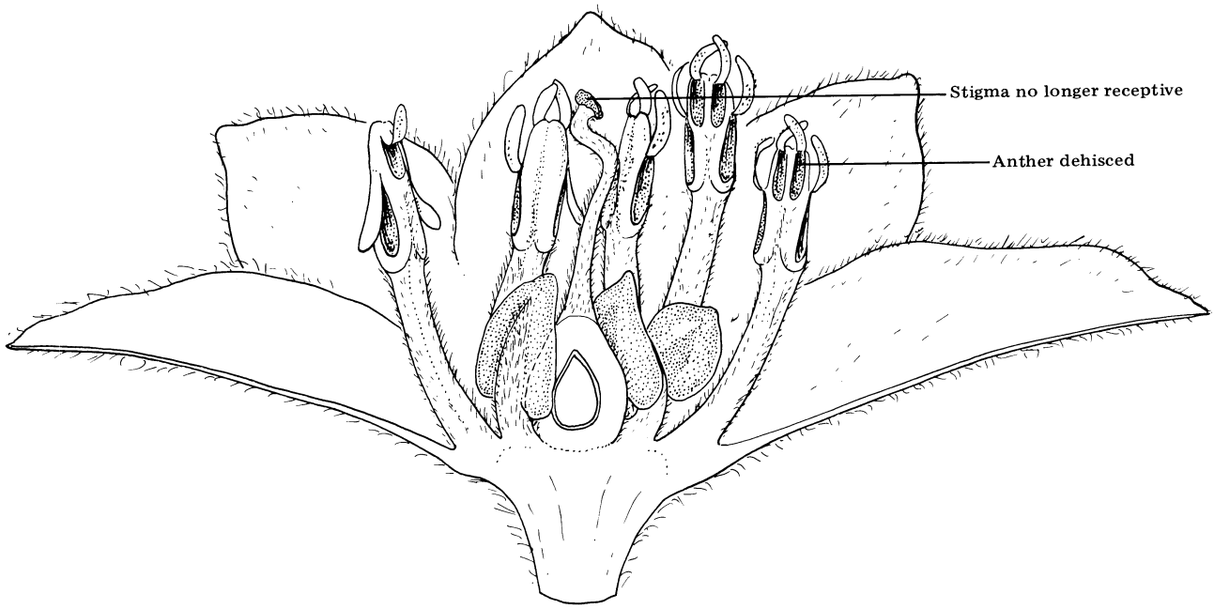
FIGURE 47.—Closeup of avocado tree in full bloom.

When the flower closes the second day, it never reopens. It is, therefore, structurally bisexual but functionally unisexual. This dichogamous condition was first noticed by Nirody (*1922*) and enlarged upon by Stout and Savage (*1925*) and Peterson (*1955a, b, 1956*).

The unusual part about the avocado flower is that in some cultivars stage 1 occurs in the morning of the first day and stage 2 in the afternoon of the second day. These cultivars are referred to as type A. In other cultivars, referred to as type B, stage 1 occurs in the



A



B

FIGURE 48.—Longitudinal section of 'Fuerte' avocado flower, ×18. *A*, Stage 1: stigma receptive, but stamens bent outward and anthers not dehisced; *B*, stage 2, the second day, with stigma no longer receptive, but stamens upright and anthers dehisced.

afternoon, and stage 2 occurs the following morning. If cultivars of both types are interplanted within the same orchard, pollen should always be available when the stigmas are receptive (Stout *1932*, Robinson *1930*, *1933*, Ward *1933*, Bergh and Gustafson *1958*, Bergh and Garber *1964*). At least one cv., 'Collinson', produces no pollen; therefore, it is incapable of setting fruit unless pollen is transferred to it from other cultivars that release pollen when its stigmas are receptive (Anonymous *1930*).

If the temperature is too low, some flowers, for example, those on the 'Fuerte' cv., may fail to open in the female stage, making fruit set impossible. On the other hand, hot weather and low humidity are not conducive to fruit set. Also, too much disturbance of the flowers by wind can cause shedding. A mild climate with calm humid days is best for the flower.

Bergh (*1968*) showed that trees set more fruit when there are flowers of different avocado cultivars nearby. This may not be true for all cultivars or all years, but such effects have been thoroughly demonstrated. For example, he showed that the 'Fuerte' and the 'MacArthur', which are considered to be self-fertile, increased production as much as 50 percent when exposed to pollen of other interplanted cultivars.

Avocado flowering may extend from one to several months depending upon conditions affecting fruit setting. A sufficient supply of pollinating agents will tend to shorten the period of flowering. The number of flowers that may set fruit has been variously estimated by different people. Purseglove (*1968**) stated that only one in 5,000 flowers produces a fruit. Gustafson and Bergh (*1966*) considered that a set of less than 1 percent of the flowers is usually sufficient for a good fruit crop. Chandler (*1958**) stated that flower clusters containing 1,000 or more flowers may be found on a branch less than a foot long in space enough for no more than two fruit. He stated that less than one flower in 500 on a 'Fuerte' tree set fruit. If a tree produces a million flowers and there are 90 trees per acre, 90 million flowers should be produced. If one flower in 5,000 produces a fruit that weighs 12 ounces, the grower should harvest 18,000 fruits, or over 6 tons per acre. That this is seldom done is a good indication that only a small fraction of 1 percent of the flowers produce fruit.

Pollination Requirements

Peterson (*1955b*) showed that the pistillate stage, or stage 1, of the 'Rincon' cv. was open for 3 hours 40 minutes, the maximum time in which pollination of this cultivar could take place. He showed that the flower was incapable of selfing because first flowering began at 7:25 a.m. and ended by 11 a.m.; whereas the second stage of the 2-day-old flower did not begin until 11 a.m., by which time the current-day stigma had withered and was no longer receptive. In the 'Zutano' cv., stage 1 extended from 2:50 p.m. to 6:20 p.m., and stage 2 (the next morning) from 8:40 a.m. until after 11 a.m. Therefore, when the flowers of type A, for example, 'Rincon' cv., are receptive to pollination, the pollen is being shed by flowers of type B, for example, 'Zutano' cv., and when flowers of the 'Rincon' are shedding pollen, flowers of the 'Zutano' are receptive to pollination. This condition is considered by horticulturists to be highly fluid and influenced by the cultivars involved and various environmental conditions.

Peterson (*1955a*) showed that at least the 'Zutano' and the 'Haas' cvs. were capable of setting fruit when isolated from other cultivars if honey bees were present in abundance. He caged four individual trees, two of each cultivar with one tree of each group in a cage with honey bees during the flowering period. When flowering was over, the bees and cages were removed and the fruit counted. The results concerning the treatment and fruit produced were as follows:

Cultivar	*No bees in cage*	*Bees in cage*
'Zutano'	4	120
'Haas'	5	284

Whether the pollen was carried over on the bees from the normal time of anther opening until the time of stigma receptivity, whether the opening phases overlapped, or whether the bees forced open the anthers when the stigma was still receptive was not determined, but in any event the effect of the bees was striking.

The evidence is clear that avocados must be insect-pollinated, and that production is best when varieties are interplanted. Bees usually transfer avocado pollen no greater distance than two avocado rows (Bergh *1961*). The varieties should intermesh in their blooming dates so that pollen is available on one cultivar when the stigmas on another are receptive, and vectors should be available to move the pollen to the receptive stigmas. Maximum set can only be achieved through adequate provision for cross-pollination—the interplanting of appropriate flowering types and the availability of adequate pollinating agents (Bergh *1969*).

Pollinators

Various pollinating agents visit the avocado flowers for nectar and pollen. These include the honey bee, various species of wild bees, wasps, flies, and hummingbirds (Chapman *1964**).

The consensus of various research workers who have studied the flowering and fruiting of the avocado is that only honey bees are sufficiently abundant on the blossoms at all times to set satisfactory crops of fruit (Clark *1923*, *1924*; Clark and Clark *1926*; Boyden *1930*; Traub et al. *1941*; Lemmerts *1942*; Lesley and Bringhurst *1951*; Winslow and Enderud *1955*; Lecomte *1961*; Popenoe *1963*).

Many observers have noted that a bee tends to visit a single tree and thus fails to afford the cross-pollination desired. This can occur when the trees are separated by some distance, for example, when they are small or spaced too far apart (Bergh *1966*). It also occurs when there is an insufficiency of bees in relation to the number of blooms available.

When the ratio of bees per bloom is high, the bees are required to visit many blossoms to obtain a load of food and their efficiency as cross-pollinating agents is increased. Ruehle (*1958*) stated that good crops are set consistently in groves a considerable distance from any bee hives, but that the presence of bees would increase

production. Wolfe et al. (*1942, 1946*) stated that it is quite possible that a hive of bees per acre with sets of five in the middle of each 5-acre tract would materially increase production. Popenoe (*1963*) stated that honey bees are probably necessary for good pollination unless there is an abundance of wild bees in the area.

In an excellent survey of the reasons for low yield of avocados in California, Bergh (*1967*) unequivocally stated: "Practically every avocado fruit set means that a *honey bee* transferred pollen to that flower from some other flower. Gravity or wind may act, but they are so rare they can be ignored by the practical avocado grower." Further on, he stated, "At the present time the California avocado industry is dependent upon the honey bee. The greater the bee population, the more likely the bees are to travel from flower to flower and so make the best of such inter-flower overlap in male and female stages as may be present. This is probably the chief source of avocado set in California."

Pollination Recommendations and Practices

Peterson (*1955a*) stated that there was no evidence that addition of bees to the "natural population of wild bees and other large insects" would increase fruit set. He gave no indication as to the population of wild bees, honey bees, or other large insects present on the trees. Wolfenbarger (*1954*) showed that honey bees were more abundant within 375 feet of a 64-colony apiary than at more remote distances, and more avocados were harvested per tree within 250 feet of the apiary than at a distance of 1,000 feet. Wolfe et al. (*1946*) and Ruehle (*1958*) recommended that one colony of bees per acre be used with five colonies set in the middle of each 5-acre tract. Stout (*1923*) recommended providing "bees in abundance" and control of other plants in the area that might attract the bees. LeComte (*1961*) suggested one colony per acre. Stout (*1933*) went even further by stating that one hive per acre for other fruit is satisfactory, but the flowering habits of the avocado make it desirable to employ more than one hive per acre to supply the honey bees in abundance.

Bergh (*1967*) stated that the average California avocado grower would have better crops if he would use more honey bees. He recommended that growers use two to three strong colonies per acre, the colonies placed in groups no more than one-quarter mile apart with 0.1 mile being preferable.

Bergh (*1967*) made the following recommendations: (1) Place hives or have them placed by the beekeeper after the avocados begin blooming so the bees will "get the avocado habit" right away; (2) place hives in the grove if possible, at least avoid locations where the bees must fly past citrus or other attractive pasturage; (3) control other blooms, such as mustard; (4) avoid use of insecticides during the blooming season, (5) and for cross-pollination, interplant types A and B to increase production 50 to 150 percent.

Thus, after careful study of the research by these scientists, one must conclude that for commercial production of avocados bees are essential, that honey bees are the primary pollinators, and that two to three colonies per acre should be used, the colonies placed within or alongside the groves, and that steps should be taken to insure protection of the bees and discouragement of associated plants attractive to them.

The majority of avocodo growers only passively encourage the keeping of bees in the area of their groves. Few if any actively contract for the bees or pay any type of pollination fee to insure the presence of adequate numbers. Many of them know that beekeepers usually move the colonies to the avocado growing areas to obtain nectar and pollen for buildup of the colonies. The bee population the beekeeper desires on the flowers for colony buildup, however, is far short of the population needed for maximum avocado pollination. Colonies vary enormously in strength and pollination effectiveness. Also, unless contracted for, the colonies may be transported to avocados when forest, range, or desert conditions are unfavorable for beekeeping, but may be placed elsewhere at avocado flowering time if the other flora is more favorable. For dependable pollination and maximum avocado fruit set, the grower should see that his trees are amply supplied with strong colonies of honey bees.

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BALL CLOVER[14]

Trifolium nigrescens Viv., family Leguminosae

Plant

Ball clover is a reseeding, annual, hollow-stem, creeping legume that does not root at the nodes. It reaches 18 to 36 inches high, and resembles Persian clover. It is grown to a minor degree in the Gulf Coast States and has been grown as far north as Maryland and as far inland as Missouri.

Inflorescence

The flowers are smaller than those of white clover, highly fragrant, and highly attractive to bees. The flower heads have an average of 38 florets. Ball clover blooms over a period of 7 to 8 weeks and has a high density of blooms (840/yd^2). Perkins (*1961*) counted 2,285 full to partly open florets per square yard. He also (*1960*) recorded 840 mature flower heads per square yard, compared with 315 white clover and 300 crimson clover heads.

Ball clover is an excellent honey plant, and bees show a strong preference for it over other true clovers. Other bees are also attracted to it.

Pollination Requirements

Weaver and Weihing (*1960*) obtained more than 100 times as much seed from caged plots with bees as from plots caged to exclude bees. They concluded that pollinating insects are necessary for seed production. Perkins (*1961*) stated that "ball clover is self-fertile but, like crimson, pollinators increase seed yields." His observations indicated that because of its attractiveness to honey bees there should be little trouble in getting bees to visit the flowers. The desired visits per unit of flowers for maximum seed production are unknown.

Pollination Recommendations and Practices

There are no recommendations for the use of pollinating insects on ball clover, nor is there an indication that growers take steps to utilize such insect activity to obtain maximum seed production.

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BALSAM-PEAR, BITTER CUCUMBER, OR PERIA

Mormordica charantia L., family Cucurbitaceae

This is a minor crop that occurs in the Old World tropics, but its fruit is much esteemed by Malayans and Chinese. In some areas, it is considered a weed; in others, it is cultivated.

Plant

Balsam-pear is a slender, smooth, high-climbing, leafy annual that lives about 3 months. Its fruit is oblong or oval, narrowed toward both ends, 4 to 8 inches long, orange-yellow, and covered with blunt warts. The fruit bursts upon maturity showing its scarlet aril surrounding its numerous seeds.

Inflorescence

The yellow flowers are solitary in the leaf axil, monoecious, or rarely hermaphrodite. The staminate flowers are 1 to 1½ inches long, the pistillate ones slightly smaller. Flower opening is similar to our cucumber.

Pollination Requirements

The pollen must be transferred from the staminate to the pistillate flowers.

Pollinators

In Kuala Lampur, this plant is pollinated by small bees (Sands *1928*).

Pollination Recommendations and Practices

None.

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[14] See "Clovers, General," p. 158.

BEAN[15]

Phaseolus vulgaris L., family Leguminosae

The common bean includes the edible fresh, and processed, green snap, green-shelled, and dry beans. In 1969, about 1,872,000 acres were devoted to the many types and scores of cultivars of beans, which had a farm value of more than $243 million. Fresh snap beans are primarily produced in Florida and along the eastern seaboard; processed beans, in New York, Oregon, and California, and along the eastern seaboard. Dry beans are produced in two main areas, in the West (Idaho, Colorado, and New Mexico) and in north central U.S. (in and around Michigan).

Plant

The vast majority of *P. vulgaris* cultivars are bush type annuals that reach a height of about 2½ feet and are grown in rows about 3 feet apart. The leaves are dense, heart-shaped, and 3 to 6 inches long. The fruit is a pod, straight or slightly curved, 4 to 8 inches long, with a prominent beak. The seeds may be white to red, brown speckled, or blue-black; globular to oblong; and from ¼ to 1 inch long. Pods may contain from one to a dozen seeds.

Inflorescence

The bean flower is of the typical legume shape; usually whitish, but may be tinged to deep violet, purple, or red; and is ½ to ¾ inch long. The keel is prolonged in a spirally twisted beak. The style follows the spirals of the keel. There are the usual 10 stamens, the upper one free while the other nine are united into a tube enclosing the long ovary and part of the style. The blooms are loosely scattered along a 2- to 3-inch rachis (stem). They usually open between 7 and 8 a.m., and never close. The corolla sheds after a few days. The anthers dehisce the evening of the day before the flower opens (Jones and Rosa *1928**). Weinstein (*1926*) reported that many pollen grains germinate in the anther, but whether such pollen plays a part in fertilization is unknown. Knuth (*1908*, p. 339*) stated that although the anthers surround the style and the pollen is released before the flower opens, the pollen does not get onto the stigma before tripping occurs. When pressure, for example, the weight of a large bee, is applied to the wing petals, the style, with pollen adhering to the brush of hairs on it, projects from the tip of the keel. When pressure is released, the style retracts into the keel, sometimes leaving some pollen exposed.

When the stigma is first exposed, it is free of pollen, and may touch a pollen-coated bee during its brief period of exposure. If this happens, cross-pollination can occur. As the stigma retracts into the keel, it comes in contact with the pollen released by the anthers and selfing may also occur. Bean breeders state that beans excluded from insect visitors set a full complement of pods and seeds. although there seems to be no data on the relative time interval required for isolated plants and for bee-visited plants to accomplish this.

Pollination Requirements

Bean breeders state that they plant different lines and cultivars alongside each other without fear of cross-pollination, indicating very reliable self-pollination. The flowers of most bean cultivars are capable of self-pollination although cross-pollination can and does occur to varying degrees, depending upon the cultivar and the pollinator population (Hawthorn and Pollard *1954**, Mackie and Smith *1935*, Barrons *1939*). Much of the research on bean pollination has been concerned only with the impact of the cross-pollination on varietal seed contamination, not on quantity or quality of fruit set. Rutger and Beckham (*1970*) stated that *P. vulgaris* is primarily a selfing species, but studies of controlled insect pollination are needed. Free (*1966*) concluded that the pollination requirements of different species of beans could not be predicted so they must be studied individually. Thorough studies on the possible benefits of maximum pollinator activity on the various types and cultivars would appear to be highly worthwile.

Darwin (*1857*) noted that the movement of the pistil by the bee would appear to aid in the fertilization of the flower by its own pollen. When he tested this effect, he found that flowers not disturbed in any way set no seed, but flowers manipulated by the wing petals set a great number of seeds. From this, he deduced that "if every bee in Britain were destroyed, we should not again see a pod on our kidney beans." Just what species or cultivar he dealt with is not clear.

Knuth (*1908*, p. 339*) stated that the anthers surround the style and shed their pollen upon it, but the stigma is never dusted until the keel is depressed. Then the style, with its pollen-covered brush, springs out of the opening. If the stigma is touched by the bee, coated with pollen from other plants, before being contacted by its own pollen, cross-pollination results. However, Taylor (*1919*) stated that the flowers are entirely self-fertile as is abundantly proved by their productiveness when grown in greenhouses where bees are not present. Yet, he stated that they can be cross-fertilized by bees, although the percentage of crossing is not great. Mackie and Smith (*1935*) and Barrons (*1939*) indicated that cross-pollination may amount to more than 8 percent. The pollinator population associated with the crossing was never measured.

Jones and Rosa (*1928**) stated that because the stigma and the anthers are enclosed within the keel, insects reach them only with difficulty; however, visitation occurs and crossing results. They considered the amount negligible. They also stated that selfing occurs freely when flowers are enclosed. Kristofferson (*1921*) reported 0 to 1.4 percent crossing, and Emerson (*1904*), 0 to 10 percent crossing. Free (*1966*) working with 'Processor' cv. of *P. vulgaris* concluded that "honey bees are unlikely to have much effect on the yield." His

[15] See also: "Broad Bean and Field Bean," pp. 117; "Lima Bean," p. 244; and "Scarlet Runner Bean," p. 332.

data, however, showed that the plants in the cages with bees produced 21 percent more seed weight, with 6 percent more pod weight than plants from which bees were excluded.

Beans are visited only sparingly by honey bees, and beekeepers do not consider this crop of significance as a source of nectar or pollen. What the visitation or its effect on beans might be under a high concentration of bees is unknown, but the information would be of interest and possibly of considerable value to bean growers.

Pollinators

Mommers (*1971*) studied the pollination of beans grown under glass and concluded that bees do not influence development of *P. vulgaris*.

Diwan and Salvi (*1965*) stated that beans in India are eagerly visited by *Apis dorsata*, *A. florea*, and *Trigona* spp., but the flowers are generally ignored by *A. cerana*. Those who have studied the problem agree that bumble bees and honey bees are the most frequent visitors to bean flowers in the United States. Darwin (*1858*) and Palmer (*1967*) indicated that bees are of benefit to beans, but the kind of bean they referred to is not clear. The data indicate that, if pollinating insects are of benefit, the bumble bee is the best pollinator. Honey bees are apparently next in importance. The latter can be increased in numbers where desired. They visit the blossom for both pollen and nectar. The exact effect on the flower or value to the different cultivars of *P. vulgaris* has not been well established.

Pollination Recommendations and Practices

There are no recommendations on the use of bees as pollinators of beans. In fact bean breeders, knowing the plants will set fruit in greenhouses where bees are excluded, feel that pollinating insects are entirely unnecessary. On the other hand, some growers "like to see bees around," believing that their activity results in fuller pods. For such an important crop, more precise information should be obtained on its pollination requirements, and the possible value of pollinating insects. The effect of saturation pollination, as practiced on other crops, might be effective.

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BEET

Beta vulgaris L., family Chenopodiaceae

The term "beet" is used to include both the garden beet and sugar beet grown in the United States. The former were grown on 17,930 acres in 1969 and were valued at $4.8 million; the latter were grown on about 1.5 million acres with a farm value of $353 million.

Plant

The beet is normally an herbaceous biennial. The first year it develops a rosette of large leaves and a fleshy root. The second year it develops a seed-stem, which draws upon the food stored in the root, and after the seed crop is produced the entire plant dies. The whitish root of the sugar beet (from which sugar is obtained) may be 6 to 8 inches thick and up to 2 feet long. The reddish garden beet root is more or less oval and 2 to 4 inches across. The leaf of the sugar beet rosette may reach 2 feet high by 6 to 8 inches across. The garden beet leaves are much more delicate. Whether the plant is grown for its root as a vegetable or as a source of sugar, the growth characteristics are similar. The second year

the seed-stem appears and a seed crop is obtained. Both types of beets are cultivated in rows.

Inflorescence

The many-branched seed stem, which produces the inflorescence and which may reach 4 to 6 feet, is composed of large paniculate open spikes. The small, greenish, sessile flowers (fig. 49) are usually in clusters of two or three, one of which bears a single, extended bract. The flowers are perfect although they rarely self, because the stigma is not fully mature when the flower opens (Artschwager *1926*). The flower opens in the morning, and the anthers dehisce before noon. The stigmatic lobes open gradually in the afternoon and are not fully open until the second or even the third day. By then, the anthers of the same flower have shriveled and no longer produce pollen. Once open, the stigma may then be receptive for more than 2 weeks. Shaw (*1914*) indicated that a pungent nectar is present and that there is an abundance of pollen. Jones and Rosa (*1928**) also reported that a large amount of pollen is produced, which is carried long distances by wind. Meier and Artschwager (*1938*) reported that beet pollen was collected by airplane 5,000 m above beet fields.

Pollination Requirements

Poole (*1937*) stated that the beet is an example of a wind-pollinated species that is also insect pollinated to some extent. Shaw (*1916*) stated that self-incompatibility seemed to be the general rule in beets. Owens (*1945*) reported that male-sterility existed in sugar beets. Mikitenko (*1959*) trained bees to collect nectar from beets, which resulted in an increase in seed production of 14.3 percent compared with the control. Stewart (*1946*) concluded that wind alone is sufficient to transfer the pollen from anthers to stigmas, but unfortunately the conclusion was based on production of plants in the open compared to plants in cages that excluded larger insects. No attention was paid to "larger insects" on the open plants or to small insects in the cages.

Although beets are basically wind pollinated, some benefit may be derived from insect pollination. The lengthy period that the stigma is receptive to pollen doubtless contributes to the chances that windborne pollen will encounter it in time to effect fertilization and the production of seed.

Pollinators

Wind is doubtless the major pollinating agent of beets. However, Shaw (*1914*) reported that thrips cross-pollinate some flowers. Treherne (*1923*) considered syrphids the most prevalent cross-pollinating insects present on beet flowers, but honey bees, solitary bees, and various Hemiptera were also important. Sharma and Sharma (*1968*) reported that honey bees were "prominent" on sugar beet flowers. Popov (*1952*) (according to Free *1970**) stated that Halictidae, Megachilidae, and Anthophoridae were most abundant on beet flowers. Mikitenko (*1959*) and Archimowitsch (*1949*) reported that bees will visit beets in large numbers for pollen if nothing else is available, and Mikitinko (*1959*) stated that they may increase yield of beet seeds. The finding of numerous honey bees or wild bees on beet flowers in the United States is unlikely if there is other pollen available in the area.

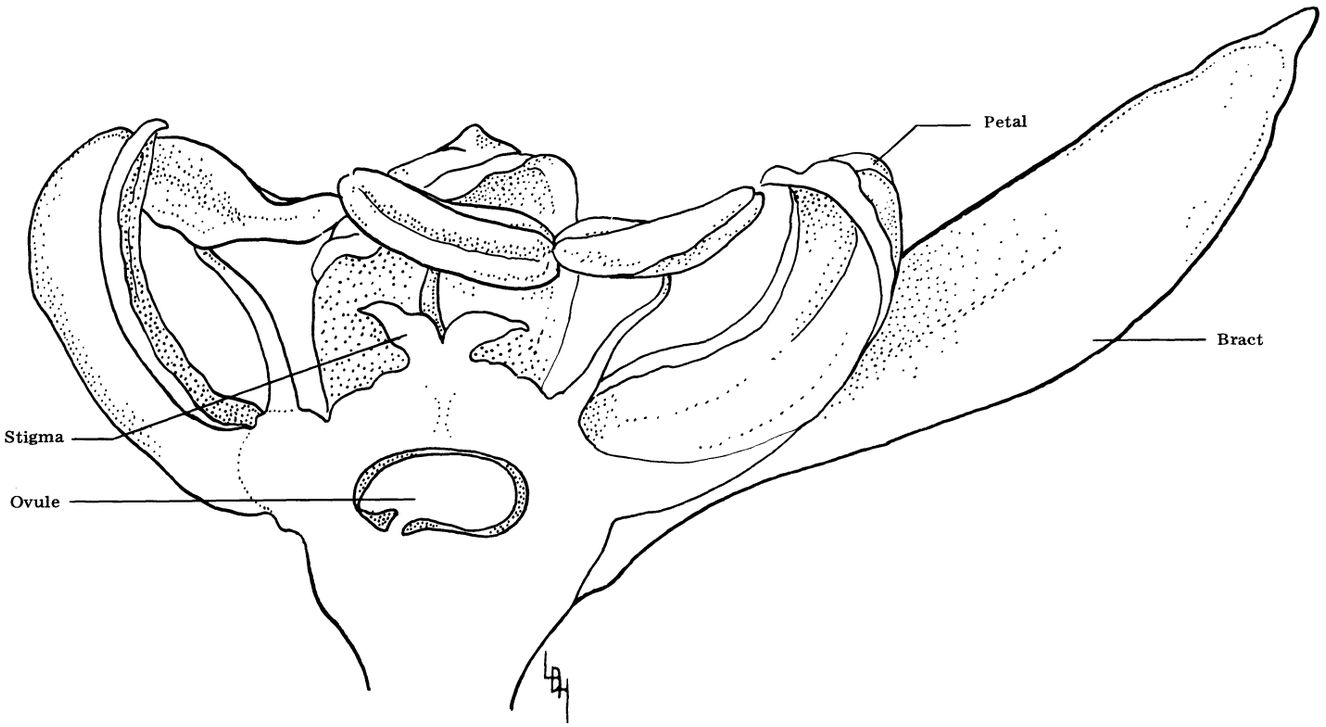

FIGURE 49.—Longitudinal section of beet flower, × 33.

Pollination Recommendations and Practices

Although the evidence indicates that pollinating insects may cause some increase in beet seed yields, their value is given no consideration in the usual recommendations for beet seed production. The evidence indicates that they may be beneficial, and for that reason their activity in flowering beet fields should be encouraged.

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BERSEEM CLOVER[16]

Trifolium alexandrinum L., family Leguminosae

Berseem, or Egyptian clover, is a little-known legume in the United States. It is grown to a small extent in southern California, Arizona, Texas, and in other States near the Gulf of Mexico where freezing rarely occurs (Wheeler and Hill *1957**). Temperatures below 25° F are frequently fatal to berseem plants (Bashaw and Riewe *1955*).

Plant

Berseem is an erect, 18- to 36-inch, nonreseeding, cool-season, hollow-stem, annual clover, recognizable by its typical cloverlike appearance (Kretschmer *1964*). It is a heavy forage producer and grows extremely fast in the mild winter areas. It is grown primarily for its succulent, high-quality forage, which cattle prefer over alfalfa. Hassanein (*1953*) considered berseem to be the most important forage crop in Egypt. It grows from October to May but produces forage principally from December to March. Seed yields vary from 150 to 500 lb/acre (Wheeler and Hill *1957**).

Inflorescence

The round to oblong yellowish heads, similar in size and structure to white clover heads, appear shortly after the first of the year. The florets (fig. 50) form one seed each.

Berseem is highly attractive to bees, which visit it avidly for nectar and pollen. It sets seed abundantly, more than 70 per head, if pollinating insects are present (Narayanan et al. *1961*). Unlike alfalfa, the most vigorous berseem plants set the most seed (Kennedy and Mackie *1925*).

Pollination Requirements

For such a minor crop, the pollination of berseem is quite well established. Chowdhury et al. (*1966*) stated that it is self-compatible, but tripping is essential for seed set. They stated that wind was an important pollinating agent but presented no data to support this statement. Shamel (*1905*) reported that bees are absolutely necessary for pollination. This has been verified with caged and open plots by Hassanein (*1953*), Latif (*1956*), and Narayanan et al. (*1961*). The reports leave little doubt that insect pollination is absolutely necessary for profitable seed production. Narayanan et al. (*1961*) obtained from 19.58 to 70.54 seeds per head of open pollinated berseem plants but only 0.27 to 0.64 seed per head where insects were excluded by 16-mesh wire gauze cages.

Pollinators

Honey bees are the primary pollinators of berseem. They collect both nectar and pollen (Narayanan et al. *1961*).

[16] See "Clovers, General," p. 158.

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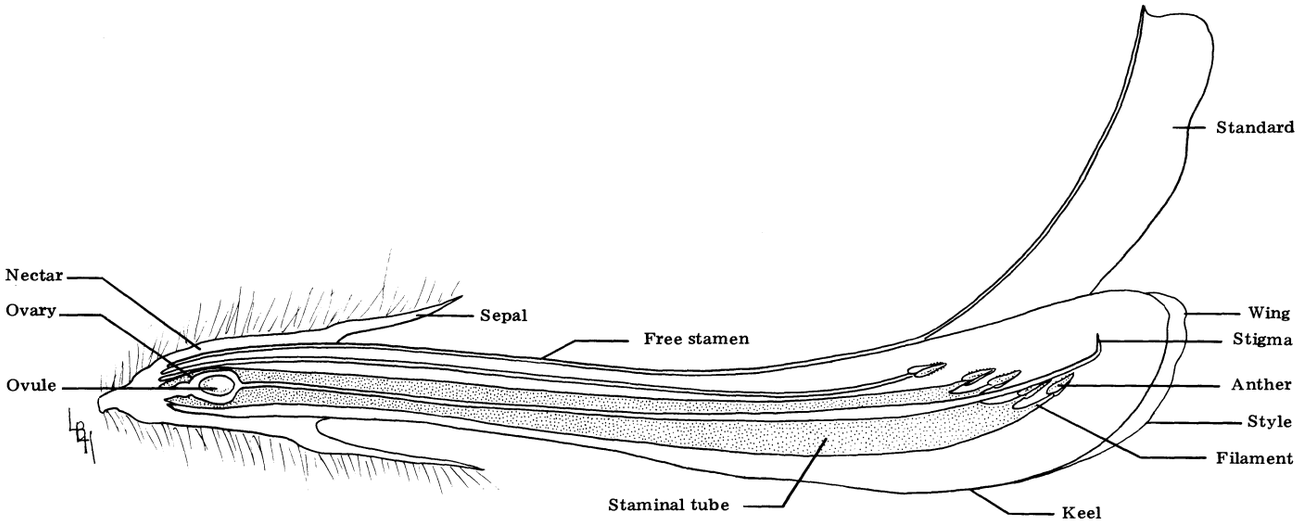

FIGURE 50.—Longitudinal section of berseem clover flower. ×12.

Pollination Recommendations and Practices

There are no recommendations on the use of insect pollinators on berseem. Considering its flowering characteristics, the absolute necessity of bees in its pollination, and the time of year it blooms, the equivalent of two to four bees per square yard should be sufficient to set a maximum crop of seed.

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BLACKBERRY

Rubus spp., family Rosaceae

Blackberries grow wild throughout the United States, but commercial production is limited largely to Oregon and Washington with small acreages in California, Michigan, New York, New Jersey, Florida, Texas, and some other southeastern States. This acreage includes erect, semierect, semitrailing, and trailing blackberries, as well as boysenberries, loganberries, and youngberries. Production has decreased considerably from the 43,684 acres in 1959 (Darrow *1967*), probably because of increased harvesting costs. In 1969, production from 6,850 acres in Washington and Oregon amounted to 41.7 million pounds valued at $6.9 million (USDA *1971*).

Plant

Cultivated and wild blackberries comprise a large but inexact number of species and hybrids. Bailey (*1949**) stated that more than 400 species are known in North America. He listed eight species grown for ground cover or ornament and 31 species grown for the fruits. Many of the cultivated blackberries are hybrids.

Instead of grouping the plants according to species, most authorities group them according to growth habits. The prostrate or trailing blackberry, which may spread over brush or small shrubs in the wild state, is

sometimes called "dewberry." The erect untrained blackberry may reach a height of 10 feet.

The loganberry was considered to be a cross between the 'Antwerp' red raspberry and the 'Aughinbaugh' blackberry (Lewis and Cole *1909*, Aspinwall *1911*, and Logan *1955*). Darrow at first (*1918*, *1937*) considered it a kind of the Pacific Coast blackberry (*R. ursinus* Cham. and Schlecht.), but later he (*1967*) agreed that it was indeed the blackberry-raspberry cross.

The youngberry or Young dewberry is generally considered to be a cross between the 'Mammoth' and 'Mays' (syn. 'Austin Mays').

Bailey (*1949**) placed the loganberry and boysenberry under the subspecies *loganobaccus* Bailey of *R. ursinus* and stated that the youngberry is "probably a derivative of *R. ursinus*, perhaps of hybrid origin." Hence, boysenberry, loganberry, youngberry, and "dewberry" are grouped herein as blackberries.

Most blackberries have a biennial "cane" or stem rising from a perennial root system. The cane usually produces its growth the first year; the second year it bears fruit and dies back to the crown. A few thornless cultivars have been developed, but most cultivars bear stiff thorns (correctly prickles) to one-quarter inch along the branch and smaller ones on the stems and leaves. The leaves are usually deciduous, but on some cultivars they are persistent. The fruit clusters of the trailing blackberries are usually less numerous, more open, and ripen earlier than those on the erect blackberries.

The fruit consists of many one-seeded fleshy drupelets or carpels on the receptacle. In the blackberry, the receptacle, unlike that in the raspberry, is retained in the harvested fruit making it more firm than the raspberry.

Blackberry plants are usually set in rows (fig. 51). To facilitate harvest of the fruit, the vines are usually trained to a trellis or tied alongside uprights.

Inflorescence

The erect blackberry inflorescence is usually a cluster of 10 to 20 flowers, whereas the trailing blackberry is more likely to have 1 to 10 flowers in the cluster. Intercrossing has produced all variations of this cluster size in different types and cultivars. Also, there are many more flowers per square yard of erect than of trailing blackberries. Otherwise, the whitish flowers, 1 inch or more in diameter, are similar in size and shape. There are usually four white petals and 50 to 100 stamens clustered around and overshadowing about the same number of pistils (fig. 52). Nectar is secreted in a shallow nectar cup at the base of flower. Secretion begins just before the petals start to unfold and continues until petal fall (Percifal *1946*).

Blackberry nectar and pollen are both quite attractive to pollinating insects, and the plants are a source of surplus honey for bees in some of the Southern and Pacific States. Pellett (*1947**) stated that the honey was light-amber in color, had a good flavor, and was very thick and slow to granulate. Gates (*1917*) indicated that some forms of blackberries are more readily visited by bees than others.

Pollination Requirements

Some of the hybrids of blackberries are self-sterile, but many of the species are partially self-fertile (Darrow *1924*, *1942*, Darrow and Waldo *1948*). Darrow (*1967*) stated that self-sterility is very widespread in wild blackberries, and he gave credit to bees for performing the necessary cross-pollination. Hedrick (*1938**) called attention to the sterility in blackberries and noted that the pollen is frequently shrunken or otherwise malformed. Detjen (*1916*) also mentioned the variations in fertility of different blackberry groups and gave pollinating insects credit for transferring the pollen. Hartman (*1923*) considered most species self-fertile, but not all. He noted that insufficient pollination not only reduced the number of flowers that set but also resulted in imperfect fruit. Auchter and Knapp (*1937**) mentioned that most cultivars are self-fruitful but some are self-unfruitful. Hooper (*1912*) pointed out that logan-

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FIGURE 51.—'Lucretia' blackberries trained upright on individual posts.

berries need insect pollination, and he recommended the keeping of hive bees for pollination in suburban gardens and fruit farms and where large areas of the same kind of fruits are grown. Shoemaker (*1961*) reported the commercial blackberry cv., 'Flordagrand', was self-unfruitful and that wild blackberries were suitable pollinators.

Whether the self-fertile cultivars are capable of pollinating themselves in the absence of pollinating insects has not been determined on all cultivars of blackberries. The structure of the blossom strongly indicates that insects are necessary to transfer the pollen from the appropriate anthers to all of the receptive stigmas if maximum production of highest quality

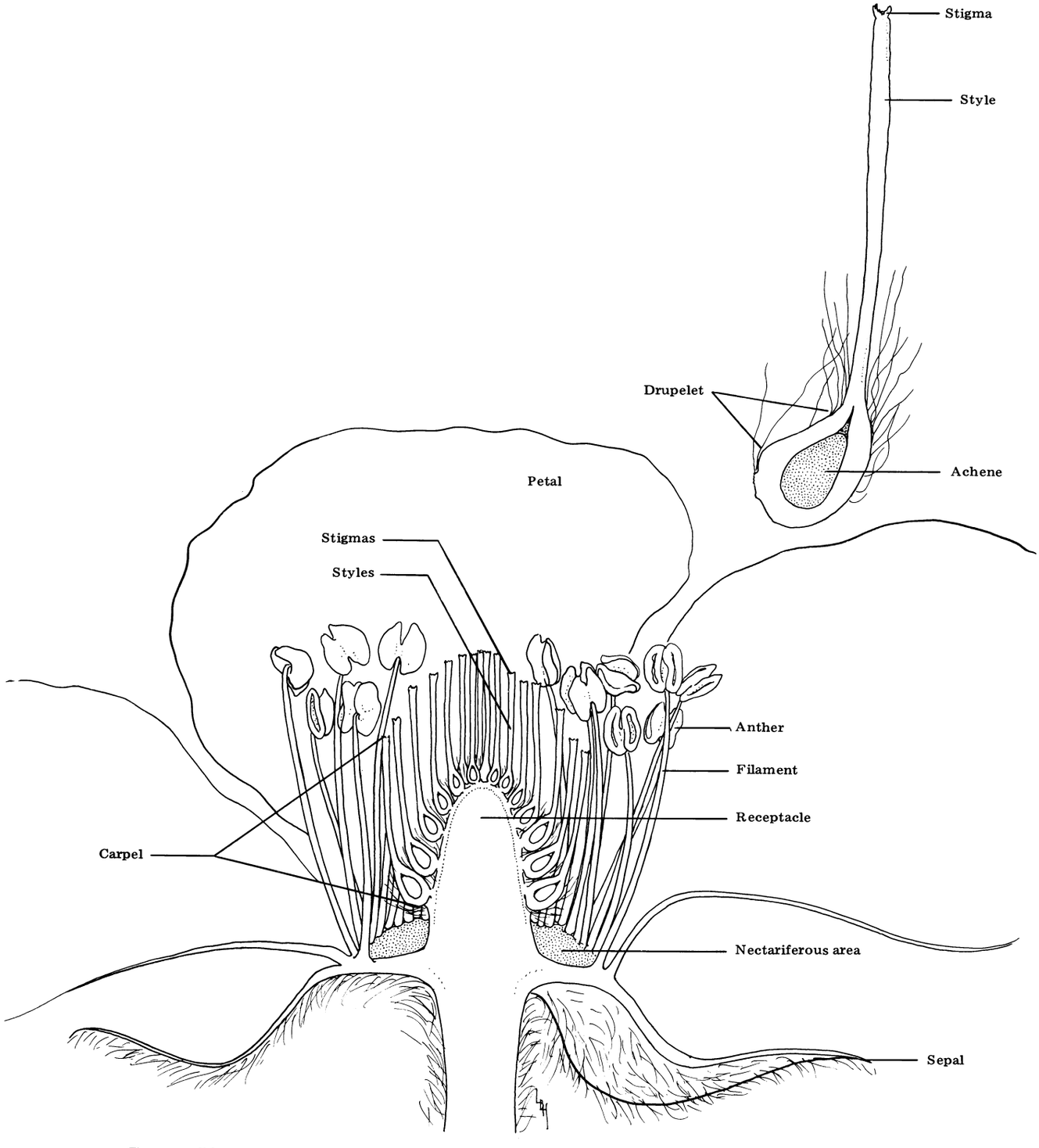

FIGURE 52.—Longitudinal section of 'Olallie' blackberry flower, × 6, and individual floret, enlarged.

berries is obtained. Hartman (*1923*) noted that the 'Mammoth' and 'Cory Thornless' cvs. of blackberries in Oregon were "more or less self-sterile and require cross-pollination. Insufficient cross-pollination of these not only reduces the total set but results in imperfect fruit."

Shoemaker and Westgate (*1966*) stated that the 'Flordagrand' blackberry is self-sterile but can be pollinated with pollen from the native trailing type of blackberries, but the native plants must be growing "in quantity near the cultivated plants and overlapping must occur in bloom." The 'Oklawaha' cv. was developed precisely to provide a pollen source for 'Flordagrand' and to yield a marketable crop as well. The 'Oklawaha' sets no fruit with its own pollen but produces abundantly if cross-pollinated (Shoemaker and Westgate *1966*).

Yields largely depend upon the degree of insect cross-pollination. Shoemaker and Davis (*1966*) stated that if a perfectly formed berry is to be obtained most or all of the pistils of the blossom must be effectively pollinated by some "mass" method such as the visits of honey bees. They recommended that colonies of honey bees be placed in or near the plantings just before bloom. They also recommended the planting of alternate rows of 'Flordagrand' and 'Oklawaha' to provide the supply of pollen for crossing. They concluded that in all of the trailing cultivars the yields depended on the degree of effective cross-pollination. Sherman and Westgate (*1968*) pointed out that differences in size of berries may be due to imperfect pollination.

The effective time period of pollen transfer within an individual flower, as well as between flowers of blackberries has not been determined. Most pollination probably takes place the first day the flower is open with the remainder occurring the second day, although flowers will stay receptive for 3 days in a greenhouse at 75° F. Petals will hang on for 4 days if the weather is cool, but they usually drop off the second or third day.

The USDA (*1967*) recommended the removal of all wild blackberry and raspberry plants in the vicinity of blackberry fields. From the standpoint of disease and harmful insect control, this is good advice but from the standpoint of cross-pollination and the production of the largest quantity of highest quality berries, it may be questionable if only one cultivar is in the field.

With recent development of mechanical harvesting, the need for firmer berries has been emphasized. Such berries are more likely to be obtained if they are adequately pollinated.

Pollinators

There is little information on the pollinating insects of blackberries. Honey bees eagerly visit the blossoms if the weather is favorable and are credited with much of the cross-pollination that occurs. Bumble bees and various other wild bees also visit the flowers, but where the berries are grown commercially, there are not likely to be enough of these insects in the wild to provide the mass pollination desired for maximum crop production. Honey bee colonies can be moved to such fields as desired.

Pollination Recommendations and Practices

Hooper (*1913*) and Shoemaker and Davis (*1966*) recommended the placement of colonies of honey bees in or near blackberry plantings, and the evidence is strong that commercial production would be enhanced by supplying adequate pollinating agents. Even self-fertile cultivars can benefit by having bees transfer pollen to every receptive stigma of the blossom at the earliest possible moment. An adequate supply of pollinating insects should be highly remunerative both in volume and quality of berries produced.

The number of bee visitations per number of flowers that would provide this service is unknown, but considering the time a bee spends in a flower and the number of stigmas that need to be pollinated, the recommendation of one honey bee for each 100 (muskmelon) flowers (McGregor et al. *1965*) might be a conservative recommendation on berries. Such a rate of bee visitation might require the placement of several strong healthy colonies of honey bees per acre in the field at flowering time.

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BLACK MEDIC OR YELLOW TREFOIL

Medicago lupulina L., family Leguminosae

Black medic or yellow trefoil, a near relative of alfalfa and burclover, is widely distributed in the South but is seldom abundant in one location.

Plant

The annual or biennial plant that reseeds readily has slender, finely pubescent, procumbent stems from a few inches to two feet long, with hairy leaflets ¼ to ¾ inch long. It is an introduced yellow-flowered European legume that has escaped in waste places throughout the country (Graham *1941**, Martin and Leonard *1949**).

Inflorescence

Black medic bears small, bright-yellow flowers in dense heads, ½ inch or less in length. The mechanism of the small (2 mm) flower is similar to that of alfalfa. An insect visit causes the sexual column to trip, but, unlike the alfalfa sexual column, it does not return to its original position in the keel when the pressure is removed.

Pollination Requirements

Bohart (*1960**) stated that black medic is self-fertile and self-pollinating and thus has no need for pollinating insects.

Knuth (*1908*, p. 279–280*) also stated that automatic self-pollination takes place readily, but that it is far less productive than cross-pollination. Apparently, like ball and crimson clover, black medic will set seed in selfed flowers, but more seeds will set if crossing occurs. Todd (*1957**) listed black medic as a crop whose seed production is increased by bees.

Hartwig (*1953*) stated that florets were more likely to be fertilized if visited by insects.

Pollinators

Honey bees are the chief visitors to black medic flowers. They visit a few flowers on an inflorescence then move to other inflorescences, thereby increasing possible crossing. Many other bees are of some value as pollinators.

Pollination Recommendations and Practices

No recommendations have been made for use of insect pollinators on black medic; however, the meager data available indicate that many bees are needed for maximum seed production.

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BLACK PEPPER AND WHITE PEPPER[17]

Piper nigrum L., family Piperaceae

The plant that yields ground pepper is not grown commercially in the United States, but it is an important one worldwide. In terms of usage and value, pepper is the most important of all spices in world trade. The United States imports 35 to 40 million pounds annually. India and Indonesia account for about two-thirds of the

[17] See "Pepper, Green," p. 292.

world production. Some pepper is produced in Brazil (Kevorkian *1964*). It has been grown experimentally under glass in Maryland (Creech *1955*).

Plant

Piper nigrum is a strong, somewhat woody, perennial evergreen vine that may climb to 30 feet in its preferred hot, wet, nonseasonal climates. Under cultivation, growth is usually held to 10 to 15 feet. The plant has oval, dark-green leaves, as much as 7 by 4 inches in size, that arise at the nodes. Hardwood posts or trees provide columnar support for the vines that may reach 5 feet in width (Purseglove *1968**). There are many cultivars.

The fruit, called a corn, is 1/4 to 1/5 inch in diameter and is picked just before it ripens. The corns are separated from the stems, then dried in a manner similar to coffee drying. Within 2 to 3 days, the pericarp turns black. If the corns are ground while in the pericarp, the product is black pepper. If the black pericarp is removed before the fruit is ground, the product is white pepper (Blacklock *1954*, Gentry *1955*).

Inflorescence

The flowers are borne on the vine, at the node opposite the leaves, in catkins or spikes. A spike may have 50 to 150 rather inconspicuous yellowish green apetalous florets only 1 to 3 mm in diameter. The florets are usually hermaphrodite but may be unisexual, with staminate and pistillate flowers on the same plant or on separate plants. Frequently, the florets are unisexual near the base of the spike and hermaphrodite toward the tip. Flowering begins at the base and continues to the tip over a 7- to 8-day period (Ridley *1912** Gentry *1955*).

The hermaphrodite floret is protogynous, the two to three stamens appearing at the base of the ovary only after the star-shaped stigma with its three to five rays has matured (Cobley *1956**). The stigma may be receptive for 10 days with peak receptivity at 3 to 5 days (Purseglove *1968**). The pollen is then released in gelatinous masses to pollinate receptive stigmas of other flowers. The unilocular ovary produces only one seed. The stigmatic rays are coated with long tubular hairy growths with their tips somewhat bulbous. The feltlike surface acts as a medium for trapping the pollen grains (Anadan *1924*).

Pollination Requirements

Because of the protogynous nature of *Piper nigrum*, self-pollination of the floret is impossible. Cobley (*1956**) stated that cross-fertilization was the rule, but he apparently referred to transfer of pollen between flowers on a plant rather than between plants. Martin and Gregory (*1962*) concluded that self-pollination between flowers on a plant was undoubtedly the rule. Free (*1970**) stated that the stigma may be receptive for 10 days but that it is at its peak of receptivity after 3 to 4 days.

Pollinators

Anadan (*1924*) and Menon (*1949*) considered rain as the pollinating agent of *Piper nigrum*. This was supported by the observation by Anadan (*1924*) that a vine protected from rain failed to set fruit. Martin and Gregory (*1962*) stated that wind pollination, with or without rain, was not very effective. They believed that self-pollination was undoubtedly the rule, but they did not explain how the pollen might have been transferred from the anthers of one flower to receptive stigmas of another. Cobley (*1956**) attributed the transfer of pollen to wind, rain, and ants. Free (*1970**) stated that pollination was the result of gravity possibly aided by rain or wind. Purseglove (*1968**) stated that although the pollen was in gelatinous masses, a light rain would break up these masses, then the pollen grains would be dispersed and finally caught in the papillae of the stigma. He concluded that the degree to which insects assist in pollination is not known. Martin and Gregory (*1962*) stated that no insects, large or small, visited the spikes. Anadan (*1924*), as previously mentioned, stated that a vine protected from rain failed to set, even with bees. He did not elaborate on the kind or activity of the bees. No other observer mentioned visitation of the flowers by bees. It is not clear, therefore, the degree to which insects pollinate *Piper nigrum*.

Pollination Recommendations and Practices

None.

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BLUEBERRY

Vaccinium spp., family Ericaceae

The blueberry industry in the United States is concerned primarily with three distinct types of blueberries: highbush, lowbush, and rabbiteye. In the lowbush type, the two most common species are *V. angustifolium* Ait. and *V. myrtilloides* Michx. The highbush type developed mainly from *V. australe* Small and *V. corymbosum* L. (Goheen *1953*). The rabbiteye type consists of one species, *V. ashei* Reade. Some hybrids, relatively unimportant in the United States, have been considered as a halfhigh group. Darrow (*1966*) stated that there were millions of clones—covering tens of thousands of acres from New Hampshire to West Virginia—of segregates of highbush-lowbush hybrids that are called lowbush. Numerous other species of minor importance are mentioned in the excellent book on blueberries by Eck and Childers (*1966*).

The 1964 United States Census of Agriculture reported 43,114 acres of blueberries in 20 States, with production of 46 million quarts of berries valued at $15 million. However, Darrow and Moore (*1962*) stated: "Although the blueberry crop from all cultivated varieties had a value of more than $13 million in 1960, the total value of the industry in the United States is much greater, as wild blueberries are harvested in several widely separated areas." Further on they continued: "About 150,000 acres of native blueberries in Maine are given some care." Eck and Childers (*1966, p. 5*) stated: "At present more than 100,000 acres of the lowbush species are under cultivation in the United States. Two-thirds of this acreage is harvested annually, and one-third is burned over each year." These statements would indicate that the 1964 United States Census of Agriculture data dealt only with tilled acreages, whereas the wild or burned over acreages were in addition.

This would indicate that about 200,000 acres may be concerned to some degree with blueberry production in the United States.

The bulk of the lowbush berry crop comes from plants to which some attention is given, such as burning over the area every 2 to 3 years, treating with insecticides and herbicides, fertilizing, and providing insect pollination. In recent years, more attention has been given to the care and harvesting of the lowbush type than formerly. By contrast, the bulk of the highbush and rabbiteye blueberry crop comes from plants that receive intensive cultivation.

Plant

Lowbush blueberries may be less than a foot tall, but highbush types may grow to 30 feet. With one exception, the plant is grown only for its fruit, the delicious blue-black berry, ¼ to 1 inch in diameter. The evergreen blueberry (*V. ovatum* Pursh), which grows along the Pacific coast, not only yields berries, but florists also use its branches of green leaves as ornamentals.

The lowbush blueberry plant develops from an individual fertile seed but spreads as a single clone by underground growth to form a colony as much as 40 feet across. Most seeds develop as a result of cross-fertilization, giving rise to thousands of different kinds in the field. The highbush and rabbiteye develop as individual isolated plants with one to several stems and an oval canopy of growth above.

Before the arrival of the white man on this continent, the Indians intermittently burned over the lowbush blueberry growth, their only effort at cultivation of this plant. Burning prevents overgrowth of other plants and promotes new growth by the lowbush blueberry. Unfortunately, it also destroys many pollinating insects.

Starting in 1906, highbush blueberry selections were taken from the wild and crossed and back-crossed to form improved cultivars and an intensively cultivated crop (Coville *1937*). The rabbiteye blueberry, which is a southern type, has also recently been included in the intensively cultivated crops.

The fruit of a few wild highbush species, for example, *V. alto-montanum* Ashe and *V. membranaceum* Dougl., are handpicked. The berries from the lowbush plants are harvested with hand rakes. Berries from the cultivated highbush and rabbiteye types are handpicked or mechanically harvested.

Inflorescence

The blueberry inflorescence is usually a raceme on the last several inches of a branch (fig. 53). In the

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FIGURE 53.—Branch of highbush blueberry in flower.

mountain blueberry (*V. membranaceum* Dougl.), the flowers are borne singly or in pairs on the leaf axis.

The white or pink petals of the flower are united to form a tubular or bell-shaped corolla, ¼ to ½ inch long, that hangs open end downward before pollination (fig. 54). After the flower is pollinated, it points skyward (Oldershaw *1970*). Eight to ten stamens are inserted at the base of the corolla, around a much longer style that is receptive only on its tip. Pollen is released through pores on the end of the anther, during the period of stigma receptivity. Nectar is produced in the base of the corolla; after fertilization, the ovary matures into the

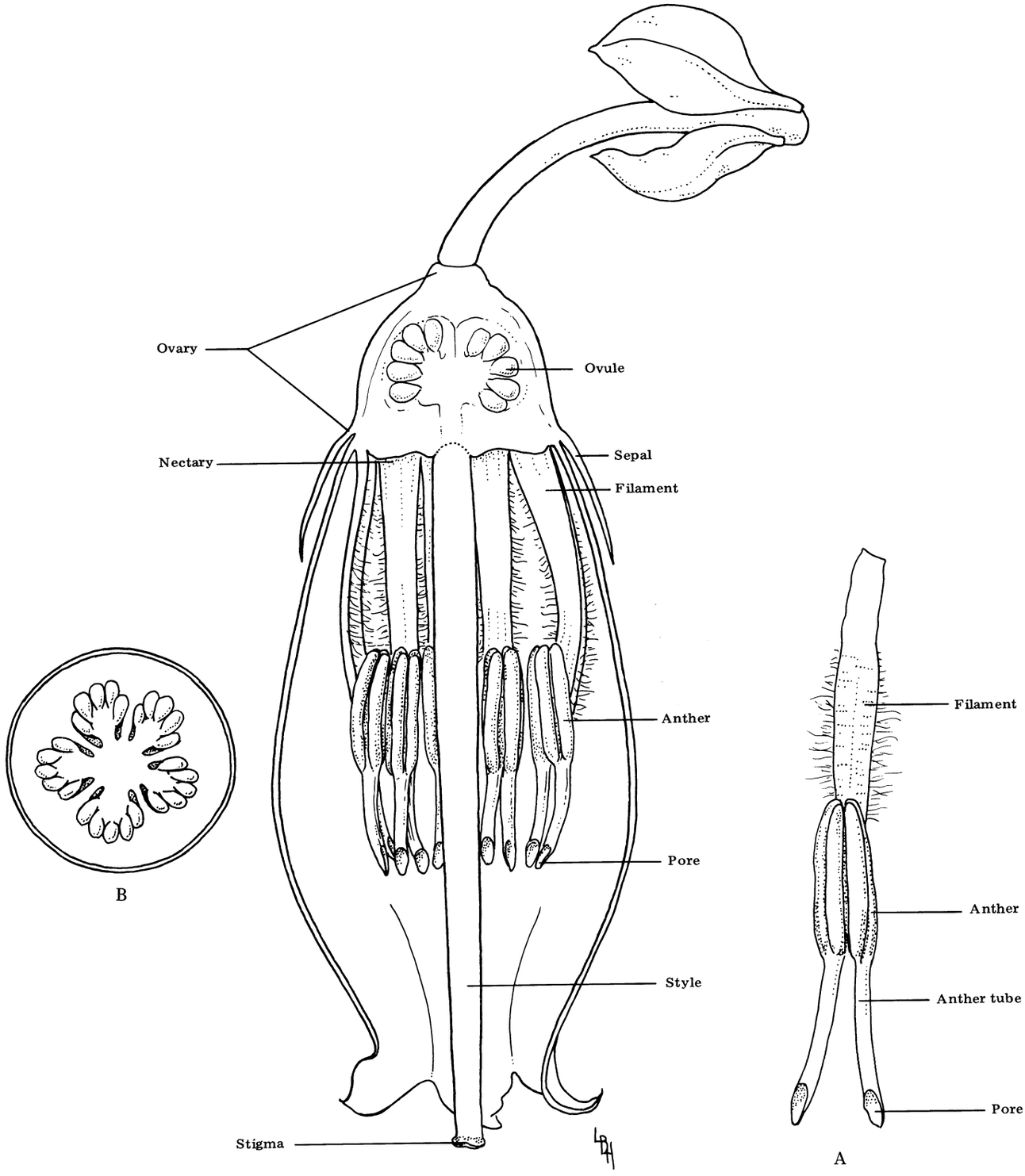

FIGURE 54.—Longitudinal section of 'Tifblue' rabbiteye blueberry, ×12. *A*, Individual anther, ×17; *B*, cross-section of ovary, ×12.

many-seeded blueblack berry that ripens 2 to 3 months after flowering. The berry may contain as many as 65 extremely small seed, which do not interfere with the fruit's palatability. In fact, Barker and Collins (*1965*) stimulated seedless fruit development with gibberellic acid, but the product was a bland fruit with only half of the expected amount of sugars present. Berry size increases with seed number (Eaton *1967*, Brewer and Dobson *1969a, b*).

Beekeepers sometimes obtain honey crops from blueberries (Filmer and Marucci *1964*). Both nectar and pollen from blueberries are attractive to bees although some cultivars are more attractive than others (Brewer *1970*, Wood et al. *1967*). The reason for this difference has not been determined but should be given more serious study. Incorporation of the attractive factor in new cultivars could increase berry production.

Pollination Requirements

Properly pruned and nurtured highbush or lowbush blueberry plants growing under favorable conditions are capable of setting almost 100 percent of their blossoms. A set of 80 percent is required to yield an excellent commercial crop of highbush blueberries—50 percent for lowbush—but Karmo (*1957*) stated that many growers do not get over 10 to 20 percent set.

Aalders and Hall (*1961*) and Wood (*1968*) found considerable self-sterility and some cross-sterility in lowbush blueberries. More specifically, Hall and Aalders (*1961*) found that over 5 percent of the lowbush plants were male-sterile and that 45 percent produced less than abundant pollen or practically none. With so much sterility and pollen scarcity, it becomes evident that free transfer of pollen between plants is essential to maximum fruit production.

Early in the study of blueberries, Coville (*1910*) stated that pollination was effected by some insect. Later, Coville (*1921*) observed that when blueberry flowers were pollinated with their own pollen, and fruit was obtained, the berries were smaller and later in maturing than when pollen came from another plant, and some plants were almost completely sterile to their own pollen. Bailey (*1937*), Beckwith (*1931*), Lee (*1958*), Phipps (*1930*), Phipps et al. (*1932*), Shaw and Bailey (*1937*), Schaub and Bauer (*1942*), and Shaw et al. (*1939*) also concluded that cross-pollination was a requirement for good blueberry production. This was further confirmed by Meader and Darrow (*1944, 1947*) and Wood (*1965*). Eck and Childers (*1966*) stated that the rabbiteye blueberry is so nearly self-sterile that compatible cultivars must be interplanted. Morrow (*1943*) showed that even when selfing occurred the cross-pollinated flowers produced more seeds and were larger and earlier in maturing than those produced from selfed flowers. Boller (*1956*) and Darrow and Moore (*1962*) recommended that at least two cultivars be included in every planting to provide adequate cross-pollination possibilities.

Insect pollination is essential for maximum blueberry production. Failure to produce good crops is frequently the result of poor pollination (Filmer and Marucci *1963*). Chandler (*1943*) stated that growers frequently blame frost for their low yields when in reality poor insect pollination is the cause. The plants set more fruit, larger fruit, and set it earlier when there is adequate cross-pollination.

The blossom is well adapted for insect pollination, with its fragrance, its nectaries at the base of the corolla, and its receptive stigma and heavy pollen, both so placed in the narrow throat of the corolla that the bee must come in contact with each when foraging. The structure and position of the blossom—hanging downward with the 10 stamens forming a tight circle around the pistil, which extends beyond them—ideally facilitates cross-pollination. A mere touch of the blossom will dislodge some of the pollen and cause it to fall downward, but the likelihood is small that it will land on the stigma of its own or another blueberry blossom, unless it falls first upon a bee's hairy body and is then transferred to the stigma. If pollination does not occur, the pistil continues to elongate until it extends beyond the corolla, which enhances its possibility of contact with pollinating insects.

Stigma receptivity may last 5 to 8 days (Merrill *1936*, Moore *1964*, and Wood *1962*). However, if pollination does not occur within 3 days after the flower opens, fruit set is unlikely (Chandler and Mason *1964*).

Knight and Scott (*1964*) made cross-pollination studies in the greenhouse with four cultivars under cool and warm conditions. They reported that warm temperature hastened pollen tube growth and improved fruit set. They also found that cross-pollinated fruit ripened earlier than selfed fruit. They concluded that the larger, earlier berries and increased percentage of fruit set from cross- as compared to self-pollination indicated that growers would be economically justified in promoting cross-pollination.

As soon as fertilization occurs, the flower begins to lose attractiveness and development of the ovary begins.

Merrill (*1936*) and Merrill and Johnston (*1939*) erroneously concluded that blueberries were self-fruitful, and they encouraged growers to plant single cultivars in solid blocks. This advice, which was still being given as late as 1959 (Johnston *1959*), seriously curtailed maximum blueberry production in Michigan for years (Martin *1967*).

The inability of blueberries to set commercial crops in the absence of pollinating insects is now well established in different areas and under different conditions. However, Darrow (*1966*) stated that much more information seems to be needed on pollination of both lowbush and highbush blueberries. This is still true.

One of the major problems in highbush blueberry pollination is that the bulk of the commercial plantings consist of solid clonal blocks, which afford little opportunity for cross-pollination. For most efficient pollination and highest production, such blocks should be interplanted with compatible cultivars. The self-sterile rabbiteye must be interplanted with compatible cultivars.

Pollinators

There has been considerable lack of opinion in the past as to which pollinating agent is most effective in

pollinating blueberries (White and Clark *1938*). In Massachusetts, Beckman and Tannenbaum (*1939*) recorded more bumble bees (46 percent) than honey bees (38 percent) on blueberry blossoms. In Michigan, Merrill (*1936*) stated that both bumble bees and honey bees played a major part in blueberry pollination, but he considered bumble bees the primary agents. Wood (*1961*) stated that the importance of honey bees as a supplement to native bees had not been clearly established in Canada. Filmer and Marucci (*1963*) noted that bumble bees are good pollinators of blueberries in New Jersey, but their numbers fluctuate so they are not reliable. Later Marucci (*1966*) conceded that bumble bees and other wild bees were inadequate. Numerous references show that modern agricultural practices have greatly reduced the bumble bee population in many areas. Other native pollinators are usually insignificant. Brewer et al. (*1969a*) showed that neither airblasts nor vibrations gave a commercial fruit set for either 'Jersey' or 'Rubel'. The only recourse for adequate pollination in the absence of native pollinators is to move honey bee colonies to the blueberries.

Boulanger (*1964*) and Boulanger et al. (*1967*) noted that there were too few native pollinators to set an adequate crop in many fields in Maine, and they recommended the introduction of honey bees. Darrow and Moore (*1966*) also stated that, in general, native bees are inadequate and should be supplemented with one to five strong colonies of honey bees per acre. Dorr and Martin (*1966*) stated that the scarcity of bumble bees and other bees in Michigan blueberry plantations had previously been an important factor in limiting optimum production. They recommended both the placement of honey bee colonies in the field and bumble bee conservation practices. Eaton and Stewart (*1969b*) and Oldershaw (*1970*) mentioned the well-known fact that bumble bees frequently "burglarize" the blossoms by cutting a hole in the base of the corolla and stealing the nectar without contributing to pollination. Honey bees frequently visit these holes so their pollinating efficiency is also reduced. Helms (*1970*) attributed these holes to honey bees which he—we believe erroneously—considered to be "parasites."

With the populations of bumble bees decreasing as a result of various agrotechnical factors, the repeated results of various researchers previously mentioned as well as others (Eaton and Stewart *1969a*, Filmer *1963*, Filmer and Swift *1963*, Hansson *1969*, Karmo *1958*, *1966*, *1972*, and Marucci *1965*) plus practical experience strongly indicate that the value of the honey bee has gradually become fairly well recognized in most areas as the primary pollinator of blueberries. Some questions not conclusively answered about the honey bee include the appropriate number, strength, placement, and various problems of management of the colonies to be used.

The number of colonies per acre recommended by various researchers varies and lacks strong supporting data. Wood (*1971*) reported no increase in perfect seeds per berry when up to eight colonies per acre of lowbush blueberries were used. Brewer et al. (*1969b*) compared berry production and seeds per berry with colonies per acre. They obtained 160 ounces of berries with 4.9 seeds per berry per plot in fields not supplied with bees; 290 oz with 23 seeds per berry per plot in the fields supplied with two colonies per acre; and 335 oz with 28 seeds per berry in plots of a field supplied with five colonies per acre. Yet, for unexplained reasons, they stated that slightly more than two strong colonies per acre will provide an adequate pollinating force.

Marucci (*1966*) recommended one colony per 2 acres of highly attractive cultivars, one colony per acre of 'Weymouth', and two colonies per acre of less attractive cultivars such as 'Coville' and 'Earliblue'. Lathrop (*1950*, *1954*) recommended one strong colony per acre on small acreages. Darrow and Moore (*1966*) recommended one to five strong colonies per acre. Increased production of lowbush blueberries has been shown with up to 10 colonies per acre (Boulanger *1966*).

Howell et al. (*1970*, *1972*) introduced honey bees into cages with blueberries at 0, 25, 50, and 100 percent of full bloom. They concluded that 25 percent of full bloom is the latest time for bees to be added to insure maximum yield.

According to E. C. Martin (personal commun., 1973), there was a rather dramatic acceptance of the information on the value of bees to blueberries in Michigan following publication of papers by Martin (*1966*) and Dorr and Martin (*1966*). Within 3 years, growers of 9,000 acres of blueberries were using between 12,000 and 15,000 colonies of honey bees (Mich. Agr. Expt. Sta. *1970*), and this activity was primarily responsible for that State being the leading producer of blueberries. He stated that two colonies per acre has become the accepted optimum for commercial growers, and some growers were convinced that higher numbers of colonies per acre were economical.

Boulanger (*1966*) compared blueberry production in fields where the colonies were shifted from one field to another every few days (rotated) with fields where the colonies were left in the field throughout the period of bloom (static). The fields were supplied with 3.5, 4.5, 7.9, and 10 colonies per acre. Production varied considerably between fields and years and within treatments, but the highest yield, 80 bu/acre, was obtained from the field that contained 10 static colonies per acre. Nevertheless, he concluded that colony rotation held promise as a future management practice. Karmo (*1961*) also showed that colony rotation increased blueberry production. However, Karmo (*1972*) suggested that the bees be present for 4 to 5 days during the peak of bloom then moved to later blooming fields for more efficient use of the bees.

Sharp (*1970*) reported increased efficiency in pollination by the bees when the colonies were rotated. The theory involved in this shifting of the colonies is that the first day or so after a colony is reoriented the bees forage only near the hive. This subject has not been sufficiently explored to determine if the extra effort is worthwhile.

Filmer and Marucci (*1963*) considered one bee visitor per square yard of lowbush blueberries in full bloom on days of good weather as adequate. When the population goes below this level, they recommended supplementing the local supply of pollinators with honey bees.

Eaton and Stewart (*1969a*) showed that some

colonies of honey bees collected much more blueberry pollen than other similar colonies. The genetic inheritance of this character has not been studied although other studies have shown that the tendency to collect specific pollens is inherited.

The greatest benefit in blueberry pollination seems to be derived when there are sufficient pollinators to distribute the pollen freely, not only from anthers to stigma of self-fertile flowers, or between plants of a cultivar some of which may be self-sterile, but also between self-sterile cultivars (Hall and Aalders *1961*). As Eck and Childers (*1966*) pointed out, when the bee population is high, the more attractive blossoms become pollinated and fall rapidly, forcing the bees to work sooner on the less attractive blossoms; thus, the higher the bee concentration the more efficient the bees become.

Pollination Recommendations and Practices

The recommendations for the supplemental use of honey bees on blueberries range from less than one colony to five colonies per acre. Frequently, the lower recommended number seems to stem from the beekeeper's reluctance to overstock an area from the standpoint of honey production or colony buildup. The actual usage varies from none to three, and State averages of honey bee colony rentals for blueberry pollination are less than one colony per acre.

Evidence indicates that the grower would profit most, in terms of quantity and quality of berries produced, earliness of harvest, and greatest percentage harvest at first picking, if the highest possible bee population were maintained at flowering time. This might mean five or even 10 colonies per acre; doubtless under most conditions it should be greater than one or two.

Most growers make some attempt at having honey bees in or near their fields; however, this supply is seldom adequate. During optimum bee flight weather, there should be sufficient colonies to provide several bees per square yard of highbush plants in full bloom and at least one bee per square yard of lowbush plants.

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BROAD BEAN AND FIELD BEAN[18]

Vicia faba L., family Leguminosae

Broad bean and field bean, also known as faba, fava, horse, spring (pigeon), tick, and windsor beans (Robinson *1968*), are relatively unimportant in the United States, but they are important in England, parts of western Europe, and Australia. Yields vary considerably for these crops. Hawthorn and Pollard (*1954**) stated that broad beans yielded an average of 1,300 to 1,700 lb/acre in England. Bond et al. (*1966*) reported yields of about 700 lb/acre. Scriven et al. (*1961*) reported field bean yields of 4,520 kilograms per hectare (3,978 lb/acre). Watts and Marshall (*1961*) reported yields of 3,377 kg/ha (2,971 lb/acre) from plots caged with bees as compared to yields of 2,687 kg/ha (2,365 lb/acre) on plots caged to exclude bees.

Plant

Broad bean and field bean are coarse, erect, smooth-stemmed annuals, 2 to 6 feet tall, with pods 2 to 10 inches long, producing two to four flat brown seeds ½ inch to 1½ inches across. They are cool-season crops, tolerant to light frost, that are planted in the fall in areas of mild winter climate or in early spring in areas of cold winters.

Extrafloral nectaries are on the underside of the stipules, the small leaflike parts at the base of the leaf. Koreshkov (*1967*) showed that these nectaries function throughout the vegetative period of the plant, and that repeated removal of the nectar stimulates further production.

Inflorescence

There are two to four white, blotched, deep maroon or blackish-violet flowers, each an inch or more across, in clusters at the base of the leaf. Free (*1970**) stated that a normal field bean plant has 50 to 80 flowers, but a large proportion of these flowers or the young pods shed—86.7 percent according to Kambol (*1969*). Soper (*1952*) stated that less than a dozen pods per plant are harvested, although isolated plants may set over 60 pods. He concluded that this heavier set on the exposed plant was associated with better insect pollination. Rowlands (*1960*) recorded an average of 24 percent set in the open but only 7.3 percent set in the glass house. He concluded that some plants are highly self-sterile and

[18] See also: "Bean," p. 100; "Lima Bean," p. 244; "Scarlet Runner Bean," p. 332 and "Vetch," p. 369.

some cross better than others. Free (*1970**) stated that the amount and concentration of field bean floral nectar was relatively low, so the flowers are not overly attractive to nectar collecting insects.

In discussing the field bean inflorescence, nectar secretion, and bee visitation, Free (*1970**) stated that bee visitors to extra-floral nectaries were more numerous at midday, whereas those visiting the flowers were most numerous from 2 to 4 p.m., when pollen was available. He concluded that pollen was more attractive to bees than the floral nectar.

Pollination Requirements

The pollination of broad bean and field bean was studied by Free (*1966*) who concluded that insect pollination greatly increased production of broad beans but had little effect on production of field beans. Later, Free (*1970**) concluded that the pollination requirements of broad bean and field bean were similar although inadequate pollination limited seed production in broad beans more so than in field beans. Darwin (*1889**) showed that 17 broad bean plants covered with a net to exclude pollinators produced only 40 seeds, whereas 17 exposed plants produced 135 seeds.

Probably the most important observation concerning the pollination of field bean was that by Drayner (*1956*, *1959*) and confirmed in more elaborate detail by Bond and Fyfe (*1962*) who showed that continued inbreeding causes a progressive loss in the ability of the plant to set selfed seed, but upon hybridization (cross-pollination) this ability is restored. This means that the plant can survive several generations (not indefinitely) without cross-pollination although production continually decreases. A similar situation apparently exists in many other so-called self-pollinated crops; continued inbreeding leads inevitably to elimination of the strain.

Holden and Bond (*1960*) concluded that 30 to 40 percent cross-pollination may represent an equilibrium point in a balanced breeding system in which the cross-pollinated third of the flowers self and the selfed flowers produce one-third selfed and one-third crossed seed. Such a system, they concluded, would be self-perpetuating, yielding one-third cross-breds and two-thirds inbreds each generation. They also observed that the pollen is in contact with the stigma 24 hours before the flower opens, therefore the cross-breds are capable of selfing.

The value of hybrids or cross-pollinated plants within the cultivar as shown by Bond (*1968*), is in their ability to self in the absence of bees, whereas inbreds would not set seed. However, Rowlands (*1958*) showed that only 2.3 percent of flowers set if they were not tripped or manipulated, whereas 12.4 percent set if they were gently hand manipulated but not tripped. This indicated that insects or the elements can influence the set of fruit without actually crossing the flowers. His open-pollinated flowers set 23.1 percent, showing that cross-pollination was more beneficial than mere manipulation.

Free (*1966*) showed that plants caged with bees produced about twice as many seeds as similar plants caged without bees. Scriven et al. (*1961*), Cooper (*1966*), Mart'yanova (*1967*), National Agricultural Advisory Service (*1964*, *1967*), and Oschmann (*1957*) showed similar results. Fyfe and Bailey (*1951*) reported about 30 percent cross-fertilization of field bean in eastern England. Hua (*1943*) reported an average of 32.9 percent cross-pollination over a 3-year period in China.

The grower wants the plant to set its crop of seeds as soon as possible and to produce as much as possible. Bees can contribute in this respect. Wafa and Ibrahim (*1960*) excluded insects from some plants by use of cages and included bees in other cages over plants. At harvest time, the bee cage had ceased flowering and most of its pods were ripe. The plants from the cages without bees had many green pods when the cages were removed. This showed that bee pollination accelerated the rate of set of bean pods. Hanna and Lawes (*1967*) showed that the percentage of crossing was higher on the lower nodes (51 percent below, 33 percent at upper ones), showing that the plant strives first for cross-pollination then for survival.

Pollinators

Bond and Hawkins (*1967*) and Free (*1962*) have studied the behavior of bees on field bean. Free (*1962*) concluded that the activity of the honey bees may vary. They may visit only the extrafloral nectaries, they may visit only the holes cut in the bases of the corollas by bumble bees, or they may visit the corolla for nectar and pollen. Only in the latter case are the bees of value to the beans as a pollinating agent. Bond and Hawkins (*1967*) placed two colonies by an acre of field bean, and the bees collected sizeable amounts of pollen. However, these workers concluded that bumble bees were primarily responsible for the cross-pollination that occurred. Wafa and Ibrahim (*1960*) concluded that the carpenter bee, *Xylocopa aestuans* (L.), was the most important wild pollinating insect in the Gaza region. Free (*1959*) concluded that better visitation to the bean flowers resulted when the honey bee colonies were moved to the crop after it started to flower.

Watts and Marshall (*1961*) showed about 26 percent increase in seed production due to the presence of bees. They also showed the value of bees in setting the seed early. In their plots caged with bees and also in their open plots, they found an average of nine, nine, and two pods, respectively, on the bottom, mid- and top portion of the plant, but in the no-bee cage three, five, and four pods were in the same areas.

Free (*1970**) concluded that only insects with long tongues could reach the nectar in the bean flower and that honey bees and short-tongued bumble bees that enter the flower probably obtain only pollen most of the time. However, some bumble bee species with short tongues, male carpenter bees (*Xylocopa aestuans*), and certain ants (*Cataglyphis bicolor* (F.)) bite holes in the base of the corolla and "rob" the nectar without contributing to pollination. Honey bees do not make holes, but they will rob nectar from holes made by other insects.

Pollination Recommendations and Practices

Allen and Scriven (*1957*) concluded that one colony of honey bees per acre should give adequate coverage of field beans, but that most of the work by these insects resulted in self-pollination. In this respect, honey bees are no different from bumble bees. Brandenburg (*1961*) reported that the placement of colonies on the bean plots doubled the yield of seed. He suggested the bringing in of a new group of bees every 7 to 14 days.

Riedel and Wort (*1960*) studied set of pods in relation to their location on the plant and concluded that uniform set along the body of the plant was an indication of inadequate pollination.

Because bees collect pollen from beans mostly between 2 and 4 p.m., a study of the degree of collection might be used to determine the degree of pollination anticipated. For example, a grower might observe the number of bees per unit of flowers, then, later, the set of beans along the stalk, and, finally, the volume of seed harvested. In this way, he could determine the bee population needed for maximum production of both broad bean and field bean. This information should be determined experimentally also.

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BROCCOLI

(See "Cole Crops")

BRUSSELS SPROUT

(See "Cole Crops")

BUCKWHEAT[19]

Fagopyrum esculentum Moench, family Polygonaceae

Buckwheat, once a highly important crop in the United States, appears to be in the twilight of its day. In 1918, more than a million acres were grown (Quisenberry and Taylor *1939*). Over half of that acreage was in Pennsylvania and New York. Twenty years later the total acreage was less than one-half million. By 1954, only 150,000 acres were harvested, and in 1964 when USDA crop production records for buckwheat were discontinued, only 50,000 acres were harvested. Seed production ranged from 500 to 1,700 lb/acre, depending on various cultural factors, not the least of which was completeness of bee pollination (Carmany *1926*, Kopel'skievsky *1960*, Martin and Leonard *1949**). However, Root (*1891*) reported a phenomenal yield of 3,840 lb/acre in one instance.

The limited acreage of buckwheat in the United States is in the Great Lakes region and eastward. In 1970, Russia led all other countries in buckwheat production with more than 4.5 million acres (United Nations Food and Agriculture Organization (FAO) *1971, p. 80*).

Buckwheat is grown primarily for the seeds, which are ground into flour and used in buckwheat cakes.

Plant

Buckwheat is an annual, 2 to 4 feet tall, with a single stem and several branches bearing heart-shaped leaves (fig. 55). The green to red stem turns brown with age. More reddening is evident with poor seed set. The 1/5-inch flowers are in clusters mostly at or near the top of the plant (fig. 56). Flowering is indeterminate, and the plants which are usually broadcast are often harvested with some immature seeds and even flowers present. A field in flower is chalky white and has a pronounced aroma that some people consider unpleasant. Flowering in a field may begin 5 to 6 weeks after planting and may continue for 25 to 30 days (fig. 57).

Inflorescence

The buckwheat flower has no petals—the sexual parts, the ovary, three styles and eight stamens being enclosed in the petallike sepals. Four of the anthers bend out but turn their pollen inward. The other four turn their pollen outward (Knuth *1909*, pp. 341–342*). Some plants have flowers, referred to as the "thrum" type, with short styles and long filaments so the stamens extend above the styles. Other flowers, referred to as "pin" types, have long styles and short filaments so the stigma is above the anthers. Occasionally, the styles and stamens are at the same height. The long stamens and filaments are fully 3 mm; the shorter ones, about 2 mm. Although each plant bears flowers of only one form, the seeds from either form will produce plants having the dimorphic forms in about equal numbers. The three styles lead to a single ovary with one ovule, so a flower can produce only one seed, which is about one-quarter inch long.

The flower, which opens in the morning around 8 a.m., has eight yellow nectaries alternating with the eight filaments at the base of the ovary, bound together by a cushionlike swelling (Knuth *1909*, pp. 341–342*). The flower (fig. 56) secretes nectar in copious amounts, but only in the morning hours, during which time it is highly attractive to bees (Phillips and Demuth *1922*). Toward noon, the flow lessens, and during the afternoon honey bees usually abandon the plants. Pollen is also collected by honey bees from buckwheat.

[19] Tartary buckwheat, *Fagopyrum tartaricum* (L.) Gaertn., is a more slender plant than *F. esculentum*, with smaller greenish or yellowish flowers and not as aggregated. According to Naghski (*1951*), extensive plantings of tartary buckwheat have been made in recent years because it is a good source of rutin, a drug used to reduce capillary blood pressure and relieve atomic radiation injury. This species is seldom visited by bees and is self-fertile (Garber and Quisenberry *1927*).

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A colony of honey bees having access to a field of flowering buckwheat may store 10 to 15 pounds of honey per day (Versehora *1962*), and collect 90 to 290 pounds of nectar per acre (Free *1970** Martin and Leonard *1949**). The honey produced by buckwheat is dark with a strong flavor that is usually relished only by people who are accustomed to it; however, there is a greater demand for this honey than can be supplied. The honey is used primarily in the baking of foods. During a buckwheat nectar flow, the apiary may have a strong sometimes nauseating aroma which can be detected for some distance (Pellett *1947**). Mel'nichenko (*1963*) thought that removal of nectar by bees stimulated greater secretion. He stated that secretion ceases after the flower has been fertilized.

Bukhareva (*1964*) and Leshchev (*1952*) reported that some trace elements caused an increase in buckwheat nectar secretion and seed yields. This was supported by Kopel'skievsky (*1955*, *1960*), Leshchev (*1952*), and Skrebtsova (*1957*) who found that the fertilizers calcium, nitrogen, and phosphorus increased the pollination effectiveness of honey bees. Demianowicz and Ruszkowska (*1959*) found that all the cultivars tested were important sources of pollen, but some were

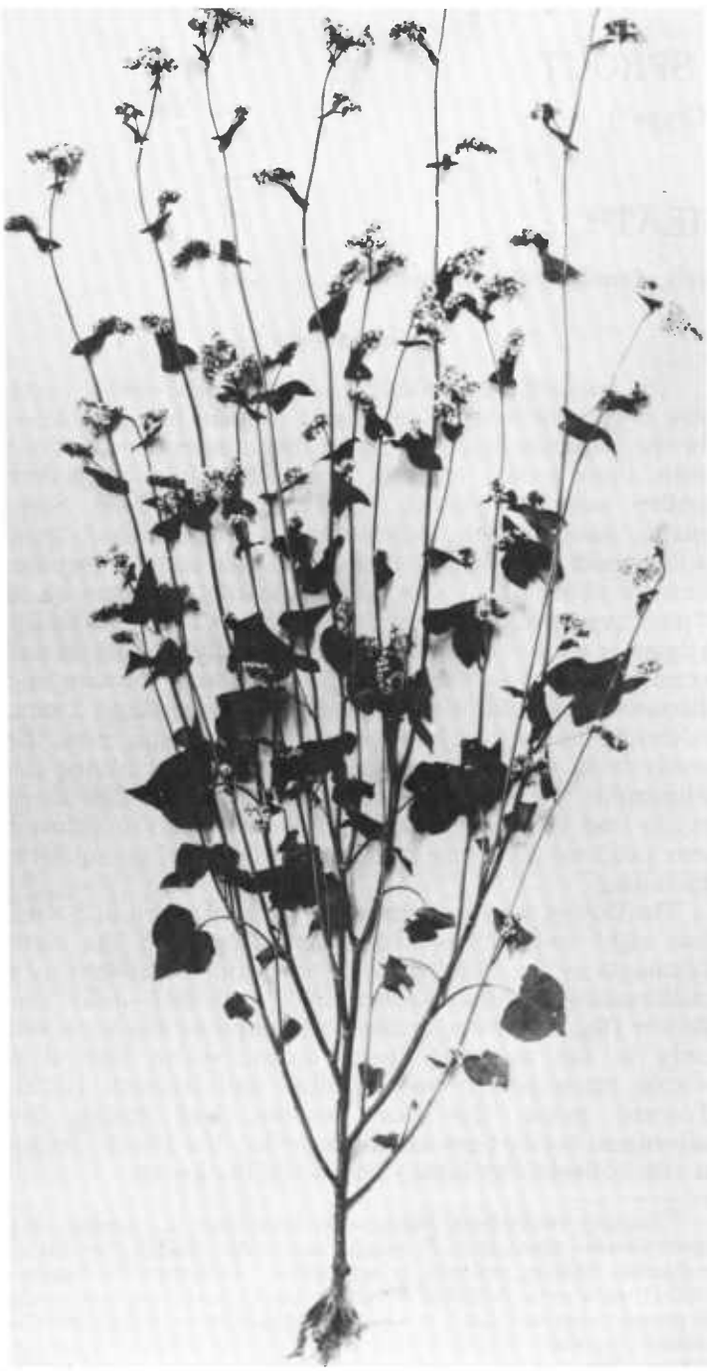

FIGURE 55.—Buckwheat plant in bloom.

FIGURE 56.—Buckwheat flowering branch.

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FIGURE 57.—Field of buckwheat in full bloom.

much better sources of nectar than others. With many nectar-producing plants decreasing or disappearing from a beekeeper's area he might encourage buckwheat planting nearby to supplement his bee forage.

Pollination Requirements

The buckwheat flower is usually unable to self-pollinate. The flower type prevents the pollen from automatically coming in contact with the stigma. Exceptions include the occasional flowers with pistil and stamens of the same length, which usually have a low degree of self-fertility. A recent selection (*F. sagittatum* Gilib.) has been developed which has stamens and pistil at the same level, with a high degree of self-fertility, but of no direct commercial value (Marshall *1970*). Buckwheat pollen is not windblown, therefore insects are necessary for the transfer of the pollen. Davydova (*1954*) found that, as is customary for dimorphic flowers, the pollen grains on the two types of stamens are different in size, the flowers with longer stamens having larger grains (46 to 67 by 39 to 55 microns, versus 35 to 44 by 29 to 40 microns for grains on the shorter stamens). The analyses by Davydova (*1954*) of pellets of pollen taken from honey bees working buckwheat, showing that both types of pollen were present, was confirmed by Roz[s]ov and Sc[k]rebtsova (*1958*). This proved that the bees move freely from one type of flower to another and are thus effective pollinating agents of this crop.

The necessity of insect pollination for commercial seed production of buckwheat has been well established by Garber and Quizenberry (*1927*) in the United States and numerous workers in Russia, where this crop is grown so extensively (Elagin *1953*, Glukhov *1955*, Kashkovskii *1958*, Mel'nichenko *1962*, and Sevcuk *1946*). Free (*1970**), after reviewing the pollination of buckwheat, pointed out the need for some controlled cage tests on this crop to determine the degree of self-pollination if any occurred and the quantity of seed that might be expected under different pollination conditions.

Pollinators

Unquestionably, the honey bee is the best pollinator of buckwheat because it is highly attracted to the buckwheat flower and efficiently and effectively transfers the pollen from anthers to stigmas, whether collecting pollen or nectar.

Leighty (*1919*) stated that many buckwheat growers believed that the weight per bushel of seed was heavier where the crop had been worked heavily by bees. Elagin (*1953*) showed the following correlation between the 2-year average yield of buckwheat seeds and distance in meters from the apiary.

Distance from apiary in meters	*Yield of buckwheat seed in kilograms per hectare*
"Near"	850
500	770
1,000	720
1,500	575

The number of colonies in relation to the area of buckwheat was not given by Elagin (*1953*), although where five colonies per hectare were present, 80.4 percent of the seeds set, but with only one colony per hectare, the set was only 57.8 percent. The transportation of colonies to the buckwheat fields was encouraged because of their value as pollinators.

Glukhov (*1955*) obtained 1,700 kg buckwheat seed per hectare within 500 m of the apiary, but production dropped to 1,200 kg in the 500- to 1,000-m range, and only 500 kg/ha at 2,000 to 3,000 m from the apiary. In another field, he obtained 2,500 kg/ha of seed adjacent to the apiary, 1,900 kg at 500 m and 1,300 kg/ha 1,000 m from the apiary. Similarly, Kopel'skievsky (*1960*) obtained 1,470 kg/ha seed adjacent to an apiary, but only 840 kg/ha 2,000 m away.

Pollination Recommendations and Practices

There are no recommendations in this country in relation to bee populations and buckwheat seed production. In Canada, one colony per acre is recommended (Smith et al. *1971*). In Russia, Kashkovskii (*1958*) stated that there should be enough bees for each flower to receive five or six visits. Mel'nichenko (*1962*) stated that about two colonies per acre were needed for saturation pollination and highest buckwheat yields; however, when he used about three colonies per acre, he obtained 1,250 to 1,500 lb per acre. Doubtless, the colonies per acre necessary to supply the five to six visits per flower varies with location and conditions.

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CACAO

Theobroma cacao L., family Sterculiaceae

Cocoa is the processed product derived from the beans of the cacao plant.

World production of cocoa exceeds a million tons, with Ghana producing 429,000 tons; Nigeria, 201,000 tons; Ivory Coast, 105,000 tons; Cameroon, 73,000 tons; Brazil, 94,000 tons; and Ecuador, 35,000 tons, with other countries of North and South America, Africa, Asia, and Oceania producing the balance. Of this amount, the United States consumes 25 percent; Germany, 13 percent; United Kingdom, 10 percent; and the Netherlands, 9 percent (Purseglove *1968**). Europe, as a whole, takes over 50 percent and the American countries, about 40 percent of the entire crop.

Plant

The evergreen cacao tree grows 15 to 25 feet primarily between latitudes 10° N to 10° S, usually below 1,000 feet in altitude, and in areas with a monthly average rainfall of about 4 inches. Various cultivars, propagated by seed, are grown. The oblong or oval fruit (fig. 58), commonly called a pod, is 4 to 12 inches long, and green when immature, but may be yellow, red, purple, or green when ripe. It contains from 20 to 60 reddish-brown beans ¾ to ½ by ½ to 1 inch in size, usually arranged in five rows (fig. 59). Pods are produced throughout the year, but the main harvest usually begins at the end of the wet season and may extend for 3 months. From 7 to 14 pods will produce a pound of dry beans. Yields range from 200 to 3,000 pounds dry beans per acre, but 600 lb/acre is considered a good yield (Purseglove *1968**).

Inflorescence

The cacao flowers arise in groups directly from old

wood of the main stem or older branches at points which were originally leaf axils (fig. 60). Each flower has five prominent pink sepals, five smaller yellowish petals, each of which forms a pouch, an outer whorl of five staminodes, and an inner whorl of five double stamens, each stamen bearing up to four anthers. The staminodes are about as tall to twice as tall as the upright style and form a "fence" around the style. The stamens are curled so that the anthers develop inside the petal pouches. The ovary consists of five united carpels each having four to 12 locules, and one style that has several linear stigmatic lobes (van Hall *1932*). According to Cheeseman (*1932*) and Urquhart (*1961*), the flower produces no nectar and has no discernible scent. However, Stejskal (*1969*) stated that there are two types of microscopic nectaries, (1) the cylindrical multicellular ones, 60 to 450 microns in size, on the pedicels, sepals, and ovaries, and (2) the conical unicellar ones 20 to 25 microns in size, located on the "guide lines" of the petals and on the staminodia. He showed that they secrete nectar, which has an odor that attracts male mosquitoes and lepidopterous insects.

The flower opens about dawn, and the anthers dehisce just before sunrise. The stigma is usually pollinated 2 to 3 hours later but is receptive from sunrise to sunset of the day of opening (Cheeseman *1932*). The stigma is receptive to pollen along its whole length, and not merely at the apex as in most flowers. If the flower is not pollinated, it usually sheds the following day (Sumner *1962*). Pollination before noon is best (Chatt *1953*).

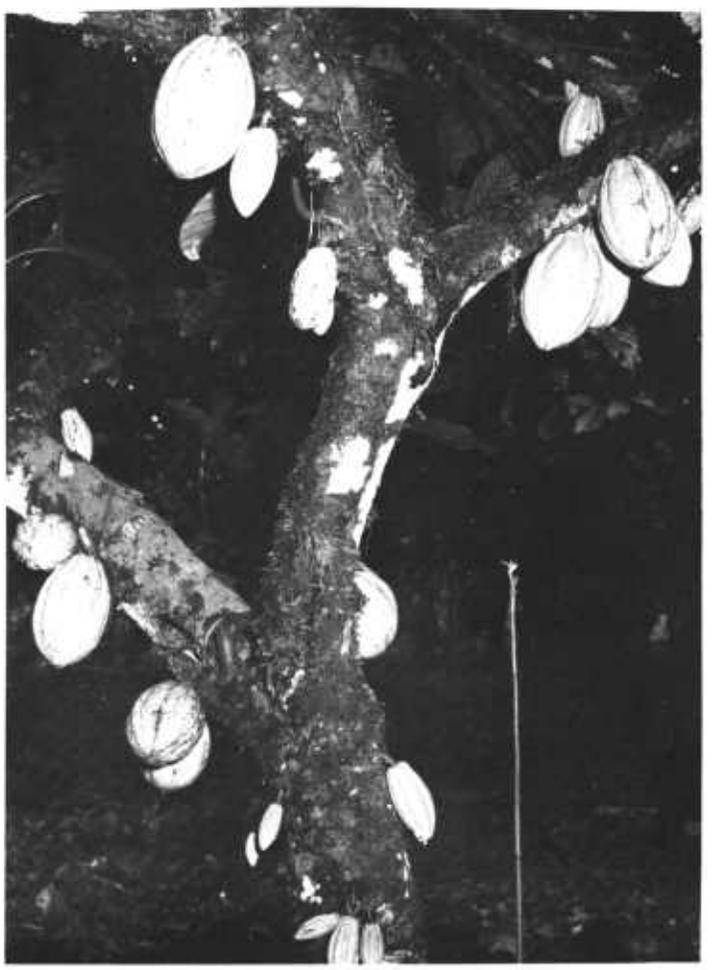

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FIGURE 58.—Maturing cacao fruit on the tree.

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FIGURE 59.—Ripe cacao fruit opened to show the beans.

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FIGURE 60.—Cacao flower cluster growing on the trunk of the tree, showing the open flower, a flower ready to open, and a small fruit.

Pollination Requirements

Although the full story of cacao pollination is not yet known, there seems little doubt that the flower is not self-pollinating, as flowers bagged to exclude insects invariably shed (Gnanaratnam *1954*). Also, some plants are self-incompatible but set fruit well if pollinated with pollen from compatible trees (Chatt *1953*, Cope *1958*, Knight and Rogers *1955*). The method of the transfer of the pollen in nature is the somewhat questionable factor. The sticky pollen is not carried by the wind. Furthermore, it is produced and released in the petal pouches where wind is unlikely to disturb it (Cobley *1956**, Gnanaratnam *1954*). Glendenning (*1962*) noted that pollen found on a stigma was usually from more than one flower, but the amount of foreign pollen depended on proximity to other plants. Little pollen seemed to move more than a couple of trees' distance.

Pollinators

There is general belief that small insects are the primary pollinating agents of cacao, but no general agreement as to which insects are responsible. Numerous authorities credit midges, especially *Forcipomyia quasiingrami* Macfie and *Lasiohela nana* Macfie (Barroga *1964*, Chatt *1953*, Fontanilla-Barroga *1965*, Macfie *1944*, Saunders *1959*, Toxopeus *1969*). Others credit ants (*Crematogaster* spp.), aphids (*Aphis gossypii* Glover and *Toxoptera* spp.), thrips (*Frankliniella parvula* Hood), and unidentified wild bees (Billes *1941*; Cope *1940*; Harland *1925a*, *b*; Hernandez *1965*; Jones *1912*; Muntzing *1947*; Posnette *1942a*, *b*, *1944*, *1950*; Posnette and Entwistle *1957*; Urquhart *1961*; Voelcker *1940*).

Thrips and aphids move about but slightly from tree to tree, yet Glendenning (*1958*) reported, after a study of albino trees, that a considerable proportion of pollination takes place across two intervening trees, though less than over shorter distances. This would indicate an agent with considerable movement between trees.

The ants *Wasmannia suropunctata* (Roger) and *Solenopsis geminata* (F.) and the wild bee *Trigona jaty* Smith were occasional visitors. Glendenning (*1958*) concluded that the midges (*Forcipomyia* spp.) were the main pollinators, accounting for twice the pollination service performed by all of the other species combined. This was verified in various experiments with different numbers of insects per cage over cacao flowers. Hernandez (*1965*) reported pollination percentages ranging from 1 to 52 percent when he used midges, bees, thrips, and ants. However, Hernandez did not indicate how pollination was accomplished.

Although midges seem to get the most credit as pollinators of cacao, there is clearly a lack of knowledge as to which insects are responsible in the different areas for the commercial set of fruit of this important crop.

Harland (*1925a*) found that of 5 percent of the flowers on trees not infested by ants and aphids, only 0.3 percent set fruit; whereas, on trees heavily infested by these insects, 35 percent of the flowers were pollinated and 2 percent set. At the same time, 5 percent of the hand pollinated flowers set fruit.

Little has been said about the adequacy of pollination of the individual flower or the minimum number of seed in relation to fruit set or shedding. However, at least as many pollen grains must fall upon the stigma as there are subsequently developed seeds. Thus, a minimum of 60 pollen grains is necessary to set the highest number of seed.

Many of the flowers are never pollinated (Harland *1925b*), at least under Trinidad conditions. Apparently, wherever the crop is grown the lack of adequate pollination is a strongly limiting factor in production of the beans. Sumner (*1962*) stated that most of the pollination occurs 2 to 3 hours after dawn with a second much smaller peak in the afternoon, but only 2 to 5 percent of the flowers ever get pollinated, and these may not set if pollinated too late or with incompatible pollen. Urquhart (*1961*) stated that only about 5 percent of the stigmas ever get pollinated; Harland (*1925b*) found only 9 percent to be pollinated. Because some plants are self-incompatible—some are male sterile or sterile (Gnanaratnam *1954*)—many of the flowers would appear to be doomed to shed. Knoke and Saunders (*1966*) tried a mist blower for mechanical transfer of pollen but achieved uneconomical success.

The use of honey bees under saturated pollination conditions has never been tried, probably because the blossom has no aroma and produces no nectar. Quite conceivably, however, honey bee colonies could be concentrated in numbers sufficient to exhaust the supply of pollen and nectar on competing plants and the bees induced to visit the flowers of this important crop for pollen and increase the percentage of cross-pollination and fruit set. A search for a selection of cacao pollen-loving honey bees might produce an acceptable and controllable pollinating agent. One or more of the various species of pollen-foraging wild bees might be found that could be controlled and used as a profitable pollinating agent of cacao.

Pollination Recommendations and Practices

There are no recommendations on the use or manipulation of insect pollinators of cacao. According to Faegri and van der Pijl (*1966**), the *Forcipomyia* spp. in Africa breed mainly in decaying pods. If the pods are removed by too scrupulous cleaning of the plantations, these midges might also be removed. This would result in deficient pollination of the flowers. Otherwise, the presence or numbers of insect pollinators are left entirely to chance on this billion-dollar crop.

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CARAMBOLA

Averrhoa carambola L., family Oxalidaceae

Carambola is a crop of no importance in continental United States. Knight (*1965*) stated that there was one commercial planting in production in Sarasota County, Fla., but otherwise production was limited to dooryard plants of southern Florida.

Plant

The carambola is a many-branched, frost-susceptible evergreen tree to 30 feet (Bailey *1949**). It is grown for its waxy-yellow, 2- to 5-inch long fruit, which are

characterized by four or five sharp ribs. When the fruit is sectioned, the star-shaped pieces are used ornamentally in salads and punchbowls. The juice is rich in vitamin C. The fruit may also be stewed, preserved, or made into jams and jellies. A fruit has from 1 to 15 pendulous seeds in each rib or segment, depending upon the completeness of pollination.

Inflorescence

The clusters of fragrant whitish to rose-colored flowers are borne in the leaf axils. They are about five-eighths inch across. There are five petals and 10 stamens in at least two whorls alternating long and short, five without anthers. The ovary has four or five cells with two to four ovules per cell (Ochse et al. *1961**, Purseglove *1968**).

Pollination Requirements

The flowers are self-incompatible, and not wind pollinated; therefore, insects are necessary in the production of fruit (Knight *1965*). Honey bees visit the flowers freely. Nand (*1971*) stated that honey bees, flies, and other insects are the chief pollinating agents of this completely cross-pollinated plant.

Pollination Recommendations and Practices

None.

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CARAWAY

Carum carvi L., family Umbelliferae

Caraway is grown almost exclusively in The Netherlands on about 10,000 acres for its seeds, which are used to season breads, meats, cheeses, and drinks (van Roon and Bleijenberg *1964*). A small acreage is grown in the northern and northwest part of the United States (Rosengarten *1969**).

Plant

The plant is a slender, smooth, erect, annual, or biennial herb, 1 to 3 feet tall, with thick tuberous roots and narrow leaves (fig. 61). It is planted in the spring (fall of the mild-wintered Southwest) in 15- to 30-inch rows, and may produce 800 to 2,000 pounds of seed per acre (Hawthorn and Pollard *1954**, Rosengarten *1969**).

Inflorescence

The yellowish-white flower is markedly protandrous. The stamens release pollen during the first 2 days the flower is open, then wither on the third day. The stigma does not become receptive until the sixth to seventh day. The primary umbel is usually in the female stage of flowering when the lateral umbels are in the male stage. Self-fertilization in a flower, and usually within an umbel, does not occur (van Roon and Bleijenberg *1964*, Knuth *1908*, p. 477*). Both nectar and pollen are easily available and attractive to flies and hymenopterous insects.

Pollination Requirements

Because of the protandry, pollen must be transferred from pollen-producing flowers to receptive stigmas. The pollen is not windblown but must be transferred by insects.

Pollinators

Bees are the primary pollinators of caraway flowers.

FIGURE 61.—Caraway leaves and flowering stems.

Pollination Recommendations and Practices

Although there are no recommendations on the pollination of caraway, the flower type and the need for pollinating insects would indicate that where maximum commercial production of seed is desired the grower should provide an ample supply of bees to the field.

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CARDAMOM

Elettaria cardamomum (L.) Maton, family Zingiberaceae

Most of the cardamoms are produced in southeast Asia and the southern tip of India. The cardamoms of commerce are the seeds, which are used as spices in seasoning and in medicine (Bailey *1949**, Ridley *1912**).

Plant

The plant, a shrub, forms a clump 7 to 9 feet tall, that is more or less cultivated in the jungle areas. It requires some shade from taller plants. It produces rhizomes, by which it is propagated, although seeds are also planted at the rate of 650 to 1,000 per acre. The plant will flower 2 years after it is planted and will yield for about 15 years. About 5 months after the flower opens, a three-celled pod is harvested. Each cell of this pod produces seven to nine dark-brown aromatic seeds, the cardamoms or cardamons.

Inflorescence

The slender flowering stems arise 2 to 3 feet from the rootstock or rhizomes, and produce toward the apex numerous florets in two- to three-flowered racemes. The green calyx tube is 1½ inches long, and the pale green ½-inch corolla lobes are narrow and spreading. The flowers open singly or two or more at a time over a long period.

Pollination Requirements

Ridley (*1912**) stated that the flowers require insect pollination. He concluded that the lack of adequate pollination often contributed to reduced crops.

Pollinators

Ridley (*1912**) stated that the flowers are pollinated by insects, probably some species of bees or a fly.

Pollination Recommendations and Practices

None.

CARDOON

(See "Artichoke")

CARROT

Daucus carota L., family Umbelliferae

Carrots were grown on 78,530 acres in the United States in 1969, with a farm value of $82,967,000. The seeds, about a million pounds, were produced on about 2,000 acres, primarily in California, Idaho, and Oregon (Whitaker et al. *1970*).

Plant

When grown for seed (fig. 62), two methods may be employed. If the seed-to-seed method is used, the seeds are planted in the late summer, the root overwinters in the soil, and the following year the growth produces a seed crop. In the root-to-seed method, the roots or stecklings are removed from the soil in the fall, stored at 33° F until the following spring, then transplanted, and the seed crop is harvested from the plant in the fall. In both instances, the crop is grown in rows and cultivation is necessary. Franklin (*1948*) concluded that proper storage of stecklings was the greatest single problem in carrot seed production.

Inflorescence

The inflorescence, typical of the umbelliferae, consists of a terminal or primary compound umbel of white flowers, 5 to 6 inches across, and a system of second-, third-, and fourth-order umbels, named in relation to their appearance on the plant below the primary umbel. The umbels decrease in size as the order number increases. The first and fourth order umbels are of little importance in seed production (Borthwick *1931*). The individual flower is usually perfect (Knuth *1909**, *p. 502*), although Braack and Kho (*1958*) reported that a tendency to produce only male flowers occurs and with increasing frequency in the umbels of high orders. A flower normally has five functional

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FIGURE 62.—Carrot seed field about ready to harvest.

stamens and two styles, which lead to the two locules of the ovary. Each locule contains a single ovule, thus two seeds can be produced. Braak and Kho (*1958*) obtained only 1.4 seeds per flower from flowers in a room free of harmful insects and supplied with flies to pollinate the flowers.

Nectar is secreted from a swollen disk on the upper surface of the ovary and is easily available to all types of insects. Pellett (*1947**) reported that 100,000 to 150,000 pounds of honey is produced from carrots annually, but its quality is poor. Carrot pollen is attractive to numerous insects (Bohart and Nye *1960*). Gary et al. (*1972*) showed that carrot blossoms were much more attractive to honey bee pollen collectors than onion blossoms, as only 7 percent of the visitors to onion flowers were collecting pollen compared with 66 percent of the visitors to carrot blossoms. Flowering extends over about a month, and dehiscence within an umbel covers about 7 days. Within a floret, the anthers dehisce over a 1- to 2-day period, and stigma receptivity begins on the third or fourth day. The stigma may remain receptive a week or possibly longer (Hawthorn and Pollard *1954**, Hawthorn et al. *1960*, Franklin *1953*, Poole *1937*).

Pollination Requirements

Jones and Rosa (*1928**) and Enzie (*1943*) stated, without supporting data, that carrots were "mostly insect-pollinated." Rather thorough studies of carrot pollination were made by Hawthorn et al. (*1960*) (fig. 63). By comparing production from open plots with that from plots caged (a) to exclude all insects, (b) to exclude all but tiny insects, or (c) to enclose a colony of honey bees, they proved that insect pollinators were essential for commercial seed production. In cages excluding all insects, an average of only 128 pounds of seed per acre was produced. When tiny insects were permitted to visit the flowers 453 pounds of seed per acre developed, open plots exposed to pollinators in the area yielded 711 lb/acre and plots caged with honey bees produced 840 lb/acre. Hawthorn et al. (*1960*) concluded from their close studies of the 'Red Core Chantenay' cv. that "limited but significant opportunity existed for self-pollination from one umbellet to another by jarring or wind action, and a greater opportunity (on a time basis) for cross-pollination by accidental rubbing together of umbels on adjacent plants."

However, their test established that such self- or mechanical pollination in the absence of pollinating insects was of little value in the commercial production of seed. Slate (*1927*) concluded that only about 15

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FIGURE 63.—Carrot pollination studies, showing flowers tagged to indicate mode of pollination.

percent of the carrot plants set seed from their own pollen. Even though apparently only two pollen grains are essential in the fertilization of the two ovules of the flower, and the stigma is receptive to pollen either from flowers of the same plant or from others for as much as a week, Paci (*1956*), Pankratova (*1957*), and Hawthorn et al. (*1960*) concluded that there is sufficient transfer of such pollen without pollinating insects. Thompson (*1962*) reported that more than 95 percent crossing occurred in the field at Ithaca, N.Y., but he gave no indication as to the pollinating agents.

The value of hybrid vigor in carrots has been known for years (Poole *1937*) and male sterility, essential in its utilization, was reported shortly thereafter (Welch and Grimball *1947*), but only a few hybrids have been produced commercially. Whitaker et al. (*1970*) stated that the uniform, smooth, highly colored roots produced by superior hybrids cannot be duplicated by the open-pollinated varieties. However, hybrid carrot seed production is so recent that time has not permitted the identification of problems that might be involved in providing adequate cross-pollination for this crop. The relatively long flowering period of carrots is favorable and so is the attractiveness of both the nectar and pollen to a broad spectrum of pollinators, particularly honey bees. For large-scale production of seeds, however, where male-sterile plants are used, there is need for pollinating agents interested only in nectar collection that will freely cross over from the normal to the male-sterile flowers and effect maximum cross-pollination.

Pollinators

Associated with the studies made by Hawthorn et al. (*1960*) on the need for insect pollinators, Bohart and Nye (*1960*) also studied the insect visitors to carrot flowers. They collected on the carrot blossoms 334 species of insects representing 71 families, which in itself shows the attractiveness of these blossoms to a wide variety of insect visitors. Most of the species of visitors were in the superfamily Apoidea, or the Ichneumonidae, Psammocharidae (Pompilidae), Sphecidae, and Vespidae families of the Hymenoptera, and the Bombyliidae, Sarcophagidae, Stratiomyidae, Syrphidae, and Tachinidae families of the Diptera. Bohart and Nye (*1960*) proposed an efficiency rating for the insect pollinators of carrots, based on the amount of loose pollen on the insects' body, the size of the insect, and its activity on the flower head. By multiplying this rating figure by the numbers of insects observed on the flowers, a pollination index was obtained for each species.

They concluded that several genera in the Apoidea were important pollinators of carrots, but from the practical standpoint the honey bee was the only species that could be manipulated and utilized in commercial seed production (fig. 64).

Pankratova (*1958*) reported that the chief pollinators of carrots near Moscow were flies (90 percent) and bees (9 percent). No mention was made of the number of honey bee colonies in the area nor the plant competition.

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FIGURE 64.—Honey bee collecting nectar from carrot flower.

The activity of honey bees on carrot blossoms was studied by Bohart and Nye (*1960*). They stated that pollen collecting honey bees "literally wade across the heads, swinging their abdomens back and forth and scraping the pollen from stamens with their forelegs. The nectar collectors stand higher on the flowers, move about less, and lap up droplets from the exposed nectaries. In other species of bees, the females usually behave like pollen-collecting honey bees and the males like nectar-collecting honey bees."

Hawthorn et al. (*1960*) reported that plants caged to exclude pollinating insects apparently reached their peak of bloom a few days earlier and held it more than a week longer than plants in the open or in cages where bees were present. This difference, however, was attributable to the dislodging of petals by bees and was only an "illusion" so far as actual flowering was concerned.

As shown earlier by Hawthorn et al. (*1960*), bees increased production of carrot seed. As a result of the bee activity, there were fewer undesirable large seed and they matured more rapidly and germinated better than seeds produced where the pollinator level was low. Also, progressive shrinkage in weight of seeds, which following the various cleaning processes, was accelerated with every decrease in pollination level. Both quantity and quality of carrot seeds are improved by high levels of bee pollination. Franklin (*1970*) reported that at one time in Parma, Idaho, the carrot fields were teeming with bees, and excellent seed crops were obtained. Then pest control methods and materials changed, competitive crops moved in, bee counts dropped, and the seed crops failed.

Pollination Recommendations and Practices

As a result of their studies Bohart and Nye (*1960*) made the following recommendations: "(1) Locate enough colonies of honey bees in the area to provide effective populations on the flower heads; (2) avoid the presence of competing bloom; (3) restrict plantings of carrots for seed to avoid dilution of the pollinator population; (4) choose areas with varied habitats capable of supporting large numbers of a wide variety of pollinators; (5) take steps to increase populations of wild pollinators in the area. For most large seed-pro-

ducing areas a combination of the first and second methods is likely to prove the most practical."

Hawthorn et al. (*1960*) gave a little more indication as to the number of pollinators needed. They stated, "Under the cultural conditions of our experiments, a honey bee population of 8 per square yard (the lowest average number for the season in our cages) is apparently as high as the plant can use to advantage. Probably a somewhat smaller number would do just as well, although we have no direct evidence to support such a conclusion."

Pankratova (*1957*) stated that the most reliable pollinators of carrots are honey bees. He recommended transporting colonies to the field, but the number of colonies was not mentioned. Hawthorn et al. (*1956*) also recommended movement of colonies of honey bees to carrot fields to provide the large numbers necessary at flowering time but did not designate the number. Naturally, the number needed would be influenced by competition from other flowers, the strength and condition of the colonies, and the attractiveness of the carrot flowers. Under most conditions where carrots are grown for seed and maximum production is desired, the placement of several colonies per acre in and around the field would probably be justified. Eight bees per square yard of flowers should be striven for regardless of the number of colonies required to provide this.

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CASHEW

Anacardium occidentale L., family Anacardiaceae

The cashew is a hardy drought-resistant tropical or subtropical tree. This limits its growth to the area of our continent from Mexico to Peru and Brazil, but includes Hawaii, Puerto Rico, and favored parts of the southern tip of Florida. Worldwide, India is the leading producer; other producing countries include Mozambique and Tanzania (Mutter and Bigger *1961*, Purseglove *1968**).

Plant

The cashew is a somewhat straggly evergreen tree, 12 to 15 m in height, seldom taller, with oblong 6- to 7-inch leathery green leaves and terminal, many-flowered panicles. It is cultivated for its delicious 1-inch-long, kidney-shaped nut (fig. 65). The nut is inedible when raw and must be roasted to drive off the highly irritating volatile oil. The nut is produced on the end of a greatly enlarged fleshy pedicel disk and receptacle, called the cashew apple. The cashew apple is about 2 inches wide and 3 to 4 inches long (Kennard and Winters *1960**), and when ripe it is shiny, red or yellow, soft, and juicy. It is used as a fresh fruit or in juices, jellies, or for making wine (Ochse et al. *1961**). The tree bark provides an indelible ink, and the shell

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FIGURE 65.—Cashew fruit. *A*, Cashew apple; *B*, cashew nut.

provides an insect-repelling vesicant oil (Purseglove *1968**).

The fruit ripens in 2 to 3 months and is harvested from the tree or picked up soon after falling. The nut is removed from the apple, dried or roasted in the shell, then hulled and vacuum packed.

Cashew plants are usually grown from seed and thinned to 30 by 30 feet. They begin bearing the second year, are in full production by the 10th year, and continue bearing for another 20 years. The yield varies from 1 to 100 pounds per tree (Purseglove *1968**, Haarer *1954*).

Inflorescence

The cashew inflorescence is a sweet-scented lax terminal, many-flowered panicle 4 to 8 inches long. Both male and hermaphrodite flowers occur on the same inflorescence (fig. 66). In Tanganyika, Bigger (*1960*) found as many as 767 panicles on a single tree, with 63 to 67 hermaphrodite and 250 to 400 male flowers per panicle. In Mangalore, Madhava Rao and Vazir Hassan (*1957*) counted 329 florets on a panicle, 316 of which were staminate and 13 hermaphrodite. Only about 5 percent of the hermaphrodite flowers produce fruit (Anonymous, *1964*). In general, the fewer the hermaphrodite flowers the lower the percent set. Usually from one to less than half a dozen fruits mature per cluster (Ochse et al. *1961**, Northwood *1966*).

The five reflexed petals of the ⅓- to ½-inch flower are pale green with red stripes, later turning to solid red (Morton *1961*). In the male flower, about nine stamens are 4 mm long and one stamen, 12 mm, not all of which may be functional. The hermaphrodite flower also has nine short stamens and one about 8 mm long. The one-ovule ovary contains a style that extends above its own anthers to the same height as the long anther of the male flowers. About six flowers open per day on an inflorescence (Northwood *1966*).

The flower opens almost any time of the day, but the peak period of opening is 11 a.m. to 12:30 p.m. The stigma is receptive as soon as the flower opens, but the anthers do not dehisce until 5 hours later, giving opportunity for crossing. The stigma is receptive for only 1 day (Madhava Rao and Vazir Hassan *1957*). The flower produces an abundance of nectar, which is highly attractive to flies, bees, ants, and other insects (Morton *1961*, Free *1970**).

Pollination Requirements

The hermaphrodite flowers are self-fertile but not self-pollinating as indicated by the fact that bagged flowers set no fruit, but when flowers were hand self-pollinated a set of about five fruits per inflorescence was obtained (Northwood *1966*). Madhava Rao and Vazir Hassan (*1957*) obtained a set of 55.5 percent of self-pollinated flowers. Because only one ovule in one ovary exists per flower, there is no need for a large amount of pollen on the stigma.

Pollinators

Madhava Rao and Vazir Hassan (*1957*) indicated that the cashew was wind pollinated, with insects being unimportant, and Bigger (*1960*) also concluded that the high percentage of male flowers suggested that wind was the pollinating agent. The study by Northwood (*1966*), however, leaves little doubt that fruit setting is the result of insect activity. He considered that flies and ants were the principal pollinators. Madhava Rao and Vazir Hassan (*1957*) stated that only black and red ants visited the flowers, but Wulfrath and Speck (*no date*) stated that the flowers are attractive to bees all day for their rich nectar. Smith (*1960*) stated that cashew can be added to the list of plants benefiting from insect pollination. Personal correspondence from bee specialists in Ghana indicates that when bees are moved to cashews the production is increased.

Pollination Recommendations and Practices

There are no recommendations on the use of insects in the pollination of cashew. The evidence strongly indicates that concentration of honey bee colonies in cashew plantings during flowering would at least alleviate the problem of poor setting of fruit. Selection for clones with a higher percentage of hermaphrodite flowers would doubtless enhance fruit production.

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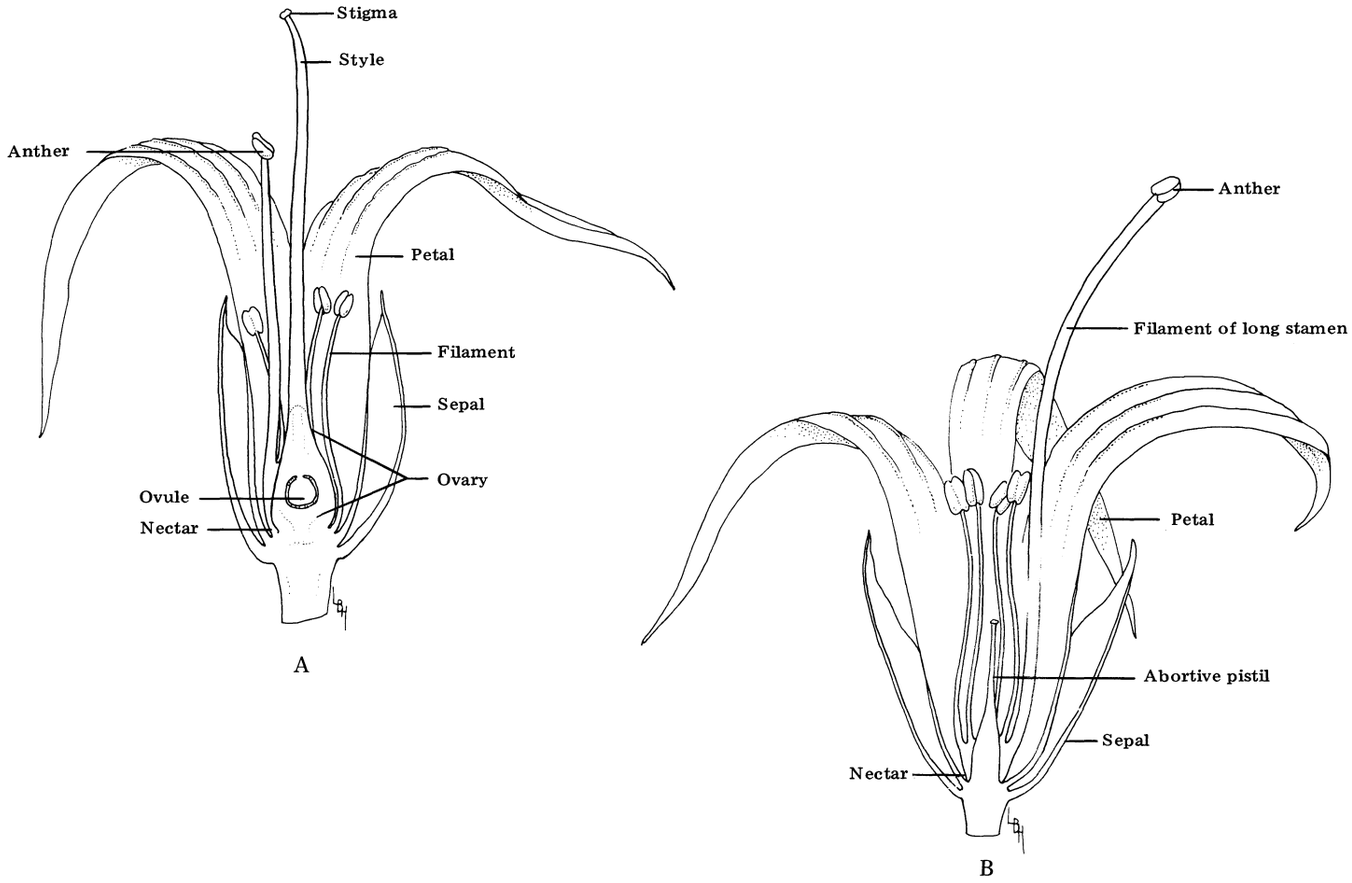

FIGURE 66.—Longitudinal section of cashew flower, × 7. *A*, Hermaphrodite flower with elongated style and short stamens; *B*, male flower with abortive pistil and elongated stamen.

CAULIFLOWER

(See "Cole Crops")

CELERIAC

Apium graveolens L. var. *rapaceum* (Mill.) DC, family Umbelliferae

Celeriac, often called knob-celery, is grown primarily for its roots (fig. 67), which are similar to turnips but with a celery flavor (James *1965*). Otherwise, so far as is known, its pollination requirements are the same as for celery (see "Celery"). Its culture for seed resembles that of carrot (see "Carrot") (Hawthorn and Pollard *1956**).

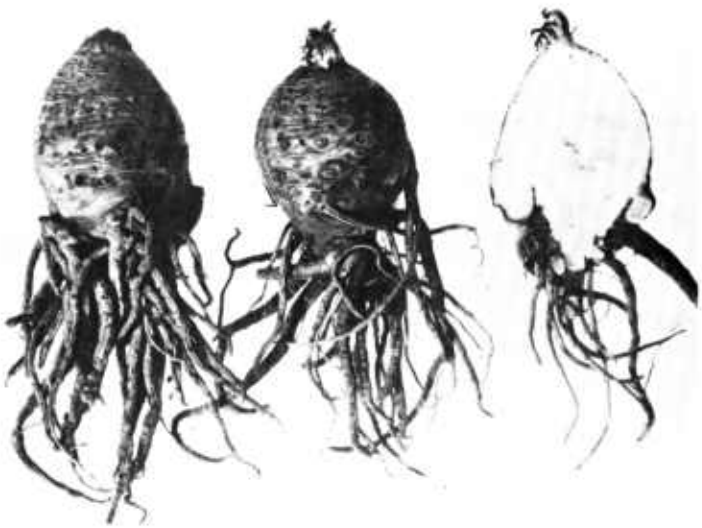

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FIGURE 67.—Celeriac roots.

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CELERY

Apium graveolens L. var. *dulce* (Mill.) DC, family Umbelliferae

In 1970, celery was grown on 31,980 acres, about half of which was in California with Florida second in production. The crop was valued at $85,657,000. The seed was produced primarily in California although some was produced in Michigan, Idaho, and Utah (Hawthorn and Pollard *1954**). Under ideal growing conditions, 3,000 pounds of seed per acre can be produced (Watson *1943*). The acreage devoted to seed production was small—100 to 200 acres (Hawthorn and Pollard *1954**).

Plant

The celery plant is a many-branched glabrous biennial. The first year it develops an upright rosette of leaves with ribbed petioles to 2 feet. This part is harvested as a vegetable. If seed is desired, the plants are left until fall or winter, depending upon the location, then the roots are dug, and stored until spring when they are re-set in another location in 3-foot rows and about 3 feet apart in the row. The plant is then allowed to develop its grooved and jointed flowering stalk about 3 feet high.

Inflorescence

The inflorescence is a series of umbels and umbellets, smaller and less compact than those of the carrot (fig. 68). The small white flowers are arranged in whorls, the outer ones opening first with successive whorls opening over a period of several days. The individual flower opens in the early morning and the anthers dehisce shortly afterwards, sometimes before the petals have fully spread. The afternoon of the following day the petals fall. On the third day, the style begins to rise but is not fully erect until the evening of the fifth day. From about then until about the eighth day, the stigma is covered with stigmatic fluid and is receptive to pollen (Emsweller *1928*).

Celery in bloom is strong smelling but yields abundant nectar and is highly attractive to bees (Root *1919*).

FIGURE 68.—Portion of celery stalk, showing leaves and flowering stem.

Pollination Requirements

The individual flower is self-fertile but incapable of self-pollination, since the pollen is shed and dissipated before the stigma is receptive. The flowers are receptive to pollen of the same plant (Jones and Rosa *1928**), but the pollen must be transferred from the anthers to receptive stigmas of other flowers by insects.

Pollinators

Because of the attractiveness of the flowers to honey bees, these insects are probably the most satisfactory as pollinating agents, provided they are present in sufficient abundance. No information is available on the desirable population density of pollinators on celery, but the eight bees per square yard suggested for carrots (Hawthorn et al. *1960*) should be satisfactory.

Pollination Recommendations and Practices

No recommendations have been made on the use of pollinating insects on celery, probably because of the small acreage devoted to seed production.

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CHAYOTE

Sechium edule (Jacq.) Swartz, family Cucurbitaceae

Chayote is also called Christophine (Purseglove *1968**), mirliton and tayote (Cook *1901*), and trellis squash (Fairchild *1947*). It is a cucurbit crop of minor importance, comparable to the gherkin and citron melon (Hawthorn and Pollard *1954**). It is grown in Australia, Guatemala, Mexico, Puerto Rico, and other subtropical countries. Bukasov (*1930*) reported that chayote was very common in Mexico and Guatemala below 6,600 feet. It has been grown in Louisiana, mainly in home gardens around New Orleans, and there was one small commercial planting in Florida in 1971 (D. O. Wolfenbarger, personal commun., 1971).

Plant

Chayote is a robust, climbing, or sprawling herbaceous perennial with tuberous roots and with vines up to 12 yards long. It resembles a cucumber but is much more vigorous. It prefers shelter from wind and a place to climb (Whitaker and Davis *1962**). The leaves are strongly three-angled, rough textured, and deep green with white veins. The plant grows best at altitudes above 1,000 feet in the tropics in areas of moderate rainfall, but will grow wherever the soil does not freeze and there is sufficient moisture. The top is killed by frost.

The green, jade, or white ivory fruit is similar in shape and size to the avocado (fig. 69), with a single short-lived seed. The fruit is an excellent substitute for summer squash, the roots are comparable to yams, the young leaves are eaten like spinach, and the shoots are acceptable substitutes for asparagus tips.

Whitaker and Davis (*1962**) stated that the cultivars are not clearly separated but are identified largely by the type of fruit such as the cvs. 'Round White', 'Long White', 'Pointed Green', 'Broad Green', or 'Oval Green'. The plant requires day lengths slightly over 12 hours before flowering can begin. For this reason, they do not flower in temperate regions before fall. The fruit reaches full size 30 days after anthesis. The entire fruit, with its single seed, is planted when a new plant is desired. Chayote yields 25 to 100 fruits per plant, averaging 1 pound each.

Inflorescence

Cook (*1901*) stated that the ¼- to ½-inch five-petal pistillate flower is solitary, otherwise it is not different from the more numerous staminate blossoms. The ovary is one-celled with one ovule. Knuth (*1908**, *p. 454, 458*), citing Arcangeli, stated that there are two necta-

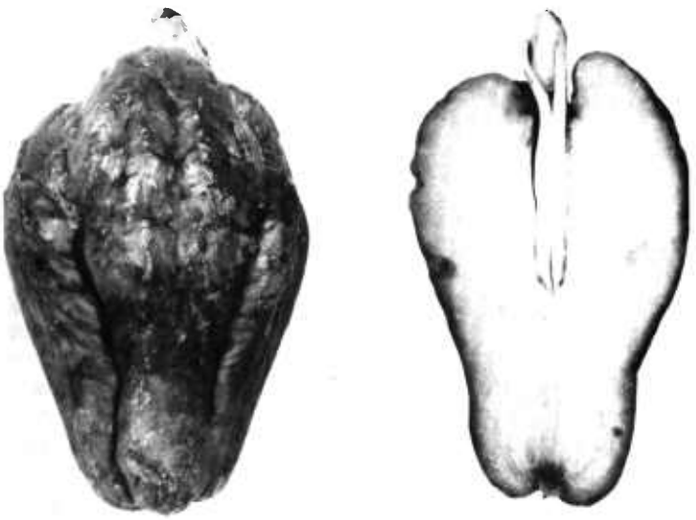

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FIGURE 69.—Complete and sectioned chayote fruit.

ries in both male and female flowers at the base of each of the five lobes of the corolla, 10 per flower. In the male, these nectaries form small narrow inconspicuous pockets, but in the female flowers they are larger and more conspicuous. The explanation offered was that insect visitors find only nectar in the female flowers, therefore the nectary must be more attractive, whereas both pollen and nectar are found in the male flowers. Cook (*1901*) reported that the vines swarmed with bees and the plant was a good honey producer. He also stated that, in the United States, fields of chayote were recognized as good bee pasture, seemingly making up in numbers what the flower lacked in size. Pellett (*1947**) listed chayote as a valuable honey plant. It blooms continually if not killed by frost. Wulfrath and Speck (n.d.) considered it a wonderful source of nectar.

Pollination Requirements

Other than that the plant is monoecious, having staminate and pistillate flowers that are insect pollinated, little seems to be known about the pollination of chayote. Because only a single ovary and seed occurs within a flower, repeated visits by bees to a flower may not be necessary. Fairchild (*1947*) stated that when the flower is fertilized and fruit sets, it grows rapidly to maturity.

Pollinators

Where honey bees are attracted to the flowers in sufficient numbers, additional steps to provide pollination is unnecessary. If production is on a big scale, there might be more flowers than the local supply of insects could pollinate. Should that occur, some provision for additional bees should be made.

Pollination Recommendations and Practices

No recommendations for the use of pollinating insects on chayote have been made.

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CHERIMOYA

Annona cherimola Mill., family Annonaceae[20]

The cherimoya occurs naturally in the Andean valleys of Ecuador and Peru (Purseglove *1968**), but it has been carried to various other subtropical areas of the world where it has become very popular. It is grown to a limited extent in Hawaii and Florida, with an estimated 50 to 60 acres in California (Schroeder *1948*, *1956*). Sarasola (*1960*) stated that about 300 acres are grown in the area of Almunecar, Spain. There are numerous cultivars (Anonymous *1956*, Brooks and Olmo *1952*). The hybrid of *A. cherimola* × *A. squamosa* L., termed "atemoya," has also been cultivated (Ahmed *1936*, Thakur and Singh *1965*).

Plant

The cherimoya tree may reach 30 feet tall but is usually much smaller, somewhat spreading or scraggly, and semideciduous. It sheds its leaves in the spring just before the flowers appear (Schroeder *1941*). It will grow anywhere the avocado will grow. The 'Bays' cv. is the most satisfactory in California (Schroeder *1956*). The plants are usually set about 12 feet apart each way in the field (Ahmed *1936*).

Cherimoyas are grown for the fruit, 3 to 6 inches in diameter and ½ to 2½ pounds in weight, which ripens 5 to 8 months after pollination. The thick brown, green, or gray-green skin has the appearance of rough leather. The fruit can be broken apart easily and the delicious white, sweet (18 percent sugar) pulp eaten out of hand with a spoon. It tastes somewhat like banana or pineapple custard. There may be 20 to 80 black or mahogany-colored oval seed ½- to ¾-inch in diameter that separate quite easily from among the delicious pulp. The fruit is seldom good more than 7 or 8 days after harvest (Sarasola *1960*).

Inflorescence

The rather primitive but scented cherimoya flower may be solitary, or there may be two or three in a cluster on a short peduncle (fig. 70). There are three light-green, fleshy petals about an inch long. Almost hidden at the base of the petals are the numerous but

[20] Other species of *Annona* that are cultivated or sometimes cultivated include: *A. diversifolia* Saff., the llana; *A. montana* Macfad., mountain soursop; *A. muricata* L., soursop or guanabana; *A. squamosa* L., sugarapple or sweetsop; and *A. reticulata* L., custard-apple or bullocks-heart. Unlike *A. cherimola*, none have floral fragrance, but otherwise their pollination requirements may be similar. They are mentioned here because of their popularity in Asia and the tropics and their potential value in our subtropical areas (R. J. Knight, Jr., personal commun., 1971).

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practically filamentless stamens, surrounding but just below the stigma, the whole androecium resembling the immature strawberry fruit. There is no nectary.

When the petals open, towards midday, the stigma is covered with a viscid material and is receptive to fertilization. Receptivity may last 2 to 6 hours depending upon temperature and humidity (Schroeder *1971*). When receptivity ceases, the stigma dries and turns brown. Later in the day, or more frequently the following morning, the stamens shed their pollen (Brooks and Hesse *1953*, Schroeder *1941*, Watts *1942*). If fertilization occurs, the petals drop within about 24 hours and fruit development proceeds. If fertilization is prevented, the entire inflorescence dries and drops within 4 days.

Pollination Requirements

The maturation of the pistil before pollen is available creates a pollination problem and prevents ample fruit set on at least some cherimoya cultivars (Watts *1942*). Schroeder (*1941*) established that the flowers are

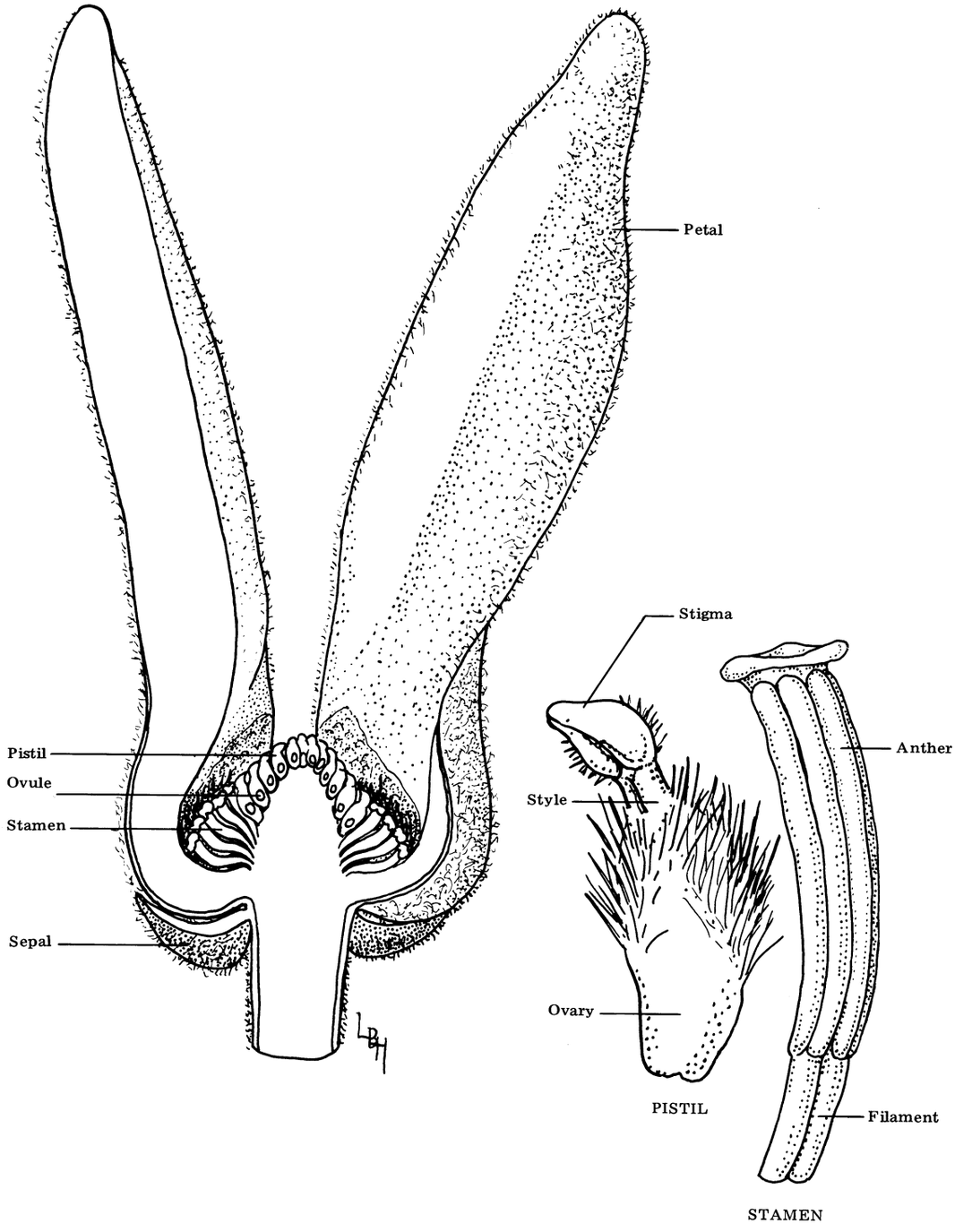

FIGURE 70.—Longitudinal section of cherimoya flower, ×5, with detail showing an additional stamen and pistil, greatly enlarged.

self-fertile but usually not capable of self-pollination. When he hand-pollinated flowers, 70 percent set perfect fruit, 17 percent were misshapen, and 13 percent were "runts." In open-pollinated flowers, only 10 percent produced perfect fruit, 39 percent were misshapen, and 51 percent were runts. The hand-pollinated fruits weighed an average of 461 g, whereas the open-pollinated fruits weighed an average of only 261 g. Thakur and Singh (*1965*) also reported 44 to 60 percent set of hand-pollinated flowers as compared to less than 6 percent of open-pollinated flowers. No explanation was given for the fruit set that occurred in the open-pollinated flowers, but Brooks and Olmo (*1952*) stated that at least the 'Carter' and 'McPherson' cvs. set well without hand pollination.

Thomson (*1970*) stated that near the ocean the stigma stays receptive longer and selfing is normal. Clark (*1925*) also reported that heavy crops result without hand pollination although he admitted that he had never seen pollen-bearing insects visit the flowers, and he thought that self-pollination occurred. Krishnamurthi and Madhava Rao (*1963*) stated that comprehensive studies on pollination of the annonas are needed, with which there seems to be no disagreement.

Pollinators

In general, cherimoya flowers have been considered incapable of self-pollination and unattractive to pollinating insects. Ahmed (*1936*) reported that the flowers do not attract bees but stated: "Insects of the lady-bird type such as *Coccinella* sp. and *Scymnus* sp. have been observed to visit the flowers either in search for one of the preys such as aphis, or mealy-bugs or feeding on the pollen-grains. . . . Ants may also be responsible to a smaller extent." He also stated, "Under normal conditions, as in the home-forests of anonas the insect agency is sufficient. But under cultivation, it has been noticed that such agents may be very scarce or absent altogether, thus inducing very low fruit-setting or none." Wester (*1910*) concluded that nonproductiveness of cherimoyas was due to the scarcity of pollinating insects, but Schroeder (*1971*) stated that insects visited the flowers upon occasions. Sarasola (*1960*) doubted that the good fruit set in Spain was the result of special pollinating insect activity but resulted from self-pollination, although he offered no proof for this assumption.

Usually, growers collect pollen by hand from dehiscing anthers, then pollinate stigmas the following day. Ahmed (*1936*) showed that a man and a little boy working full time daily throughout the 6-week flowering season could pollinate 1 acre. There seems to be no question that hand-pollinated flowers produce more and better fruit than is obtained under natural conditions, but no attempt has been made to influence the supply of pollinators available to the flowers.

Pollination Recommendations and Practices

Cherimoya growers either collect pollen and hand-pollinate the flowers or leave the plant to chance pollination and the possibility of little or no set of high-quality fruit.

Considering the high cost of hand pollination, the fact that insects visit the flowers only occasionally, and that fruit set occurs in the natural home of cherimoya, other steps should be taken to improve the production and decrease costs. A search might be made for the particular species of insects responsible for the pollination of the plants in their native habitat. Attention might be given to selecting self-fertile cultivars. An immediate step might be to supply "saturation pollination" with honey bees. This has proven feasible on some other crops. Bee visitation should be sufficient to get an ample supply of pollen to all parts of the stigma at the earliest possible moment after it becomes receptive.

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CHERRY

Prunus spp., family Rosaceae

Cherries grown commercially in the United States include sweet cherries (*P. avium* L.); tart, sour, or pie cherries (*P. cerasus* L.); and Dukes (probably *P. gondouinii* (Poit. & Turp.) Rehder). The mahaleb (*P. mahaleb* L.) and the mazzard, a wild or seedling form of *P. avium*, are used as rootstock upon which the fruiting types are grafted. The mahaleb is used much more extensively than the mazzard (Howe *1926*, USDA *1967*).

In 1970, 121,650 tons of sweet cherries, including Dukes (usually grouped with the sweet cherries), were produced, primarily on the West Coast. Oregon produced 40,000 tons; Washington, 25,800; California, 25,400; and Michigan, 21,000 tons. There were 118,640 tons of tart cherries produced—79,000 in Michigan and 18,200 tons in New York. Several other States produced smaller amounts of both kinds.

The value of the 1970 sweet cherry crop was $43.2 million, compared to $17.9 million for the tart cherries.

Plant

The deciduous cherry tree does not thrive where summers are long and hot, yet the blossoms are susceptible to injury by cold spring weather (Cullinan *1937*). For these reasons, the growing areas are limited to the more northerly States, except for some areas of high altitude and temperatures moderated by large bodies of water such as the oceans or the Great Lakes.

The trees are planted at various distances apart but most commonly 20 feet for tart cherries and 25 to 32 feet for sweet cherries. They are usually planted at equal distances apart, except when the contour or hedgerow systems are used (Griggs *1970**).

When hedgerow planting is used in California, the trees are placed 6 feet apart in the row and the rows are spaced 4 feet apart. The pollenizer trees are placed at every eleventh location in every other row, offset by five trees, about one pollenizer for each 20 recipient trees (Ryugo and Mikuckis *1969*).

Inflorescence

When in bloom the cherry tree displays white, faintly fragrant flowers in clusters of two to five on short lateral spurs on the many branches (fig. 71). The five petals of the flower are oval, white, and rather widely spread. There is a single upright pistil and about 30 loose stamens (fig. 72). The sweet cherry flower is about an inch across, the tart cherry slightly smaller. The flower remains open 7 to 8 days. When the flower opens the stigma is receptive, but the anthers are closed. Anthers begin opening shortly after flowers open and continue into the second day (Knuth *1908*, p. 703*; Srivastava and Singh *1970*). Nectar is secreted on the inner surface of the receptacle. Eaton (*1959*) stated that pollination on the first day after anthesis was much more effective than pollination on the second day, and he stressed the importance of the earliest possible pollination particularly in cultivars such as 'Schmidt'.

Both pollen and nectar are attractive to insects, particularly bees, throughout the day if weather permits. The sweet cherry nectar is much richer in sugar (55 percent sugar) than the tart cherry nectar (28 percent) (Vansell *1942**). Pellett (*1947**) stated that in California the cherry is one of the best fruit trees for honey production. Because of the time of year that cherries bloom, colonies are frequently not sufficiently strong to store surplus amounts and cherry honey is practically unknown. There are usually few other floral visitors except honey bees, although Nevkryta (O.M.)

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FIGURE 71.—Fruiting branch of cherry, showing spurs and clusters of flowers.

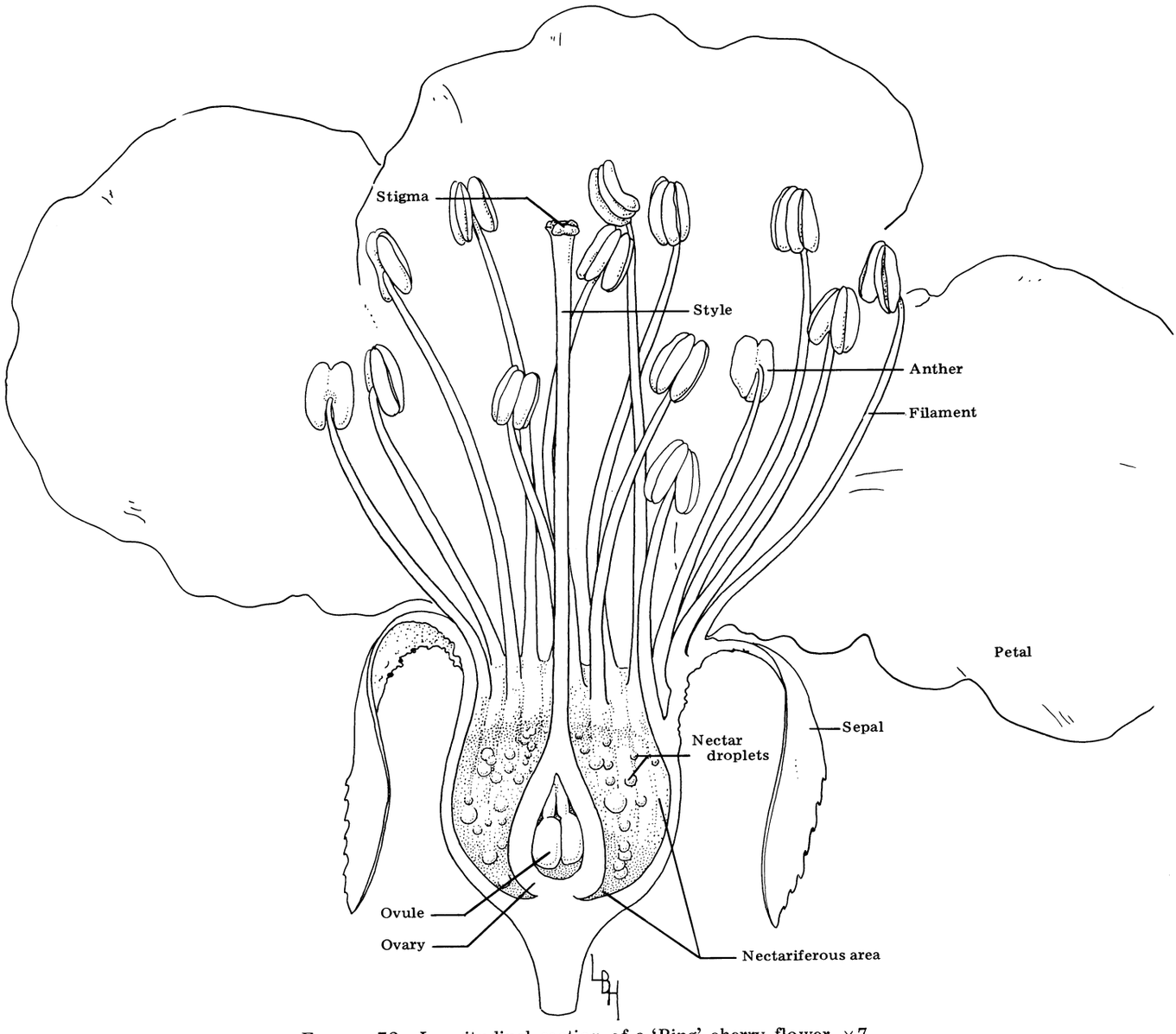

FIGURE 72.—Longitudinal section of a 'Bing' cherry flower, ×7.

(*1957*) reported that only 60 percent of the insects on flowering sweet cherries were honey bees.

Pollination Requirements

The sweet cherry was shown by Gardner (*1913*), Anonymous (*1926*), Overholser and Overley (*1931*), Crane and Brown (*1937*), and Way (*1968*) to be self-sterile or self-unfruitful, and, furthermore, the most important cvs., 'Bing', 'Lambert', and 'Napoleon' ('Royal Ann'), were shown to be interincompatible. This interincompatibility continues to be a problem (Griggs *1970**), although Lapins (*1971*) reported that the 'Stella' cv. was a self-compatible sweet cherry, derived from a radiation-induced self-fertile selection obtained from England.

The attitude toward the pollination of tart cherries has changed over the years. Crane (*1925*), Dujardin (*1921*), Hooper (*1924*), and Schuster (*1925*) stated that the tart cherry was self-sterile or nearly so. Einset (*1932*) said that there was a continuous range from complete self-fruitfulness to complete self-unfruitfulness. Roberts (*1922*) and Marshall et al. (*1929*) said the blossoms were self-fertile and that insect pollinators were not needed. Murneek (*1930*) said they were self-fertile but benefited from insect pollination in unfavorable seasons. However, Hootman (*1931, 1933*) showed that only 4 percent of screened blooms (of 'Montmorency' cv.) produced fruit as compared to 49 percent that were hand pollinated. Lagasse (*1928*) and later Vansell and Griggs (*1952**) stated that the commercially important tart cherry cultivars are self-fruitful if enough pollinizing insects are available, but better crops can be expected if the orchard contains more than one cultivar. The knowledge is now fairly well accepted that all of the important tart cherry

cultivars will set fruit with their own pollen, but only after it is transferred by some outside agency from the anthers to the stigma.

The amount of fruit set expected on cherries has been mentioned by various research workers. All concede that set of every blossom is undesirable. Shoemaker (*1928*) reported a range of 13 to 60 percent with an average of 35 percent set of sweets, 21 to 42 percent with an average of 33 percent for tart cherries, and 10 to 53 percent with an average of 20 percent set for Dukes. As previously mentioned, Hootman (*1931*) obtained 49 percent set of hand-pollinated 'Montmorency' tart cherries. Gardner (*1913*) stated that 50 percent of the sweet cherry flowers should set. Griggs et al. (*1952**) reported an overall average for several seasons of good crops at 21 to 32 percent set. Griggs (*1970**) stated that self-fruitful cultivars of sweet cherries may be undesirable if they tend to set too heavily. Also, the fruit fails to develop adequate size without expensive thinning practices.

Luce and Morris (*1928*) stated that if the cherry blossom is not pollinated, the fruit develops to the size of a garden pea, then drops to the ground.

Tukey (*1925*), Free and Spencer-Booth (*1964*), and numerous others have reported decreasing production with increased distance from the pollenizer row of sweet cherries.

In summary, all cherries are basically incapable of automatic self-pollination. Tart cherries will set fruit if the pollen is transferred from anthers to stigma of the same flower but will set more fruit if other cultivars are interplanted in the orchard. Compatible cultivars can only be determined by tests (Griggs *1953**). Sweet cherries, with the exception of the 'Stella' cv. (Lapins *1970*), will not set fruit with their own pollen, only with pollen of certain other cultivars.

Way and Gilmer (*1963*) showed that healthy trees are important in the set of cherries. When they used pollen from trees infected with tart cherry yellows disease, fruit set was only 25 to 90 percent of that with pollen from healthy trees. Such pollen would either decrease production or create a demand for more insect pollinators.

Pollinators

Wind is not a factor in cherry pollination, as has been clearly and repeatedly established over the years (Roberts *1922*, Burtner *1923*, Murneek *1930*, Claypool et al. *1931*, and Brown *1968*). Most researchers and growers give the primary credit for the pollination of cherries to honey bees. A heavy pollinator population is needed and flowering occurs too early in the year for other insects to be plentiful. Hendrickson (*1922*) stated that as early as 1894 a government report showed that a cherry crop near Vacaville, Calif., was greatly increased when several colonies of honey bees were placed in the orchard. Morrill (*1899*) also reported that bees increased cherry production. Gardner (*1913*) was the first to establish scientifically the need for pollination, and he stressed the importance of bees. This was supported with further research by various others, including Wellington (*1923*), Tuft and Philp (*1925*), Hooper (*1930*). Claypool et al. (*1932*), Weiss (*1957*), Skrebtsova and Iakovlev (*1959*), Eaton (*1959*), and Brown.[21]

The fact that possibly only one pollen grain is needed to pollinate a cherry flower would indicate that repeated bee visits may be unnecessary, providing the pollen grain is compatible and successful fertilization of the ovule ensues. To play safe, the grower should insure the transfer of many pollen grains to the stigma. Tart cherry pollen may come from the same flower or the same tree, although greater benefit is usually derived if pollen comes from another cultivar. Sweet cherry pollen must come from another—and compatible—cultivar; therefore, a high degree of bee activity on the tree and between trees is required to adequately pollinate the crop.

The proper pollinator population is not easy to establish. Griggs et al. (*1952**) counted 30 to 40 bees per sweet cherry tree that had been in production several years. The number of colonies per acre necessary to provide this population was not given. Skrebtsova and Iakovlev (*1959*) spoke of "saturation pollination" of cherries, but their data indicated that even with their maximum of 3.8 colonies per hectare (less than two colonies per acre) maximum set of all flowers was not achieved.

Pollination Recommendations and Practices

Schuster (*1925*) recommended one strong colony for each 1 to 2 acres "if the stands are strong." Tufts and Philp (*1925*) recommended at least one colony per acre. Marshall et al. (*1929*), Murneek (*1930*), Philp (*1930, 1947*), and Stephen (*1961*) concurred with the one-colony-per-acre recommendation. Hooper (*1930*) recommended that colonies be placed in the orchard during flowering. Brown (*1968*)[22] recommended four to five colonies per acre for his area of Oregon, the colonies placed in groups on each 5 to 10 acres of the orchard. Eaton (*1962*) stated that strong colonies should be brought into the sweet cherry orchard on or before the day the first flowers open, because placement in the orchard even 1 day late could result in a reduced crop. Auchter and Knapp (*1937**) recommended one colony containing 7 to 9 pounds of bees to every 3 to 4 acres but conceded that many growers use one colony for each acre or two. Coe (*1934*) and Hoffman (*1965*) urged the use of bees but did not designate the concentration. Nevkryta (A. N.) (*1957*) recommended four to five colonies per hectare (about two colonies per acre). Skrebtsova and Iakovlev (*1959*) recommended "saturation pollination" of the orchard, and showed that with 3.8 colonies per hectare, 15 percent of all flowers set fruit but with 2.8 colonies only 13 percent set.

Luce and Morris (*1928*) recommended one colony per acre. Schuster (*1925*) also reported, "It is becoming

[21] BROWN, K. BEES FOR SWEET CHERRY POLLINATION—UNDER WILLAMETTE VALLEY CONDITIONS. Polk County (Oregon) Agr. Ext. Serv. Agent, 2 pp. 1969. [Mimeographed.]

[22] BROWN, K. POLLINATION OF ROYAL ANN (A-10) IN THE WILLAMETTE VALLEY. Polk County (Oregon) Agr. Ext. Serv. Agent, 4 pp. 1968. [Mimeographed.]

the practice for cherry growers either to keep their own bees or to hire stands of bees during the blooming season." To take advantage of this needed cross-pollination between cultivars, various planting plans of trees in the orchard were recommended, ranging from one pollenizer and nine recipient trees to a 1:1 ratio.

This recommended usage of bees barely seems to be accepted by the growers. Kelly (*n. d.*) reported that during 1959–63, tart cherry growers in Pennsylvania spent only 28 cents per acre for pollination fees; when colonies were rented, the fee was $4.50 per colony. Considering the pollination needs of this crop and the apparent lack of effort expended by these growers, one is not too surprised at his statement: "In the last decade sour cherry production and growers have both declined 31 percent." However, pollination is probably not the only reason for this decline. In a similar study made in Michigan on 37 tart cherry farms, Kelsey (*1964*) reported that growers paid an average of $1.33 per acre for bee pollination. The number of colonies of honey bees utilized, for which there was no remuneration, was not disclosed.

In general, most cherry growers make some attempt to have bees present in their cherry orchards at flowering time. Frequently, if bees are rented and there are 2 or 3 days of good weather for bee flight, the tart cherry grower is ready for the bees to be removed.

The number, strength, and placement of colonies necessary to provide 50-percent set of cherry flowers (Gardner *1913*, Hootman *1931*) is not known but should be determined. Also, the difference in the need of bee pollination between sweet and tart cherries should be determined.

For highest production of cherries—the setting of the maximum number of blooms for greatest production of sizeable fruit—cross-compatible cultivars that flower at the proper time must be interplanted in sweet cherry orchards, and possibly also in tart cherry orchards, although large solid blocks are known to produce satisfactory crops. For highest production of either sweet or tart cherries as many as five strong colonies of honey bees per acre should be placed on each 5 to 10 acres just before flowering time. The colonies should contain 600 in^2 or more of brood and 7 to 9 pounds of bees.

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CHERVIL

Anthriscus cerefolium (L.) Hoffm., family Umbelliferae

Chervil, or salad chervil, is of minor importance even in California where it is grown (Rosengarten *1969**) but is of more importance in Europe. It is used primarily as a substitute for parsley (Thompson and Kelly *1957*).

Plant

Chervil is usually seeded in early spring but sometimes in the fall. The plants are usually grown in 12-inch rows, 6 to 10 inches apart in the row. The leaves may be harvested in 6 to 8 weeks after planting. Chervil produces a seedstalk to 2 feet tall, sets a crop of seed, and dies by midsummer (Knott *1949*). Its culture is similar to that of coriander (Sievers *1948*).

Inflorescence

The minute five-petaled white flowers are in umbels and are hermaphrodite or pseudohermaphrodite stami-

nate (Knuth *1908**, *p. 512*). According to Kerner (*1897**, *p. 325*), the anthers of all species of *Anthriscus* have two kinds of inflorescences. The umbels that blossom first have principally true hermaphrodite flowers with a few isolated staminate flowers. The later umbels are only staminate. The hermaphrodite flowers shed pollen before the stigma of the same flower becomes receptive. Kerner (*1897**, *p. 325*) stated: "... the anthers, borne on very thin filaments, are brought one after the other to the center of the flower, where they dehisce and scatter their pollen, and the day following they drop off. After all 5 stamens have dropped off the stigmas become mature and receptive. They continue in this condition for 2 days and during this period are liable to crossing with pollen of other plants." Then the pedicels of the umbels bearing only staminate flowers elongate, so that these flowers stand over the hermaphrodite flowers with their mature stigmas, and their anthers release pollen that falls upon the stigmas below.

Each flower has a two-celled ovary, each of which produces two seeds attached to each other by a Y-shaped stalk (Bailey *1949**). Apparently, both nectar and pollen are produced by the flowers.

Pollination Requirements

The early flowers are dependent upon pollen brought to them from other plants. Later flowers receive pollen by gravity from the anthers above them. Self-fertilization within a flower is impossible.

Pollinators

Knuth (*1908**, *p. 513*) mentioned the honey bee and various other hymenoptera, as well as coleoptera and diptera, as visitors to the chervil flowers. Gravity also contributes to the pollination. The agitation of the flowers by the insects can contribute to the rain of pollen on the stigmas below.

Pollination Recommendations and Practices

None, probably because of the small acreage necessary to produce the required seed. Large plantings would doubtless benefit if bees were plentiful within the field.

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CHESTNUT

Castanea spp., family Fagaceae

Chestnut trees are cultivated for their nuts or as ornamentals. Probably the most notable species was the large and graceful ornamental American chestnut (*C. dentata* (Marsh.) Borkh.) (fig. 73), which extended from Maine southwest to Arkansas (Munns *1938*). It has been almost completely destroyed by blight. The Japanese chestnut (*C. crenata* Sieb. and Zucc.) and the Chinese chestnut (*C. mollisima Blume*) are both cultivated for their nuts.

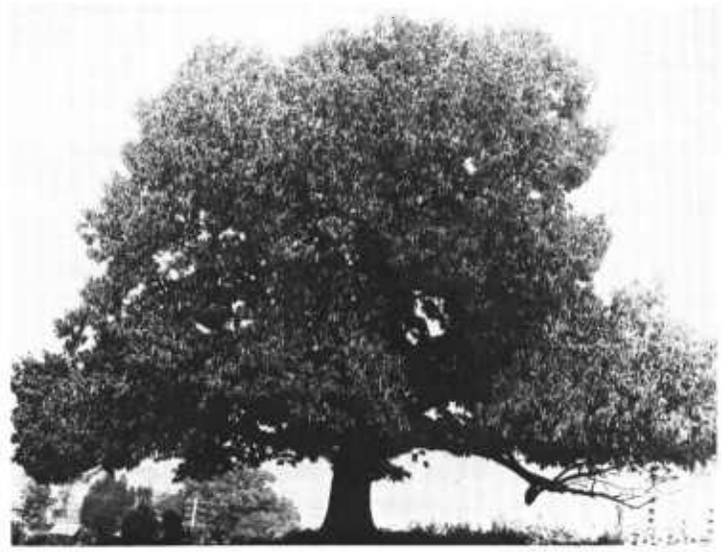
Plant

Chestnut is a deciduous tree or shrub, which is cultivated in a similar manner to other deciduous nut trees. It bears brown nuts, about an inch in diameter, which are usually consumed after they are roasted. From one to nine nuts are produced in a spiny involucre or burr (fig. 74).

Inflorescence

The fragrant inflorescence is about 12 inches long (fig. 75). It consists of a group of catkins 4 to 8 inches long. Catkins bearing only staminate florets make up the bulk of the inflorescence. Those produced near the base bear both staminate and pistillate florets. The latter, near the base of the catkin, are few in number. Usually three pistillate florets make up an involucre, each floret capable of producing three nuts.

Bees visit the staminate flowers for both nectar and pollen (Hazslinszky *1955*, McKay *1939*, Pellett *1947**). the degree of visitation depending upon competition from other flowers. The bees do not intentionally visit the pistillate flowers, but may accidentally come in contact with them while visiting the staminate flowers.



PN-3786

FIGURE 73.—American chestnut tree. (Photograph taken in 1915.)

PN-3787

FIGURE 74.— Burrs and nuts of Chinese chestnuts.

Pollination Requirements

Reed (*1941*) concluded that chestnut is self-sterile. He noted that isolated trees bear few nuts or even a fair crop, but best results are invariably obtained from trees in a mixed orchard where good pollen is available. McKay (*1939*) reported finding a *C. crenata* tree that was completely male-sterile. Its nectar production was normal, and it produced a normal crop of nuts. He also reported male sterility in *C. sativa* Mill. and *C. sativa* × *C. dentata*. Later, McKay (*1942*) reported that when flowers of *C. mollissima* were self-pollinated only 1.3 percent of the flowers set fruit, when they were cross-pollinated 34.9 percent set, but when they were open-pollinated 68.1 percent set. This showed the need for transfer of pollen between plants.

Crane et al. (*1937*) stated: "As a rule all chestnuts are more or less self-sterile and they bear better when interplanted with other cultivars."

Kawagoe (*1955*) stated that the stigmas may remain receptive as much as 45 days and that cross-pollination was best effected 8 to 22 days after stigma emergence.

Ohno et al. (*1958*), considering the effect of rain on the pollination of chestnuts, tested the effect of water on the pollen. They found that 17 to 19 percent of their pollen germinated even after soaking in water in the laboratory for 9 hours. In the field, this pollen caused 48 to 50 percent set of fruit if cross-pollinated but only 3 to 9 percent set if it came from the same plant.

Watanabe et al. (*1964*) reported much higher bur-set on adjoining rows to the pollenizer row than on the (decreasing) 3d to 10th rows. They recommended that pollenizer cultivars be set in the ratio of 1 to 1 or 1 to 2 of the main cultivar.

Pollinators

Crane et al. (*1937*) and Clapper (*1954*) stated that chestnut pollen is produced in great abundance and is carried by wind. However, J. W. McKay (personal commun., 1972) questioned this. He indicated that honey bees, rose chafers, and wild bees are highly beneficial to chestnut in the transfer of pollen, and they frequently visit the staminate flowers in large numbers. He also considered that for highest production on younger trees, a high population of pollinators is especially needed. If production of newer cultivars and hybrids expands, the value of insects in cross-pollination for maximum set should be more fully explored.

Pollination Recommendations and Practices

There are no recommendations on the use of pollinating insects on chestnut although evidence shows they are needed.

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FIGURE 75.— Chestnut inflorescence.

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CHICORY

Cichorium intybus L., family Compositae

Chicory, also known as succory, is cultivated to a limited degree as a salad or potherb, or its taproot is roasted, ground, and used as a coffee substitute or admixture (Purseglove *1968**). It is also grown in some countries for alcohol distillation from the roots (Davidovich and Davydova *1947*).

Plant

Chicory is a stout, deep-rooted perennial, 3 to 6 feet tall. It is a practically leafless herb, branching and diffuse when in bloom. The seeds are planted in the spring, and the roots are dug in the fall, stored, and replanted toward spring for foliage harvest (Jones and Rosa *1928**). The plant is most noticeable in the mornings when its azure-blue flowers are open.

Inflorescence

The composite 1½-inch flower opens early in the morning (5:30 to 7:30 a.m.) and closes about noon (Dinakaran and Sundaraj *1960*). It contains 20 to 30 drab disk flowers and about 12 beautiful, ½-inch-long, blue ray flowers. When the floret opens, the style covered with sweeping hairs extrudes through the short anther tube then twists into a one- or two-coil spiral; when this occurs, the stigma comes in contact with the pollen on the sweeping hairs (Tesi *1967*). This pollen, along with the nectar at the base of the corolla tube is available to bees and many other nectar- and pollen-feeding insects. Pellett (*1947**) stated that chicory is a good source of pollen and nectar for honey bees and that the bees produce from chicory a yellowish-green honey.

Pollination Requirements

Knuth (*1908*, p. 672*) stated that when the stigma comes in contact with the pollen adhering to the style, automatic self-pollination occurs in the absence of insects. Rick (*1953*) found that self-pollination was unsuccessful because chicory is self-incompatible. Stout (*1916*) selfed plants and obtained no seeds, but his open-pollinated plants set 61 percent of the flowers, which also showed that the plants were self-incompatible. Dinakaran and Sundaraj (*1960*) stated that fertilization occurs both within and between heads as a result of insect activity. Pecant (*1958*) found all stages of compatibility in each cultivar studied, indicating that seed production would be materially benefited by pollinating insect activity. Davidovich and Davydova (*1947*) conducted cage tests with two cultivars, 'Magdeburg' and 'Golova Ugrya', and the data below, taken from their report, shows that both cultivars benefited from insect pollination. Both cultivars had only a few empty achenes if bees were present, but many if bees were absent.

Exposure to pollinators	'Magdeburg' cv.			'Golova Ugrya' cv.		
	Full	Puny	Empty	Full	Puny	Empty
	Percent of achenes					
Caged with bees	61.4	22.7	15.9	50.0	40.5	9.5
Open	59.5	4.3	36.2	43.3	30.7	26.0
Caged without bees	14.7	5.0	80.3	10.3	7.9	81.8

Davidovich and Davydova (*1947*) also observed bees in two open fields, one of which was 300 m from the

apiary and one 3 km away. Near the apiary, 12 bees per 10 m^2 resulted in 11 g seed per plant; whereas at the distant location where only six bees per m^2 were observed, only 7 g of seed per plant were obtained. The results showed that about 1 bee per square yard resulted in almost twice as much seed as one-half bee per yd^2. This showed the value of and need for bee pollinators for commercial production of chicory seed.

Pollinators

There seems to be little information on the pollinating agents of chicory other than honey bees. The type of flower and its relationship to other better known plant species would indicate that it is not wind pollinated. This is supported by the data obtained in the above experiment by Davidovich and Davydova (*1947*). Knuth (*1908*, p. 672*) mentioned numerous insect visitors in the Coleoptera, Diptera, Lepidoptera, and Hymenoptera. Within the Hymenoptera, he mentioned the genera *Andrena*, *Anthidium*, and *Apis;* and many spp. of *Halictus*, *Osmia*, and *Prosopis*.

Of these insects, only the honey bees have been demonstrated to be effective, and they can be concentrated on the crop effectively when and where desired.

Pollination Recommendations and Practices

None.

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CHINESE GOOSEBERRY ("KIWI")

Actinidia chinensis Planch., family Actinidiaceae

The chinese gooseberry, or yangtao, is produced commercially on a few acres in California. It is produced on a larger scale in New Zealand (where it is called the Kiwi-berry) and in the orient. The name "gooseberry" is derived from the similarity in the taste of the fruit, not to a botanical relationship to *Ribes* spp. (Menninger *1966*).

Plant

Chinese gooseberry is a vigorous, deciduous, dioecious shrub that may climb to 25 feet. It has 5-inch oval leaves that are densely hairy underneath. When young, they are bright red but change to brown toward maturity. The vine is usually trained upon a trellis or pergola (Bailey and Topping *1950*). The plants are usually spaced about 15 feet apart, 175 per acre (Avent *1959*), with one staminate or male plant to 5 to 10 pistillate or female plants. Smith (*1961*) stated that no female plant should be more than three or four plants away from a male plant.

The brownish oval 1½- to 3-inch long fruit (fig. 76) may be peeled and eaten out of hand with sugar or honey, used in a salad, stewed, preserved, or used in sauces.

A single pistillate plant, if well pollinated, may produce 700 pounds of fruit in a season (Menninger *1966*).

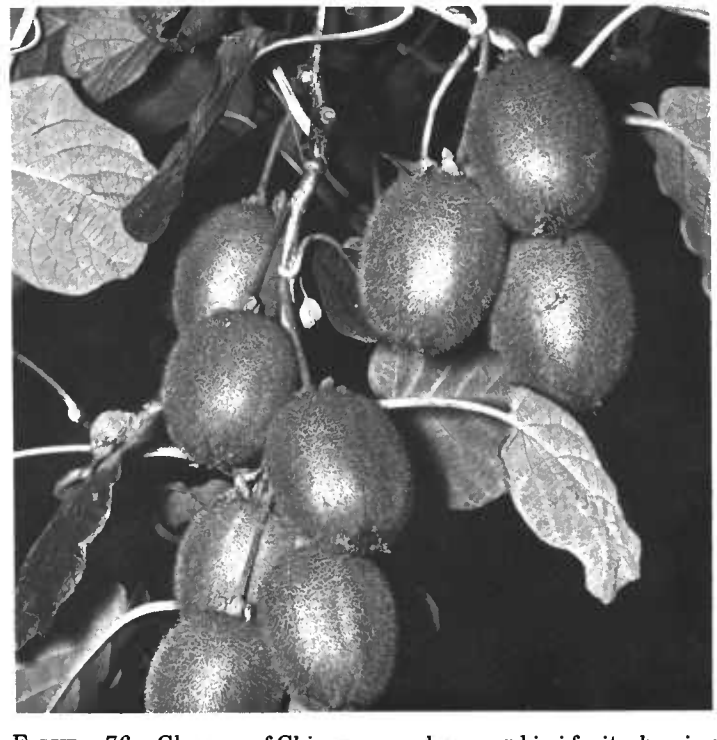

FIGURE 76.—Closeup of Chinese gooseberry or kiwi fruit, showing the fuzzy skin.

Inflorescence

The five- to six-petal flower is white, changing to yellow with age, 1½ to 2 inches in diameter, attractive, and fragrant (fig. 77). The ovary is many celled, and it produces the fruit with many seeds. The pistillate flower can be easily recognized by the swollen ovary below the base of the petals. The staminate flowers have a vestigial ovary within the corolla, surrounded by numerous stamens. There are several styles in the pistillate flower, which are also surrounded by numerous stamens that produce no viable pollen (Schroeder and Fletcher *1967*).

Pollination Requirements

Pollen must be transferred from the flowers on staminate plants to those on pistillate ones, therefore both types of plants must be present in the orchard, and they must flower at the same time.

Pollinators

Schroeder and Fletcher (*1967*) stated that wind and insects seem to be the pollinating agents. The general structure of the plant, and the need for numerous pollen grains on the stigma to fertilize the ovules and produce

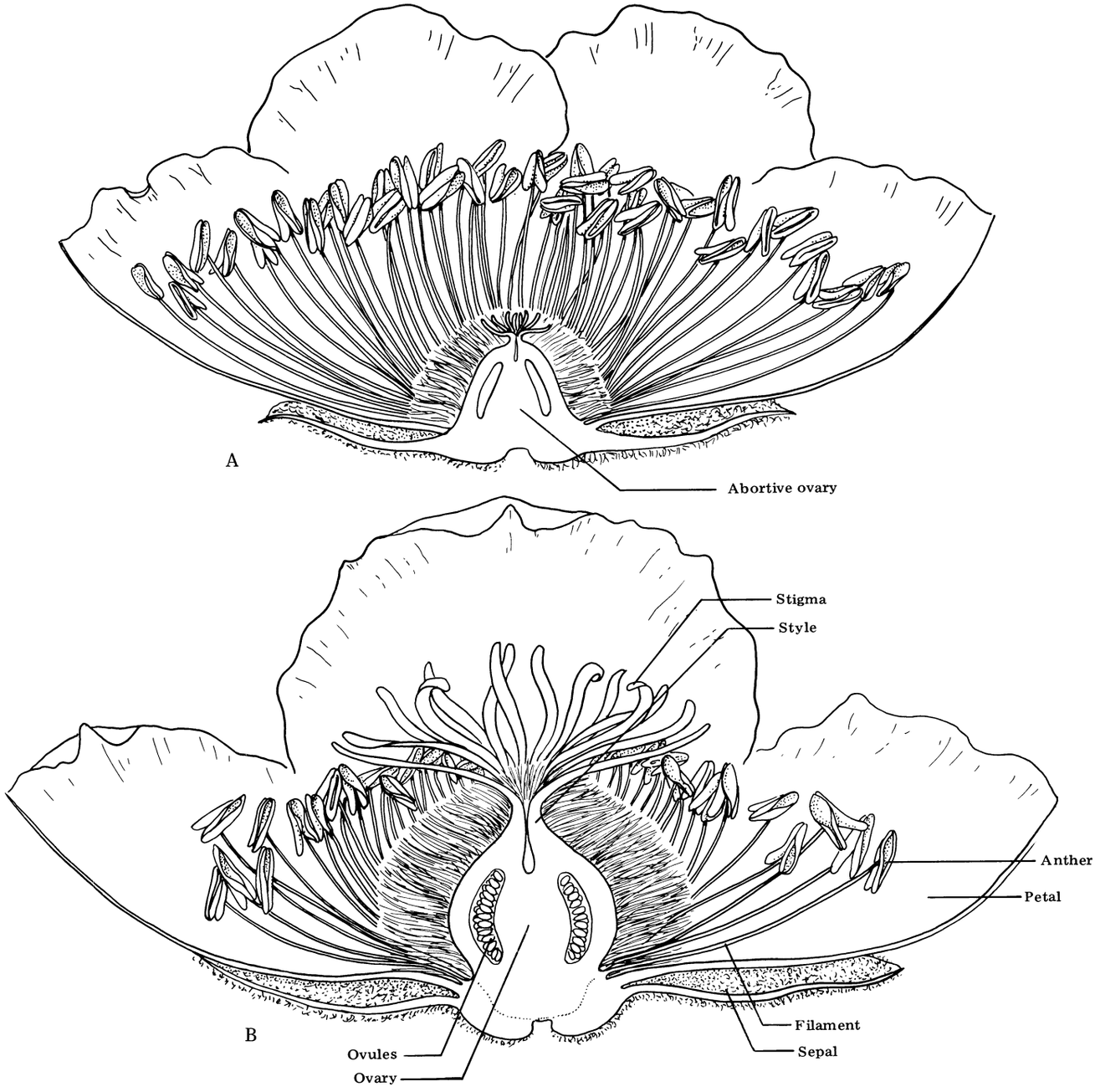

FIGURE 77.—Longitudinal section of Chinese gooseberry, or kiwi, flowers, ×4. *A*, Male; *B*, female.

the numerous seeds, indicate that wind would be a poor pollinating agent. The flower seems ideally adapted to bee pollination.

Pollination Recommendations and Practices

Some growers in California have colonies of honey bees placed in their plantings. The literature indicates that bees are essential.

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CHIVE

Allium schoenoprasum L., family Amaryllidaceae

Chive (see "Onions") seeds are produced in limited quantities in the United States because the plant can also be propagated vegetatively. Even so, chives are not grown to any great extent. The leaves are used in fresh salads and for flavoring of other foods.

Plant

Chives are perennial plants, much smaller than onions, and they grow in compact clumps or clusters. The leaves are about one-fourth the size of onion leaves. The seedstalk is short and, after the first year, appears annually (Hawthorn and Pollard *1954**).

Inflorescence

The 1-foot-tall chive inflorescence has only 25 to 100 florets, and when seeds are produced, many shatter. It is considered to be a "shy" or poor seed producer.

Pollination Requirements

Knuth (*1909*, p. 457*) stated that the flowers are feebly protandrous. The anthers release their pollen slightly before the stigma becomes receptive, and the flowers close at night so that self-pollination is possible if insect pollination fails. Kropacova et al. (*1969*) indicated that chives, like onions, require bee pollination.

Pollinators

Kropacova et al. (*1969*) reported that honey bees were the primary pollinators of chives. They indicated an insufficiency of bees on the older plants.

Pollination Recommendations and Practices

None.

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CICER MILKVETCH

Astragalus cicer L., family Leguminosae

Cicer milkvetch offers possibilities as a good pasture crop in the irrigated and dryland areas in the Great Plains and Western States. Apparently, it is not grown commercially, although Hafenrichter et al. (*1968*) considered it superior to alfalfa. Townsend (*1970*) pointed out that there is a scanty information on this crop.

Plant

Cicer milkvetch is a perennial legume, 2 to 3 feet tall, that spreads by rhizomes. In growth characteristic, it varies from decumbent to prostrate. Like most of the members of *Astragalus*, it is well adapted to arid conditions (Bleak *1969*). Although little work has been done on *Astragalus* spp., it is known that some species are useful honey plants, whereas other species are poisonous to bees and livestock (McKee and Pieters *1937*).

Inflorescence

The typical papilionaceous flowers of yellow or purple are in axillary racemes or heads with many ovules. At Fort Collins, Colo., flowering occurs during June and July (Townsend *1970*).

Pollination Requirements

Townsend (*1971a*) reported good seed-set on open-pollinated cicer milkvetch plants at Fort Collins but obtained no seed from 1,400 nonmanipulated

florets on plants in a growth chamber (*1971b*). Those that were manipulated set 5.29 seeds per raceme, whereas the open-pollinated racemes set 100 to 300 seeds each. In personal communication (1971), Townsend stated that in his opinion little seed would be set on *A. cicer* in the field without insect pollinators.

The Gifu (Japan) Agricultural Experiment Station (*1954*) conducted a test on the value of honey bees in the pollination and seed setting of a species referred to as *A. sinensis*. Seed production in cages where bees were excluded was only about 70 lb/acre; in cages with honey bees it was almost doubled, 130 lb/acre, and in open plots, 980 lb/acre. The reason for the great difference between caged and open plots was likely due to the cage effect. The relation between the pollination requirements of *A. cicer* and *A. sinensis* is not clear.

If *A. cicer* develops into a crop of importance, its need for and importance of insect pollination should be established.

Pollinators

Honey bees appear to be satisfactory pollinators of *A. sinensis*. Their value on *A. cicer* is unknown but should be determined.

Pollination Recommendations and Practices

None.

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CITRUS

Citrus spp., family Rutaceae

The kind of citrus crop produced, its volume, area of production, and dollar value are shown in table 8. As this table shows, the bulk of the citrus crop is produced in Florida, and oranges and grapefruit account for more than 80 percent of all the fruit produced.

Plant

The cultivated citrus plants are mostly shrubs or small trees with dense foliage; sweet-smelling, whitish to purple flowers that are often produced in great profusion; and greenish to golden fruit. The trees may live for more than 100 years, but citrus groves more than 50 years old are rare. Depending on the kind involved, the fruit may mature from fall until summer of the year following flower development. Some fruits, for example certain mandarins, fall shortly after they mature. Others, such as the 'Valencia' orange or the grapefruit, will remain on the tree several months after maturity. Citrus has little cold resistance and is not grown in areas where the temperature is likely to fall below 20° F.

TABLE 8.—Estimated U.S. production of citrus by State, type, number of boxes, and total value in 1970-71

Crop	Fruit produced				
	Arizona	California	Florida	Texas	Total value
	1,000 boxes	*1,000 boxes*	*1,000 boxes*	*1,000 boxes*	*$1,000*
Oranges	3,560	38,600	142,300	6,200	445,329
Grapefruit	2,520	5,160	42,900	10,100	136,905
Lemons	3,150	13,300			85,652
Tangerines	390	800	3,700		16,307
Temples			5,000		12,350
Tangelos			2,700		5,022
Limes			880		1,085
Total	9,620	57,860	197,480	16,300	$702,650

A high degree of cross-fertility exists between the species of *Citrus* as well as between the genera of *Citrus*, *Fortunella*, and *Poncirus*. This has permitted breeders to develop the various simple and multiple hybrids, some of which have become of considerable economic importance (Cameron and Soost *1969*).

The common and scientific names of the more well-known cultivars are shown in table 9. The species frequently mentioned but of minor value or used as rootstock or in breeding work are as follows:

Common name	*Scientific name*
Calamondin	*Citrus reticulata* var. *austera* Swingle × *Fortunella* spp.
Citrange	*C. sinensis* × *Poncirus trifoliata*
Citrangequat	*P. trifoliata* × *Citrus* spp. × *Fortunella* spp.
Citron	*Citrus medica* L.

Common name — (Con.)	*Scientific name — (Con.)*
Cleopatra mandarin	*C. reticulata* Blanco
Kumquat	*Fortunella margarita* (Lour.) Swingle
Meyer lemon	*Citrus limon* × *C. medica*
Pummelo (Shaddock)	*C. grandis* (L.) Osbeck
Rough lemon	*C. limon* (L.) Burm.
Sour Orange	*C. aurantium* L.
Trifoliate orange	*Poncirus trifoliata* (L.) Raf.

TABLE 9.—Common and scientific names and important cultivars of U.S. citrus crops

Common name	Scientific name	Important cultivars
Grapefruit	*Citrus paradisi* Macf.	'Burgundy', 'Duncan', 'Marsh', 'Redblush', 'Thompson'.
Lemon	*C. limon* (L.) Burm. f.	'Eureka', 'Lisbon'.
Lime	*C. aurantifolia* (Christm.) Swingle	'Key' (Mexican or West Indian group), 'Bearss' (Tahiti or Persian group)
Orange (sweet)	*C. sinensis* (L.) Osbeck	'Hamlin', 'Mediterranean Sweet', 'Parson Brown', 'Pineapple', 'Valencia', 'Washington Navel'.
Mandarin and mandarin-hybrid complex		'Algerian' ('Clementine'), 'Dancy', 'Kinnow', 'K-Early', 'Minneola', 'Murcott', 'Orlando', 'Page', 'Robinson', 'Temple', 'Wilking'.

Inflorescence

The outstanding characteristics of citrus flowers are the pleasant fragrance, the pleasing contrast between the whitish (to pink or purple in lemons) petals and the dark-green background of the leaves, and the attractiveness of the flowers to bees. Blossom size varies in grapefruit, lemon, lime, orange, and the mandarin and mandarin-hybrid complex, ranging from about three-quarters of an inch for the smaller flowers to 1½ inches for the largest (fig. 78). The flowers usually open in one great flush of bloom in the spring, although lemons and acid limes are particularly noted for their tendency to flower throughout much of the year.

The flowers are mostly hermaphrodite, releasing pollen when the stigma is receptive; however, staminate flowers occur in the lime, lemon, and citron (Purseglove *1968**) and pistillate flowers occur in 'Satsumas' (Kihara *1951*). The pollenless flowers of the 'Washington Navel' are well known for their ability to set parthenocarpic fruit (Webber et al. *1943*).

The flowers are in small clusters in the leaf axil of a preceding growth flush but single in the axils of a just-completed growth flush (Coit *1915*, Chandler *1958**, Reece *1945*). The four to eight, but usually five, oblong, glossy, flared petals arise from the base of the sexual column. The staminate portion consists of 20 to 40 upright white filaments, sometimes united into several groups at the base, with yellow anthers on the tip.

The globose yellowish stigma terminates the style. At the base, the style unites with the greenish ovary, with its 9 to 13 locules, which stands well above the disk.

Nectar is secreted from the nectary or floral disk just within and above the point of attachment of the stamens. Vansell et al. (*1942*) stated that secretion of nectar continues at least 48 hours after flower opening. Also, a thick viscous stigmatic fluid is secreted from papillose hairs on the stigma. This material serves to catch and hold pollen grains and provides suitable media for their germination. A similar material can sometimes be seen inside the style, apparently providing a route and media by which the pollen tube may reach the ovary.

The flowers open primarily from 9 a.m. to 4 p.m. with the peak period about noon (Randhawa et al. *1961*). They never close; the petals merely shed a few days later. The stigma becomes receptive just before the bud breaks open, but the stamens usually do not release pollen until several hours later, after the flower is fully open (Wright *1937*).

To determine if bee visitation altered the period of time the flower is open, I kept records of development on 20 'Clementine' ('Algerian') tangerine flowers at Yuma, Ariz., in 1954 (previously unpublished data). Ten flowers were on a tree enclosed in a cage with a colony of honey bees and 10 on a tree in a cage that excluded bees. Shedding of the petals and stamens in the no-bee cage was slightly slower than in the cage with bees but only because they became stuck in the uncollected nectar. Anther dehiscence was completed by the end of the second day, and normal petal fall was completed on the third day. Whether this applies to all other citrus or even to the same cultivar in other areas is not known but probably it is similar.

The difference in the appearance of the stigmas in the cages was significant. Pollination apparently occurred shortly after flower opening in the bee cage, after which the stigma color changed to brown. In the no-bee cage, the stigmas remained cream-colored and apparently receptive at least 4 days. This might explain the observation by Climenko (*1936*) that stigmas are receptive for 6 to 8 days.

Citrus generally yields nectar copiously. Vansell et al. (*1942*) stated that some blossoms contained 1.5 bee-loads of nectar, averaging 20 microliters, compared to 0.8 to 2.4 microliters per blossom for an alfalfa flower, another important nectar source. Because of the large amount and superior quality of honey that citrus blossoms produce, many beekeepers place their colonies in or near most groves.

The value of citrus as a source of pollen is influenced by the kind involved. Hamakawa (*1967*) reported that less than 1 percent of the bees foraging on 'Satsuma' mandarin (*C. unshiu* Marc.) carried pollen loads as compared to 95 percent on 'Hassaku' orange (*C. hassaku* Hort. ex. Y. Tanaka). In general, citrus is not considered to be an excellent source of pollen by beekeepers.

Only a small percentage of citrus flowers set and develop into mature fruit. For example, Reuther et al. (*1968*) showed that one 'Washington Navel' tree had 102,350 blooms but matured only 419 fruit, and a 'Valencia' tree with 47,112 blooms matured 708 fruit. Reed (*1919*) reported 4,440 buds on one lemon tree, 52 percent of which set, but only 6.6 percent (294 fruit) reached maturity.

Moss (*1971*) studied the relation of flowering and the tendency toward biennial bearing in the sweet orange. He recorded twice as many flowers on the trees in "on" years as in "off" years, but the percentage of flowers that set was the same. Although more flowers usually equal more fruit, if the grower can take steps to increase this percentage during the "off" years, he should do so.

Pollination Requirements

In general, citrus has been considered as a crop with little or no need for insect pollination. However, that which was said about a crop years ago may not be true today for, as Webber et al. (*1943*) pointed out, no variety is likely to remain entirely static over long periods, even when propagated asexually. The likelihood that pollination requirements of citrus have changed in this way is minor. More likely, our increased knowledge, obtained through continued studies, has enlightened us as to the range of pollination needs.

Furthermore, economic conditions may require maximum production of a crop if a net profit is to be realized. Under such conditions, a slight benefit, derived from better pollination of the crop, can become highly significant economically. Considerable attention has been given to citrus pollination recently. Krezdorn (*1970*) stated that a growing number of citrus cultivars are known to be self-incompatible and, in some cases, cross incompatible. With such cultivars, an appropriate pollen supply and pollinating agents is needed.

The pollination requirements of the different kinds of citrus are quite diverse. In some there is almost complete self-sterility. Pollen must be transferred to these flowers from those of another compatible type for maximum fruit production. In others, the plant is benefited if pollen is moved from flower to flower within the cultivar or within the species. In still others, there is no known benefit from transfer of pollen to the stigma by external agents over production caused by the plant's own pollen coming into contact with the stigma without the aid of such insects. In addition, there are

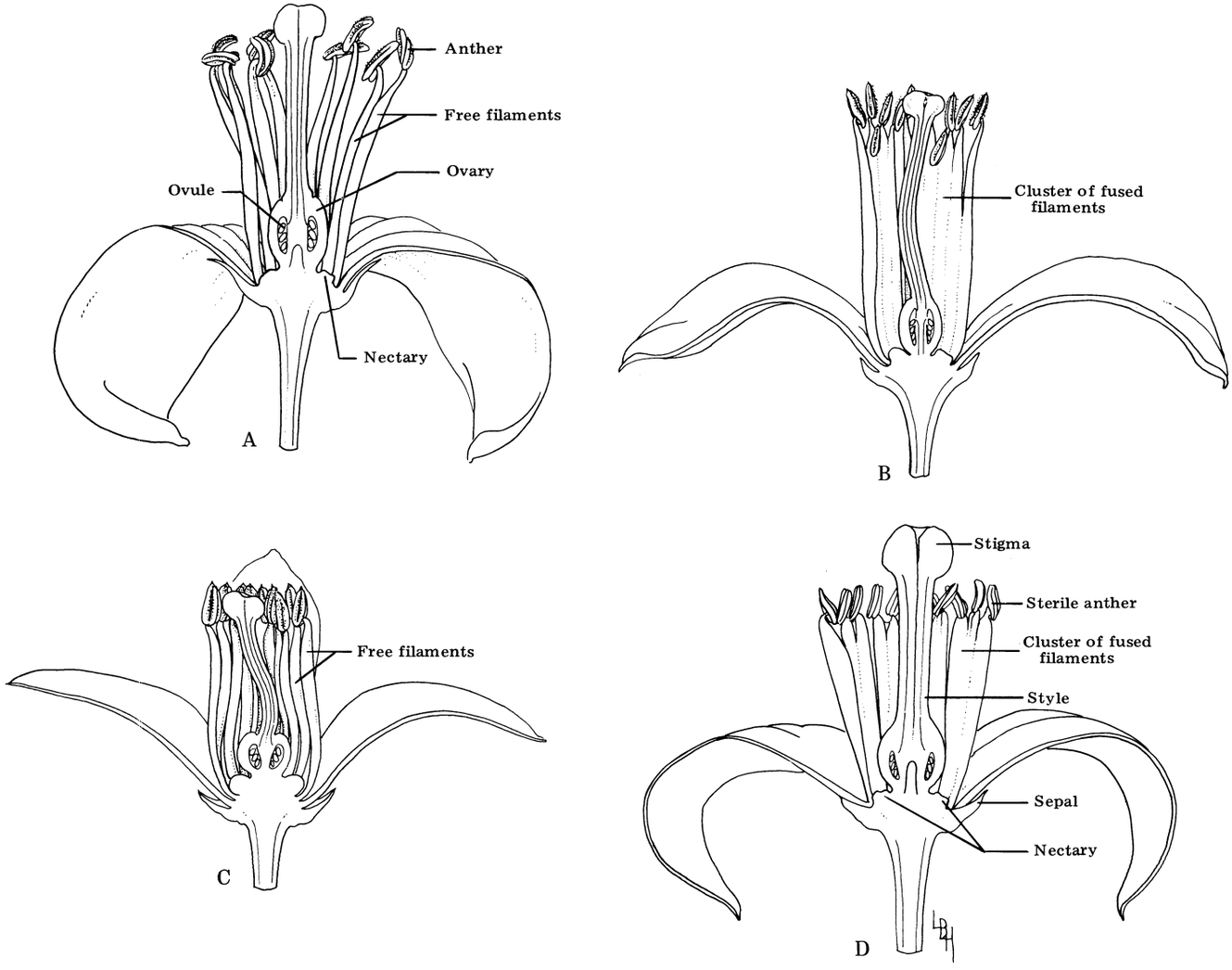

FIGURE 78.—Longitudinal section of citrus flowers, ×3. *A*, 'Red Blush' grapefruit; *B*, 'Meyer' lemon; *C*, 'Algerian ('Clementine') tangerine; *D*, 'Washington Navel' orange.

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varying degrees of parthenocarpic development of the fruit. Because of such diversity, the more important kinds of citrus are discussed separately.

GRAPEFRUIT

Authorities on citrus in the United States have consistently stated that cross-pollination is not required in grapefruit, and that grapefruit production presents no pollination problem (Coit *1915*, Frost and Soost *1968*, Krezdorn *1970*, *1972*, Soost *1963*, Webber *1930*). This does not necessarily mean that no benefit is derived from insect transfer of pollen within the cultivar.

Wright (*1937*) studied the effect of cross-pollination on seed development and fruit set of the 'Marsh' grapefruit. Although some of his data on unpollinated (emasculated and bagged) flowers are open to question, he reported that open pollinated flowers set about twice as many seeds, but more importantly four times as many fruit, as selfed flowers. The presence of seeds is generally undesired by the canners and other consumers, although the 'Duncan' grapefruit is preferred by canners in spite of its seeds. The difference in fruit set could be of considerable economic importance. Satisfactory crops of grapefruit are normally harvested from solid blocks of a single cultivar.

LEMONS

Richter (*1916*) stated that without question (but also without showing data) all the blooms of the lemon could be protected from insect visitation without the slightest reduction in set of mature fruit. Webber (*1930*) also concluded that pollination by bees was probably a negligible factor in the production of citrus fruits, at least for the 'Eureka' and 'Lisbon' lemons, the 'Valencia' and 'Washington Navel' oranges, and the 'Marsh' grapefruit. However, Webber et al. (*1943*) stated that although self-pollination occurs rather commonly without insects, seedlessness sometimes results, and seedlessness is rather generally a handicap to setting of fruit. Frost and Soost (*1968*) and Soost (*1963*) concluded that supplying pollen of another variety does not appear necessary for most of the major types of citrus.

In Russia, however, where numerous tests have been conducted on caged citrus trees, Glukhov (*1955*) stated that lemon trees isolated from bees produced only one-fourth as much fruit as trees exposed to cross-pollination by bees. Burnaeva (*1956*) reported that lemons receiving supplemental pollen from other cultivars or citrus species, produced more than trees not exposed to cross-pollination. Zavrashvili (*1964*) reported that lemon trees caged without bees produced 42.5 percent less than open-pollinated trees, whereas the trees caged with bees produced only 10 percent less, indicating that bees contribute by distributing the self-pollen on the tree. Later, Zavrashvili (*1967b*) stated that the 'Novogrusinskii' requires cross-pollination by bees for fruit production. Randhawa et. al. (*1961*) obtained four mature 'Malta' lemon fruit from 25 cross-pollinated flowers but none from 50 selfed flowers.

LIMES

There has been little research on the pollination requirements of limes. Krezdorn (*1970*) stated that the Tahiti lime is strongly parthenocarpic, and, although cross-pollination might increase the number of seed, the increase in production of fruit, if any, would be negligible. However, Motial (*1964*) reported that 80 to 100 percent of the open pollinated flowers he observed on sweet limes (*C. limettoides* Tan.) set fruit, but only 40 to 60 percent of the emasculated and hand pollinated flowers set. This indicates that strong pollinator activity might increase the set and total production of sweet limes. Motial concluded, however, that sweet lime is not self-incompatible but is merely a shy bearer because of the high percentage of staminate flowers the plant produces.

ORANGES

A general statement about the pollination of oranges is difficult because of the variation among cultivars. Coit (*1915*) stated that certain oranges require pollination to set fruit, others will set fruit parthenocarpically without the stimulus of pollination, and some will not accept pollen from some other cultivars. Because of this difference, the 'Washington Navel' and 'Valencia' and other sweet oranges will be discussed separately.

'Washington Navel'.—The anthers of 'Washington Navel' blossoms produce no pollen and the embryo sac may degenerate before tubes of pollen from other cultivars can penetrate to it, yet fruit sets and develops if conditions are favorable. However, if the tree is stressed by desiccating winds or moisture shortage, drop of young fruit can be severe. Surr (*1922*) caged six 'Washington Navel' trees to increase the humidity around them, which also excluded pollinating insects. He found that by doing this the production was not increased but instead decreased as much as 86 percent. The cages may have influenced fruit set for reasons other than pollination. Krezdorn (*1970*) stated that cross-pollination in 'Washington Navels' does not increase the yield, yet he (*1965*) obtained the following results from hand-pollinating the flowers, which would indicate that cross-pollination might influence set:

Pollen source	*No. of flowers pollinated*	*No. of fruit set*
'Pineapple' orange	1,000	2
'Temple' orange	1,000	3
'Duncan' grapefruit	1,000	5
Self (None)	3,000	0

El-Tomi (*1954*, *1957*) reported that cross-pollination of 'Washington Navels' significantly minimized the dropping of immature fruit.

An interesting report on pollination made by Zavrashvili (*1967b*) stated that 'Washington Navel' trees caged to exclude bees yielded fewer fruits than trees caged with bees or open plots. The flowers set the most fruit when crossed with the 'Grusinian' orange. He also reported that the transfer of stigmatic fluid between stigmas increased the percentage of set. No reason for

this effect was given, and its significance has not been determined.

The effect of pollination on production of 'Washington Navel' oranges seemed to be summed up by Atkins (*1963*), who stated that there is a possibility that cross-pollination by bees may cause them to retain more fruit.

'Valencias.'—Richter (*1916*) stated, without showing data, that if all insects were kept off 'Valencia' flowers there would be no less production. Francke et al. (*1969*) also concluded that bees have no effect on production of 'Valencias', but Cameron et al. (*1960*) reported that fruit size of 'Valencias' was increased as the seed number increased and that 'Pearl' tangelo pollen may increase both seed number and fruit set on 'Valencias'. This would indicate that, with cross-pollination, fruit size and possibly number of fruit set might be increased.

Other sweet oranges.—Soost (*1963*) stated that commercial plantings show no obvious reduction of yield in the absence of other varieties, but this does not mean that cross-pollination is of no benefit. Khan and Chandhri (*1964*) concluded that five unidentified cultivars were self-pollinating. Oppenheimer (*1935*) (cited by Oppenheimer *1948*) came to the conclusion that "citrus can be planted in large blocks with no admixtures of other varieties, without the least misgiving."

Conversely, Glukhov (*1955*) reported that orange trees (cultivar not given) pollinated by bees produced four times as much fruit as trees isolated from bees. Zavrashvili (*1964*) reported that the orange crop in cages without bees was 54.4 percent lower than that on trees in the open. The cultivar was not identified nor was there a measure of cage effect on the plant other than pollination effect. Wafa and Ibrahim (*1960*) obtained 31 percent increase in set of fruit on the 'Elfelaha' orange, 22 percent increase in fruit weight, 33 percent more juice, and 36 percent more seeds from fruits on trees visited by bees than on trees from which bees were excluded. Zacharia (*1951*) reported partial self-incompatibility in the 'Shamouti' orange.

Hassanein and Ibrahim (*1959*) reported a set of 2.6 percent of flowers of the 'Khalili' orange where insects were excluded, 10.4 percent set where honey bees were present, and 7.4 percent on control (open) blooms.

Krezdorn (*1967*) showed that the 'Hamlin', 'Parson Brown', 'Pineapple', and 'Valencia' orange size increased linearly with fruit set.

Although the results of tests are meager, some beneficial effects of pollination on oranges are indicated.

PUMMELO

Soost (*1963*, *1964*), working with 11 different accessions and Nauriyal (*1952*) concluded that the pummelo, which is grown commercially only in the Orient, is self-incompatible.

Aala (*1953*) conducted pollination studies on the Siamese pummelo 'Siamese 3442' in the Philippines. It produces both complete and staminate flowers. Some of the flowers were left to visits by bees, some were selfed, and some were crossed with pollen of 'Sour', 'Siaver 14', and 'Valencia' orange, and 'Batanga' mandarin. He concluded that most pummelo trees were self-incompatible and should be interplanted with other cultivars. He stated: "Bees or other insects are necessary for proper pollination and setting of fruits, whether a cultivar is self-fertile of self-sterile." He also noticed that a higher percent set of open-pollinated flowers was obtained during off seasons than regular seasons, which may indicate that an inadequate pollinator population existed at flowering time. Of course, it could also mean there was an interaction with unfavorable environmental or physiological factors.

MANDARIN AND MANDARIN-HYBRID COMPLEX

More research has been conducted on the pollination requirements of this group than of all the other citrus species combined, because the pollination problem is more acute. The problem has been recognized since Lacarelle and Miedzyrzecki (*1937*) reported that fewer fruits of the 'Clementine' mandarin set on a tree enclosed for self-pollination without bees than on 30 others enclosed with bees, either with or without pollen of other cultivars. Oppenheimer (*1948*) also showed that production of the 'Clementine' tangerine was increased when it was cross-pollinated by bees with pollen from 'Dancy', 'Temple', 'Duncan', or some other seedy cultivars. He found that the 'Valencia', 'Eureka', 'Marsh Seedless', and 'Satsuma' were ineffective pollinators.

Van Horn and Todd (*1954*) caged 'Clementine' ('Algerian') tangerine trees with and without pollinating insects (honey bees) and with and without bouquets of other cultivars. They showed that trees having both bees and bouquets yielded 16 times as many tangerines as those with no bees, had double the yield of those provided with bees only, and had better fruit quality. Miwa (*1951*) showed that the 'Hyuganatsu' mandarin was self-sterile but cross-fertile. Lynch and Mustard (*1955*), Coste and Gagnard (*1956*), Soost (*1956*, *1963*), Mustard et al. (*1957*), and Barbier (*1964*) concluded that the 'Clementine' tangerine was self-incompatible. Minessy (*1959*) found that grapefruit pollen was highly effective in fertilizing 'Clementines'. Blondel and Barbier (*1963*) accepted the fact that pollination increased production but stated that it also increased the pips or seeds present. Hilgeman and Rodney (*1961*) and Krezdorn (*1970*, *1972*) stated that yields of 'Clementine' can be improved with bee pollination.

Hearn et al. (*1969*) reported that the 'Lee', 'Page', 'Nova', and 'Robinson' were self-incompatible, but Reece and Register (*1961*) stated that the 'Osceola' was not completely so. Furr (*1964*) and Moffett and Rodney (*1971b*) reported that cross-pollination was necessary and should be provided for 'Fairchild'. Later (*1973*) they reported that bees increased the yield of 'Orlando' tangelo. Also, Moffett and Rodney (*1973*) showed that honey bee visits increased yields of 'Orlando' tangelo. Hearn et al. (*1968*, *1969*) and Hearn and Reece (*1967*), concluded that the 'Lee', 'Nova', 'Page', and 'Robinson' were all self-incompatible. Krez-

dorn (*1972*) included the 'Orlando', 'Minneola', and 'Osceola' in this group, but questioned the inclusion of the 'Lee'. Hearn et al. (*1969*) also reported that the 'Page' fruits were larger if they developed from 'Lee' pollen, the first well-defined metazenic effects reported in citrus.

Krezdorn and Robinson (*1958*) showed that crossing 'Orlando' with pollen from 'Temple' or 'Dancy' increased yields. Krezdorn (*1959, 1967*) also reported a significant correlation between fruit size and number of seeds of the 'Orlando'. Krezdorn (*1970*) stated that the 'Orlando', and 'Minneola' were self-incompatible, the 'Nova', 'Osceola', and 'Robinson' require cross-pollination, and at least in the 'Orlando' the fruit size increases with seed number. Soost (*1963*) reported that 'Minneola', 'Orlando', 'Osceola', and 'Robinson' were self-incompatible and that 'Lee' and 'Osceola' were suspect. Krezdorn (*1970*) stated that there is a growing number of self-incompatible cultivars.

The 'Satsuma' is variously referred to as 'Satsuma' mandarin (Hamakawa *1967*), 'Satsuma' orange, 'Unshiu' orange (Kresdorn *1970*), or 'Unshiu' tangerine (Mchedlishvili *1962*). Several tests indicate that it is benefited by bees—6.3 percent according to Zhgenti (*1956*); 7 to 11 percent, Zavrashvili (*1967a, b*). Soost (*1963*) recommended that the plants be set in solid blocks, although there was some risk of excessive fruit drop under some conditions. Mchedlishvili (*1962*) showed the importance of insect pollination. At varying distances from an apiary, he observed that near the apiary 42.5 percent of the flowers set and 14.6 percent were harvested. At 150 m from the apiary, 29.3 percent of the flowers set and 10.6 percent were harvested. At 350 m from the apiary, however, only 13.6 percent of the flowers set, and 5 percent were eventually harvested. This showed the value of having the colonies of bees near the trees to be pollinated. Although a few research workers have obtained substantially the same set of fruit from no pollination, self-pollination, and cross-pollination of 'Satsuma', the data indicate that for best production, an ample bee population is needed.

CALAMONDIN, CITRANGE, CITRON, KUMQUAT, MEYER LEMON, PONDEROSA LEMON, SOUR ORANGE, AND TRIFOLIATE ORANGE

No pollination problems have been observed on citron, kumquat, Meyer lemon, and trifoliate orange, but there have been problems of seed set in 'Morton' and 'Troyer' citrange (Soost *1963*).

In summary, insect transfer of pollen within the flower, between flowers of a cultivar, or between cultivars may be of slight value to oranges, grapefruit, and lemons. Many, if not all, of the mandarin and mandarin-hybrid complex are dependent upon or greatly benefited by insect pollination. The pummelo is dependent upon pollinating insects.

Pollinators

The honey bee is unquestionably the primary pollinating agent of citrus; wind is not a major factor. Other pollinating insects are minor. Beekeepers readily place their colonies near citrus groves for the delicious honey the bees store, and citrus specialists frequently intimate that an ample supply of bees is always in the groves (Krezdorn *1972*). Moffett and Rodney (*1971a*) showed this may not be true. They observed an average of slightly less than one bee per 100 blossoms at Yuma, Ariz., and concluded that the population was so low that growers of most orchards needing insect pollination should have rented colonies for that purpose. During the peak bloom, the ratio was much less than one bee per 100 flowers. Such a population would not be likely to visit individual flowers more often than about once per hour. By contrast, Mchedlishvili (*1962*) reported 12 bee visits per blossom per hour.

P. M. Packard (personal commun., 1972), State apiary inspector for Florida, estimated that only 220,000 colonies of honey bees were in the prime citrus area during bloom time in 1972—about one colony per 4 acres. He stated distribution is not systematic, with some areas overcrowded with bees and others having practically none.

Butcher (*1955*) observed a zonal production effect in relation to distance of 'Minneola' tangelos from the apiary with the most marked effect 200 to 300 feet away. However, Robinson (*1958*) stated that honey bees worked equally well in all directions and were evenly spread to 400 feet.

Honey bees collect both pollen (if it is produced) and nectar from citrus. The flower is so constructed that if the bee has visited a previous pollen-producing flower, some pollen is likely to be transferred to the next stigma visited.

Depending upon the cultivars involved, the results of insect pollination may have no effect, increase the number of fruits set, increase the size of the fruit, cause seed to be present, increase the number of seeds, or cause an overloading of the tree.

Pollination Recommendations and Practices

Little work has been done on the number of bee visits per flower, or the effect of cross-visitation between cultivars in relation to fruit set on citrus cultivars either dependent upon or benefited by bee pollination. Some recommendations have been made, without support of data, on colonies per acre and suggested placement.

Oppenheimer (*1948*) suggested bringing bees in, if they were not present, to pollinate 'Clementine' mandarins in Palestine. He did not indicate how many bees should be brought in or where the colonies should be placed.

The placement of colonies of bees in citrus orchards for pollination has often been recommended. Baldwin (*1916*) without concrete data to support his statement recommended five colonies per acre. Van Horn and Todd (*1954*) recommended one colony per acre of 'Clementines'. The Florida Agricultural Extension Service (*1961*) recommended the use of bees and pollenizer cultivars to increase the number and size of tangelos. Robinson and Krezdorn (*1962*) recommended a minimum of one strong colony of honey bees per acre of 'Orlando' tangelos. Soost (*1963*) stated that most commercial kinds of citrus set adequate crops without cross-pollination, but where insect pollination is needed "one hive per 2 acres may be sufficient although this is

not certain." Zavrashvili (*1967b*) stated that one colony per 2.5 acres doubled the crop. His research dealt with 'Washington Navels', 'Novogrusinskii' lemons, and 'Unshiu' tangerines. Haynie (*1968*) recommended one colony per 2 acres, the colonies in groups and properly spaced, for cultivars benefiting from bee pollination.

There seems to be no uniformity in these recommendations, probably because each dealt with only one or a few cultivars in different areas of the citrus world and under different conditions.

The weakness of the recommendations is that there is no indication given as to the relative bee population per unit of flowers and also no relation is shown between colonies per acre and bees per flower.

For most efficient pollination of citrus, the meager data indicate that if bees are needed they should be distributed at the rate of one-half to five colonies per acre at about ¼- to ⅒-mile intervals. Consideration in the recommendation should be given to vigor of the colonies, other colonies in the area, acres of citrus, and other nearby plants attractive to bees, size of the citrus trees, and blooms per tree. For greatest benefit, the colonies probably should be present throughout the citrus flowering period.

Beekeepers place their bees near citrus groves for the honey they obtain; however, these colonies may not be placed strategically or in sufficient numbers for most effective pollination of all areas of a particular grove. The grower would profit most by arranging for the appropriate number of strong colonies properly placed and managed for citrus pollination although the honey obtained could be a factor in relation to locations and pollination fees. The citrus grower can gain far more than the beekeeper from such an arrangement.

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CLOVE

Syzygium aromaticum Merr. and L. M. Perry, family Myrtaceae

The clove tree produces flower buds that when harvested and dried become the cloves of commerce, which are used primarily as food spices. Clove oil, distilled from the plant, is used in perfumes, medicines, artificial vanillin, dentifrices, and other ways.

Purseglove (*1968**) stated that the annual worldwide consumption of cloves was as follows: Indonesia, 8,000 metric tons; India, 3,000; Malaya, 2,000; United States, 2,000; Europe and North Africa, 3,000; and other countries, 1,000 metric tons—about 42 million pounds. Rosengarten (*1969**) stated that Tanzania produces three-fourths of the world output.

Plant

The clove tree, although related to the eucalyptus and some other large trees, is relatively small, 12 to 20 feet or, rarely, to 40 feet tall. The stem is often forked with two or three main trunks. The paired leaves are 3 to 5 inches long, 1 to 1½ inches wide, and highly aromatic.

The plants are usually grown from seed, then set about 30 feet apart in the grove.

Inflorescence

The clove tree inflorescence is a terminal branching cyme of 3 to 20 hermaphrodite florets, the whole about 1½ inches long. Each pale yellow floret consists of a cylindrical thick ovary, one-quarter inch long. Above the ovary are four fleshy ovate sepals, and above these are the four tiny petals, numerous slender white ⅜-inch filaments, and a slender central style. The flower opens early in the morning. The united petals separate from the base as a cap, similar to the grape blossom, which is pushed off by the extending stamens. In a few hours, all the anthers are open, and the stigma is receptive (Wit *1969*). There are two flowering seasons a year, July to October and November to January. Few flowers develop into fruit. The fruit, called mother of cloves, contains one seed or rarely two seeds. The ovary and sepals constitute the specific part marketed as cloves (Purseglove *1968**, Ridley *1912**).

Pollination Requirements

Purseglove (*1968**) said that no fertile fruits were obtained from bagged flowers. He concluded that cross-pollination was necessary for seed production. Tidbury (*1949*) stated that no viable seeds have been produced from selfed flowers, indicating that the flowers require cross-pollination. He also concluded that, since vegetative propagation had never been accomplished, pollination from the breeding standpoint becomes important.

Pollinators

Purseglove (*1968**) stated that the flowers are visited and apparently cross-pollinated by bees. Ridley (*1912**) merely stated that the fertilization was by some insect. Tidbury (*1949*) stated that the flowers are visited by bees.

Pollination Recommendations and Practices

No attempt is made to utilize insect pollination in the production of clove planting seed. The figures by Purseglove (*1968**) on tree spacing, tree yields, and total production of cloves would indicate that about 70,000 acres are involved, and reproduction of plants occurs at the rate of about 1,000 acres per year.

The need for sufficient pollinating insects to produce the small amount of seed required to plant 1,000 acres of cloves is probably not acute. There would be a definite need for insect pollinators if the production were concentrated in certain areas and maximum seed production desired. If such were the case, bees could be concentrated in the planting to perform the required pollination.

No known attempts have been made to use pollinating insects in clove seed production.

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CLOVERS, GENERAL

Family Leguminosae

Numerous species of plants in different genera of the family Leguminosae are called clover. They have certain characteristics in common. The leaf is normally composed of three leaflets. The papilionaceous (butterfly-like) or pealike floret of the flower head consists of a large dorsal standard petal, two lateral wing petals, and two lower keel petals. It usually has 10 stamens, one of which is free and the other nine united, that form a tube enclosing the long ovary. The flower trips exposing the stigma, which returns to its original position after pressure on the petals is removed. The plants have the ability to take nitrogen from the air and, by Rhizobium fixation, store it within nodules on the roots. This contributes to the value of the plant to the soil. The plants provide excellent forage for livestock, and they help in erosion control. Many of the species are good sources of honey and pollen for bees.

The United States Government considers legume crops so important that in 1946, when seed stocks were in short supply, Congress appropriated funds to encourage the harvesting of seeds of these crops (Johnson and Loomer *1948*).

The hay crop from clover and clover mixtures in 1969 was harvested from slightly more than 13 million acres.

There are about 250 species of *Trifolium*, the True Clovers, but only four make up the bulk of the acreage. They are alsike clover (*T. hybridum* L.), crimson clover (*T. incarnatum* L.), red clover (*T. pratense* L.), and white clover (*T. repens* L.).

There are about 20 species of *Melilotus*, the sweetclovers, but only three species make up the bulk of the acreage. They are biennial yellow sweetclover (*M. officinalis* (L.) Lam.), biennial white sweetclover (*M. alba* Desr.), the annual white subspecies (*M. a.* var. *annua* Coe), and yellow annual sourclover or sour sweetclover (*M. indica* (L.) All.).

There are about 65 species of *Medicago*, some species of which are referred to as clover, for example, the burclovers, two species of which are important. They are toothed burclover (*M. hispida* Gaertn.) and spotted burclover (*M. arabica* Huds.). Alfalfa (*M. sativa* L.) is the most important species.

There are 16 species of *Alysicarpus*, or Alyce clover, which is not a True Clover, but none are of great economic importance.

There are about 70 species of *Lespedeza* or bush clover, several of which are of economic importance.

Weaver and Weihing (*1960*) concluded, with limited cage tests, that pollinating insects were essential for adequate seed production of the experimental species *Trifolium isthmocarpum* Brot., *T. michelianum* Savi, *T. pallidum* Waldst. & Kit., and *T. xerocephalum* Fenzl.

A memorandum to USDA cooperators, from R. C. Leffel (USDA, Clover Investigations, 1971), listed the following cultivars of clover available for agronomic evaluation: Cluster clover (*T. glomeratum* L.), Kura clover (*T. ambiguum* Bieb.), Lappa clover (*T. lappaceum* L.), Large Hop clover (*T. campestre* Schreb.), Small Hop clover (*T. dubium* Sibth.), and Striate clover (*T. striatum* L.). Leffel mentioned that other species may also be present in agronomists' test plots, but none are currently grown commercially. Their pollination requirements are unknown but should definitely be evaluated by the agronomists along with their other characteristics, if release of the species for commercial production appears likely.

The important species of these different genera that are known to be dependent upon or benefited by insect pollination are discussed as separate crops herein.

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COCONUT

Cocos nucifera L., family Palmaceae

The coconut is found along tropical seashores around the world, and in some areas it is cultivated far inland. It provides man with food, drink, fuel oil, and many other products.

There are about 8.5 million acres of coconuts, of which 2.45 million are in the Philippines, 1.59 in India, 1.5 in Indonesia, 1.07 in Ceylon, 0.6 in Malaya, 0.6 in other south sea islands, and 0.7 million acres elsewhere (Minon and Pandalai *1958*, Woodruff *1970*). Apacible (*1968*) indicated that there were 4.5 million acres in 1967 as against 2.4 million in 1958. Apacible (*1968*) also stated that coconut production has increased at the rate of 5 percent a year for the last 50 years. In the United States, coconuts are found in Florida, Hawaii, and Puerto Rico. The largest coconut plantation in the United States consists of about 30,000 trees in Key Biscayne, Fla. (Woodruff *1970*).

Plant

The usually leaning, branchless trunk may reach a height of 100 feet (fig. 79). However, selections of dwarf plants as low as 6 feet are now being cultivated (fig. 80). Wrigley (*1969*) stated, however, that dwarf coconuts are short lived and inferior in copra production. The top, head, or crown consists of 20 to 30 mature feather-shaped leaves 15 to 20 feet long and 1 to 3 feet wide, with additional developing leaves. A leaf requires 1½ years to reach full size, then it will last for 2 more years. A new leaf and an inflorescence forms about once each month (Chandler *1958**). The inflorescence produces from 1 to 20, but usually about half a dozen nuts, each nut weighing up to several pounds. The nut is enclosed in a thick fibrous husk, that when removed reveals the well-known brownish fiber-coated coconut, comprising the hard shell which contains the edible meat and milk. One tree may yield 100 fruits per year, and about 90 trees per acre are used (Woodruff *1970*).

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FIGURE 79.—Grove of "standard-height" coconuts.

The plant will withstand a light frost, but is basically a tropical crop.

Inflorescence

The coconut is monoecious, having both staminate and pistillate florets on the same many-branched inflorescence, the 2- to 4-foot long spadix or fleshy panicle in the leaf axil. As many as 8,000 staminate flowers may make up most of the inflorescence, with 1 to 30 pistillate flowers near the base (Aldaba *1921*, Ochse et al. *1961**).

Flowering of larger plants begins at 5 to 8 years of age (Chandler *1958**), but on dwarf plants it begins in

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FIGURE 80.—Fruit of the dwarf coconut can be harvested from the ground.

the third or fourth year (Woodruff *1970*). Flowering occurs on the plant throughout the year.

The individual staminate flower described by Juliano and Quisumbing (*1931*), which is open only 1 day primarily between 6 a.m. and noon, and is only a few millimeters in size, has three cream-colored petals and six stamens. The stamens shed large amounts of pollen, some of it before the flower is open and altogether as much as 6.1 g per inflorescence (Whitehead *1963*). There is also an abortive pistil whose stigmatic area is divided into three parts each bearing an active nectar gland. The much larger ½- to 1-inch oval pistillate flower has three stigmas on a short style and three ovules, two of which always abort. Sholdt and Mitchell (*1967*) mentioned that honey bees collect nectar from "the nectary orifices and stigmatic region." Menon and Pandalai (*1958*) stated that nectar secretion is most profuse between the stigma and the base of the ovary. Whitehead (*1965*) stated that considerable quantities of nectar were produced from three nectaries in the pistillate flower.

Patel (*1938*) stated that when the stigma is receptive a clear sweet fluid is profusely secreted in four places, at the base of the stigma and at three pores on the pericarp toward the top of the ovary.

Not all of the pistillate flowers mature fruit. Lever (*1961*) stated that there is a normal shed, comparable to the "June drop" of fruit trees, and also a shedding caused by harmful insects.

Usually only one spadix at a time opens on a plant. Furthermore, the staminate flowers frequently complete their flowering 3 to 6 days before the pistillate flowers open; therefore, crossing between flowers on a spadix or even a plant is unlikely, although the flowering periods tend to overlap in the newer dwarf selections (Woodruff *1970*, Ochse et al. *1961**).

The period of staminate flowering on a spadix may extend from 18 to 38 days; the pistillate phase, from 2 to 12 days; and the interval between spadices, from 10 to 57 days, averaging 18 days (Kidavu and Nambiyar *1925*). Overlapping of phases on a plant ranges from "seldom" to 20 percent of the time (Sholdt and Mitchell *1967*, Ochse et al. *1961**). A pistillate flower may, therefore, receive pollen from staminate flowers of the same spadix or from a later spadix on the same plant. However, if there is no overlapping of spadices, the pollen must come from another plant (Chapman *1964**). Free (*1970**) stated that staminate flowers of tall plants begin opening about a month earlier than the pistillate flowers, but pistillate flowers of dwarfs begin opening about a week after the staminate flowers.

The flowers are visited by honey bees and many other insects attracted by the nectar and pollen (Sholdt *1966*). Nectar production, in terms of honey stored by a colony of honey bees, is not great (Pellett *1947**, Sholdt and Mitchell *1967*), and the amount stored by a colony varies with the time of the year (Wolfenbarger *1970*). Whitehead (*1965*) stated that nectar is produced in considerable quantity from the three nectaries in the female flower. During one 30-minute period, he recorded 103 visits by bees collecting nectar from one flower, and after each visit the nectar was rapidly replaced. Ochse et al. (*1961**) also referred to the large quantity of nectar that exudes from the flower.

Pollination Requirements

Pollen must move from staminate to the pistillate flowers if coconuts are produced. Sholdt and Mitchell (*1967*) showed that the source of the pollen was not important from the standpoint of fruit set for they obtained good set whether the pollen came from the same plant or from another plant. The pollen can come from the same inflorescence, another inflorescence on the same plant, or another plant.

The pollen is most effective the first day the stigma is exposed, and, theoretically, only one pollen grain per pistillate flower is sufficient to fertilize the one ovule. Aldaba (*1921*) calculated that one inflorescence produced 272 million pollen grains.

Whitehead (*1965*) studied the flowering of coconuts in Jamaica and reported all variations in the pollination requirements. He believed that to conclude that the plants are either selfed or crossed was unsafe, but the extent of crossing depended upon the relative importance of wind, insects, proximity of other trees, efficiency of selfing, presence of nectaries on male and female flowers, and the frequency of insect visitation, particularly bee visits. Copeland (*1931*) stated that the succession of clusters is normally so timed that pollen must come from another plant, which insures cross-pollination. However, Tammes and Whitehead (*1969*) stated that this applies only to tall palms. In the dwarf palms, with the exception of 'Niu Leka', the female flowers are receptive before the male flowers cease; therefore, pollen may come from the same inflorescence. Wrigley (*1969*) stated that self-fertilization between flower heads on a dwarf coconut plant is normal.

Pollinators

There has been considerable question about what agents are involved in transferring the pollen from the staminate to the pistillate flowers, a transfer that is required regardless of the flowering habits of the plant. Self-pollination is frequently mentioned, but this only refers to the source of the pollen, whether from the same inflorescence on which the stigma is located or another inflorescence. The flower cannot fertilize itself. Wind, birds, mites, and insects, including ants, bees, earwigs, flies, and wasps have been mentioned as cross-pollinating agents of the coconut (Davis *1954*, Kidavu and Nambiyar *1925*). The effectiveness of each doubtless is associated with local situations.

Furtado (*1924*) considered birds of doubtful value. Sampson (*1923*), Tammes (*1937*), and Whitehead (*1965*) stated that pollination was by insects. Huggins (*1928*) considered honey bees and various other hymenoptera important but ants unimportant. Hunger (*1920*), Patel (*1938*), and Ochse et al. (*1961**) considered both insects and wind important. Sholdt (*1966*) collected 51 species of insects on the coconut inflorescences in Hawaii, but those found most often were ants, bees, earwigs, flies, and wasps. Sholdt and Mitchell (*1967*) considered both wind and insects important, with the honey bees the most important insects of all.

The recognition of the value of honey bees on coconuts is not recent. An anonymous (*1916*) author indicated that bees played an important part in the

pollination of coconuts in Fiji. The inflorescences freely visited by bees when in flower gave a high yield of nuts, and the placement of colonies into coconut plantations was suggested. Sampson (*1923*) stated that on estates where bees were kept in large numbers for other reasons the yield of nuts was remarkably high. Huggins (*1928*) felt that the lack of adequate cross-pollination frequently depressed the yield of nuts. Haldane (*1958*) suggested that honey bees might be used to increase yields, but Tammes and Whitehead (*1969*) differed with this opinion. They stated: "There is, however, sufficient natural pollination by wild bees, as appears from trials, so the keeping of honey bees has no influence on the fertility of palms." They did not indicate what population of wild bees was adequate.

Pollination Recommendations and Practices

Except for the above references, the use of bees has not been recommended in the pollination of coconuts. Sholdt and Mitchell (*1967*) suggested that, "it would appear advantageous to bring in colonies of bees in an effort to increase yields." They gave no indication of the number of colonies per acre or bees per inflorescence that might be adequate.

The evidence indicates that the presence of honey bees in adequate numbers could increase production. There is no indication as to what might constitute an adequate population on the flowers. One might ponder over the well-known relatively low production of coconuts per acre in the Philippines, where the bee population is quite low (Morse and Laigo *1969*) as compared to the other areas of the world where coconuts are produced. The concentration of honey bees, even if it meant the development of a strong apicultural industry in the Philippines, might considerably improve the coconut industry.

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COFFEE

Coffea spp., family Rubiaceae

Worldwide about 90 percent of the coffee produced comes from *C. arabica* L., 9 percent from *C. canephora* Pierre ex. Froehner, and less than 1 percent from *C. liberica* Bull. ex. Hiern. Brazil produces about half of the world supply of coffee, about 1.5 million tons. The most important cultivar in Brazil is 'Mundo Novo' with about three-fourths of a million acres planted (Monaco and Carvalho *1969*). The combined African states are second with about 0.8 million tons. Colombia produces about 0.5 million, and El Salvador, Guatemala, and Mexico about 0.1 million tons each. In the United States, coffee is produced to an extremely limited extent only in Hawaii and Puerto Rico. In the mid-1920's, coffee production in Puerto Rico exceeded 9,000 tons, but production diminished during World War II. It is now being rehabilitated. Production of 'Koona' coffee in Hawaii is declining.

In Africa (primarily Angola, Congo, Ivory Coast, Uganda, and Madagascar), the principal coffee is *C. canephora*, which is now in great demand for the manufacture of instant coffee.

Yield per acre varies enormously from over 2,000 pounds of clean coffee per acre in Hawaii to only 360 lb/acre in Brazil (Chandler *1958**, Haarer *1962*, Purseglove *1968**, Wellman *1961*). In the United States, consumption is approximately 16 pounds per head per annum. We import annually about 1.5 million tons.

Crane and Greene (*1948-53*) made an extensive review with pertinent abstracts of the literature on coffee.

Plant

Coffee trees may grow to a height of 20 to 30 feet if unpruned, but in cultivation they are pruned to about 6 feet to facilitate harvesting of the berries. Much of the coffee in Brazil is grown in the full sun although it prospers in the shade of taller trees. Considerable care is required to keep the trees in proper productive condition. The plant is susceptible to frost, intense heat, drought, and diseases. It grows best at average temperatures of about 60° to 75° F, with 75 inches of rainfall but needs a 2- to 3-month dry period to initiate flowering. The trees are usually planted about 8 feet apart; they begin bearing at about 4 years, reach full bearing by 15 years, and may bear 6 to 100 years longer (Haarer *1962*).

The fruit is a drupe (or stone fruit), but is often called a cherry or berry. It is individually picked at the proper stage of ripeness. About 5 pounds of fruit yield 1 pound of clean coffee. One cherry, usually bearing two seeds, develops from a blossom. The less-desired, one-seeded cherry is referred to as a "peaberry." The fruit is dried or processed in water to remove the skin, cleaned, and bagged for shipment and use. The beans are roasted, ground, and brewed with hot water to produce a stimulating beverage (Wellman *1961*).

The taxonomy of *Coffea* is confused, but doubtless the three previously mentioned species are the most important. There are also many botanical varieties, mutants, and cultivars.

Inflorescence

The fragrant white flowers occur in clusters of two to 20 in the leaf axils (fig. 81). Each flower is about an inch long by an inch deep, the tubular corolla is about ⅓-inch long and the calyx is usually made up of five flared petals, forming a starlike inflorescence. There are usually five long stamens on short, curving filaments and a long style with a two-part stigma. The stamens are attached to the corolla between the lobes so that the anthers are about the height although not necessarily close to the stigma. Pollen is shed immediately after the flower opens, and the stigma is immediately receptive. Nectar is secreted at the base of the tubular corolla, but accessible to honey bees and many other insects. Both nectar and pollen are attractive to many kinds of insects.

On sunny days, the flower generally opens early in the morning and pollen shedding starts soon afterwards. The pollen is produced in comparatively small quantities and is not sticky. It may be transported by wind and insects (Carvalho and Krug *1950*). If the day is cloudy, the flower may remain closed but self-pollination can occur within the flower. Two days after opening, or fertilization within the closed flower, the parts begin to wither and fall, leaving the ovary (Haarer *1962*). Krug (*1935*) and Montealegre (*1946*) suggested that the lingering of the withered blossoms on the tree is an indication of an absence of insect pollinators, whereas if the petals fall freely and soon, they have been pollinated and a good crop should be expected.

Purseglove (*1968**) stated that approximately 40

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FIGURE 81.—Coffee in full bloom.

percent of the flowers set fruit and are harvested as mature fruit, a certain number of buds never swell, but may persist until harvest; others fall in the early stages of growth, mainly in the first 10 weeks. Ferwerda (*1951*) stated that a tree may produce 10,000 to 50,000 flowers but 70 to 90 percent of them fall. This fall may be due to self-incompatibility in the flower, incompatible pollen in general, absence of pollination, or defective embryo sac. Mayne (*1934*) kept close observation on about 20,000 original coffee buds over a 3-year period and reported that 37.6, 41.4, and 38.6 percent of them were harvested as mature coffee.

Pollination Requirements

Wellman (*1961*) stated that *C. arabica* is self-fertile, yet at times some insect pollination occurs but it is not necessary. However, he stated that the other two species, *C. canephora* and *C. liberica*, are self-sterile and require action of wind or insects. Ferwerda (*1936*) stated that *C. excelsa* Cheval., *C. liberica*, and *C. robusta* Linden [= *C. canephora*] were self-sterile. Haarer (*1962*) is in agreement with Wellman on this. Amaral (*1952*) showed that caged *C. arabica* plants produced 39 percent less coffee than open plants. Later, Amaral (*1960*) conducted another experiment using *C. arabica*, cv. 'Caturra KMC', in two flowering seasons, in which he recorded the set of fruit on branches caged to exclude bees and compared production with branches freely visited by bees. Fruit setting on the protected branches was 61.7 percent, whereas on branches visited by bees it was 75.3 percent, indicating a slightly beneficial effect. According to Free (*1970**), Sein (*1959*) had a set of 60 percent and 70 percent on bushes caged to exclude bees and bushes not caged, respectively.

Later experiments by Amaral (*1972*) leave no doubt that *C. arabica* is definitely benefited by bee pollination. He showed that bees increased set of *C. arabica* cv. 'Mundo Novo' (in cages with bees) about 82 percent over trees in cages without bees.

Carvalho and Krug (*1950*) studied the effect of cross-pollinating agents on *C. arabica* and concluded that 7.3 to 9.0 percent of seed resulted from cross-pollination. They did not indicate the intensity of activity of the pollinating agents. Lower (*1911*) claimed that honey bees are of great value in pollinating coffee in Puerto Rico during rainy seasons. Mendes (*1961*) showed that tubes from foreign pollen grew faster than self pollen, thus insuring crossing.

Montealegre (*1946*) believed that insect pollination played a much more important role in the production of coffee in Puerto Rico than was commonly thought, and he believed that honey bees increased coffee yields; however, no data was presented to support his beliefs. Nogueira-Neto et al. (*1959*) concluded that the part played by insects in pollinating *C. arabica* cv. 'Bourbon' was of only secondary importance. Sein (*1923*) concluded that bees are beneficial to coffee in Puerto Rico, and Rudin (*1942*) reported that coffee plantations were installing colonies of honey bees for pollination of coffee in Puerto Rico. Zimmerman (*1928*) believed that honey bees played only a minor role in the pollination of coffee, at least in the case of the larger plantations, and no reference is made to supplementing the number of pollinating insects in the area. The quite limited evidence indicates that *C. arabica* is not dependent upon pollinating insects, but under some conditions at least insects can be beneficial, possibly to a substantial degree to this species of coffee. *C. canephora* is self-sterile (Devreux et al. *1959*, Purseglove *1968**) as is the selection reported by Krug et al. (*1950*) and Mendes (*1949*), made up of *C. arabica* × *C. dewevrei* Wildem. & Dur.

Pollinators

Ferwerda (*1948*) stated that pollen transfer of the pronouncedly cross-pollinated *C. robusta* Linden is accomplished by wind. Carvalho and Krug (*1950*) concluded that insects and wind were of about equal importance in the cross-pollination of coffee in Brazil. Carvalho et al. (*1969*) reported 7.3 to 9.05 crossing of which 4.8 to 5.3 percent was accredited to gravity, 2 to 5 percent to wind, and 0 to 2 percent to insects. McDonald (*1930*) suggested that growers in East Africa keep honey bee colonies on their plantations. Lower (*1911*) indicated that bees benefited coffee in Puerto Rico and that colonies should be placed in the coffee plantations. Montealegre (*1946*) also indicated that honey bees benefited coffee in Costa Rica. Nogueira-Neto et al. (*1959*) stated that larger bees such as honey bees and *Melipona quadrifasciata* Lepeletier were more efficient pollinators of coffee in Brazil, but the overall benefit was considered rather insignificant. Sein (*1923*, *1959*) showed that honey bees were beneficial to coffee in Puerto Rico, and Rudin (*1942*) stated that Costa Ricans were installing colonies of honey bees in their coffee plantations for pollination purposes. Amaral (*1972*) stated that honey bees were the dominant pollinating agent in the area of his studies. He further showed that colonies in the coffee groves collected predominantly coffee pollen (80 percent of the pellets identified) during the peak of flowering.

In most instances where pollination of coffee was studied, the honey bee was the most important pollinating insect visiting the flowers.

Pollination Recommendations and Practices

The use of bees as pollinators of coffee has not been recommended on *C. arabica*, although the evidence indicates that a beneficial effect is obtained when pollinators were concentrated on this crop during the brief period of its flowering. Amaral recommended that honey bee colonies be placed every 100 m in the coffee grove just before flowering starts. The coffee specialist might be agreeably surprised to discover the increase derived from a large-scale community-type honey bee pollination program. The other two important species, *C. canephora* and *C. liberica*, are self-sterile, and they would appear to be greatly benefited by bee pollination. Considering the recent increased importance of the self-sterile African *C. canephora* in the production of instant coffee, the use of bees in its pollination would appear to be highly profitable.

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COLE CROPS[23]

Brassica oleracea L., family Cruciferae

A large number of crops belongs to the plant species *B. oleracea*, known collectively as cole crops. Considerable difference of opinion exists among authorities as to the exact classification of these crops into subspecies, varieties, and subvarieties. Also, types will intercross, and the subsequent generation adds to the confusion.

[23] For some closely related crops, see "Mustard," p. 261; "Radish," p. 314; "Rape," p. 315; and "Turnip and Rutabaga," p. 365.

Nieuwhof (*1969*) separated the species into the following classification of varieties and subvarieties:

B. o., var. *acephala* DC.	
subvar. *laciniata* L.	Curly kale
medullosa Thell.	Marrow-stem kale
millecapitata (Lev.) Thell.	Thousand-head kale
palmifolia DC.	Tree kale
plana Peterm.	Smooth-leaf kale
B. o., var. *botrytis* L.	
subvar. *cauliflora* DC.	Cauliflower
cymosa Lam.	Sprouting (Italian) broccoli
capitata L.	
f. *alba* DC.	White cabbage
f. *rubra* (L.) Thell.	Red cabbage
gemmifera DC.	Brussels sprout
gongylodes L.	Kohlrabi
sabauda L.	Savoy cabbage

Nieuwhof (*1969*) considered collards and Portugal cabbage or tranchuda kales as transitional types between kales and cabbages.

In addition to the crops mentioned above, there are some other *Brassicas* for which little or no information exists on their pollination requirements. Because of the botanical relationship these requirements may be similar to known ones, although experience with some other crops has shown that even within a species the pollination requirements can be highly variable. These less well-known cruciferous crops grown primarily for their succulent leaves were listed by Bailey (*1949**) as follows:

B. carinata A. Br.	Abyssinian mustard
B. chinensis L.	Pak-choi or Chinese cabbage
B. fimbriata DC.	Curled kitchen kale
B. narinosa Bailey	Broadbeaked mustard
B. parachinensis Bailey	Mock pak-choi
B. pekinensis (Lour.) Rupr.	Pe-tsai
B. perviridis Bailey	Tendergreen or spinach mustard
B. ruvo Bailey	Ruvo kale
B. septiceps Bailey	Seven-top or Italian kale

Cabbage and broccoli are the most important of the cole crops as indicated in table 10. Although cabbage is grown in more than half of the States on a total of 111,800 acres, Texas with 21,000; Florida with 17,600; New York with 11,200, and California with 9,700 acres account for more than half of the total production. The bulk of the broccoli, 30,600 acres of the 37,060 acres, and cauliflower, 17,900 of the 25,600 acres, produced in the United States came from California.

Table 10.—Acreage and farm value of U.S. cole crops produced in 1970

Crop	Acreage harvested	Dollar value (millions)
Broccoli, including sprouting broccoli	40,300	30
Brussels sprout	6,000	8
Cabbage	118,400	82
Cauliflower	23,900	22
Kale, including collards	(1)	(1)
Kohlrabi	(1)	(1)

[1] Estimates discontinued.

Plant

The cole crops are large-leaved, succulent, and low-growing, 1 to 2 feet, until the inflorescence is formed then they may reach 2 ½ to 7 feet in height. More are biennial than annual, although most cauliflowers are annual. Nieuwhof (*1969*) stated that when annual varieties are crossed with biennial ones in temperate zones, the F_1 is annual, but at slightly higher temperatures the F_1 might become biennial.

The plants are usually grown in cool climates or in the cooler part of the year in warm climates, and they do best under conditions of relatively high humidity. The leaves, buds, or sprouts are eaten either fresh (salad), cooked (usually blanched), or processed (sauerkraut) (figs. 82–84). The seed-stem is of value only in the production of seed. Unless seed is produced, the plant is destroyed or abandoned after the succulent portion is harvested.

There are many cultivars of the different subspecies or "varieties" of *B. oleracea* (Thompson *1964*).

Inflorescence

After leafy growth ceases, as for example the completed growth of the head of the cabbage, or the sprouts of Brussels sprouts, the flowering stem elongates. It is characterized by numerous branches (mostly from a main stem), small leaves, and numerous bright yellow or occasionally white flowers. The flowers of all Cruciferae have four petals, ½ to 1 inch long, that appear to form a cross, hence the name Cruciferae (cross bearing).

The flower opens during the morning, the anthers a few hours later, so the flower is slightly protogynous. There are six stamens, two generally shorter than the style and facing toward it but leaning away, and four erect stamens generally longer than the style and also facing it. There is a single capitate stigma terminating the style (fig. 85). In most cultivars, nectar is secreted by two nectaries located between the bases of the short stamens and the ovary. Nieuwhof (*1969*) stated that there are also two inactive nectaries outside the base of the two pairs of long stamens. The nectaries secrete freely, 0.1 cm^3 nectar each 24 hours of the 3 days the flower is open (Pearson *1933*). The flowers are highly attractive to pollinating insects for both nectar and pollen. When the seed-producing acreage is large, beekeepers nearby frequently harvest a crop of excellent honey.

The blossom forms a silique, incorrectly but commonly called a pod, 1 to 4 inches long. A silique is distinguished by the unfolding of its two outer "shells," leaving the 10 to 30 seeds enfolded in a membranous partition. A well-fruited cabbage plant may produce one-half pound of seed (Pearson *1932*); a Brussels sprouts plant, one-quarter pound (Sciaroni et al. *1953*). Yields of 1,300 to 1,700 pounds of seeds per acre of cabbage can be expected, depending upon soil, climate, and cultural practices (Schudel *1952*), although, as shown below, the average production of seed per acre is much below this amount. One acre should produce enough seed to plant several hundred acres. Nieuwhof (*1969*) recommended 1 to 5 kg seed per ha, roughly 1 to 5 lb/acre, the amount depending upon the preciseness of

the planting method. If the seeds are planted in a bed, then the young plants transplanted to the field, only 80 to 200 g of seed per acre of plants are needed.

The acreage and production of *Brassica* seeds in the United States is shown in table 11.

Pollination Requirements

The cole crops require cross-pollination. Only in some varieties of cauliflower is seed setting partly brought about by selfing (Nieuwhof *1963*, *1969*). In general, the flower is self-sterile (Detjen *1927*, Kakizaki *1922*). Many plants are self-incompatible, and some are cross-incompatible (Attia and Munger *1950*, Detjen *1927*, Garcia *1954*, Odland and Noll *1950*). The pollen must,

PN-3792

FIGURE 82.—Brussels sprouts plant, showing sprouts at proper harvesting stage.

PN-3793

FIGURE 83.—Broccoli plant with head at proper stage for harvesting.

PN-3794

FIGURE 84.—Kohlrabi plants properly spaced and almost large enough to harvest.

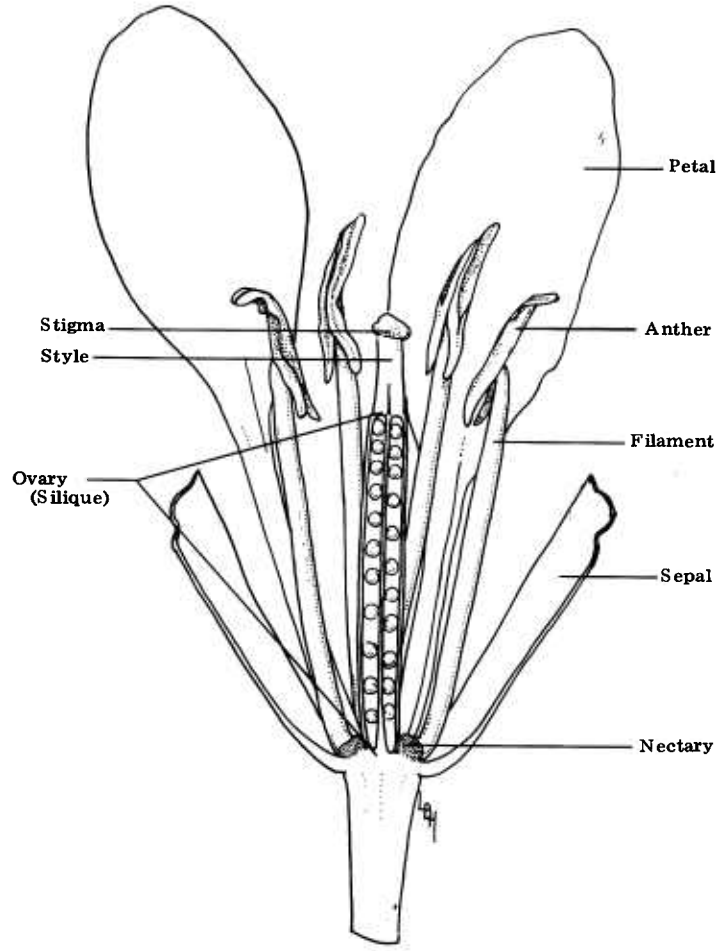

FIGURE 85.—Longitudinal section of collard flower, × 6.

Table 11.—Acreage and production of Brassica *seed crops in the United States*

Kind of seed harvested	Harvested in—			Production in—		
	1969	1970	1971[1]	1969	1970	1971[1]
	Acres			*Thousand pounds*		
Broccoli	51	97	120	56	87	85
Cabbage	358	526	664	200	351	402
Cauliflower	144	231	222	72	135	112
Kale	63	100	47	48	118	42
Kohlrabi	13	20	16	7	30	17
Mustard	379	193	204	444	288	220
Radish	1,880	1,348	1,347	1,641	1,389	1,157
Rutabaga	35	31	38	39	57	48
Turnip	591	481	422	856	758	482

[1] Preliminary estimate.

therefore, be effectively transferred between plants that are cross-compatible. Pearson (*1930, 1932*) concluded that *Brassica* plants were 95 percent cross-pollinated.

Moore and Anstey (*1954*) found up to 76 percent selfing in sprouting broccoli, but they did not indicate how much of the set was due to insect activity or if any of it resulted from the plants' own self-fertilization. Anstey (*1954*) found that 52 percent of sprouting broccoli plants were self-incompatible, 30 percent compatible, and 18 percent somewhere in between. But even with the compatible plants, the transfer of the pollen from anthers to stigma is necessary for best seed set.

Usually, plants grown in cages or otherwise isolated from pollinating agents set practically no seed even if the plants are occasionally shaken. Cross-pollinated cabbage flowers produced siliques with 10 or more seeds, but selfed flowers produced less than one seed each. Nieuwhof (*1969*) attributed this self-incompatibility to the fact that pollen on the stigma of the same plant germinates poorly, and he agreed with Knuth (*1908*, pp. 74–128*) that this incompatibility is strongest in freshly opened flowers. This illustrates Nature's abhorrence of selfing, accepting it reluctantly only as a last resort to preserve the species. The pollen must be transferred by an outside agent, and wind is not an important factor in its transfer, although Haskell (*1943*) and Jenkinson and Glynne-Jones (*1953*) stated that some pollen is moved by wind.

Many plants in the cole crops are male-sterile (East *1940*, Nieuwhof *1961*), and the use of this factor has been proposed in a hybrid seed production program (Attia and Munger *1950*, Skrebtsova *1964*). Sun (*1937*) showed that self-pollination of *Brassica* resulted in decreased yields in subsequent generations.

Increasing interest is developing in the production of hybrid seed. Legg and Souther (*1968*) showed that open-pollinated broccoli cultivars are unlikely to be used in a hybrid program, but Cole (*1959*) and Dickson (*1970*) reported finding a male-sterile mutant in sprouting broccoli, that might make hybrid seed production practical. Borchers (*1968*) showed that broccoli hybrids produced larger heads; 36 percent matured earlier and more uniformly than nonhybrids. Later, Borchers (*1971*) reported on the production of hybrid broccoli by using male-sterile plants with honey bees to do the crossing. Johnston (*1964*) demonstrated that hybrid vigor exists in the marrow-stem kale.

The most effective time for pollination during the 3 days the flower is open and the stigma is receptive has not been determined (Kakizaki *1925*). More than one pollen-application period is probably necessary for fertilization of all the ovules in the ovary to produce a full silique.

Pollinators

The construction of the flower is such that many kinds of insects can reach the pollen and nectar, including honey bees, wild bees, and flies. Blowflies have been used in cages where the pollination of only a few plants was involved (Faulkner *1962*), but no practical method has been developed for their use in open-field pollination. Pearson (*1932*) considered bees of the family Andrenidae, Megachilidae, and Nomadidae [= *Nomada* spp. of Anthophoridae] more important than honey bees in the pollination of cabbage, but he did not say what the relative populations were, either on the plants or in the area. Sneep (*1952*) mentioned *Bombus* and *Psithyrus* but only incidentally.

Because cole crops flourish in cooler areas, the plants may come into bloom at temperatures below the minimum of about 55° F at which honey bees fly. A few wild bees sometimes forage below this critical temperature, and if they are abundant, under such a climatic condition they could be important.

In general, the honey bee is the primary pollinator of cole crops (Hawthorn and Pollard *1954**, Jones and Rosa *1928**, Nieuwhof *1969*, United Nations *1961*). It can be transported to the fields to be pollinated when desired. In the U.S.S.R., Skrebtsova (*1964*) reported that 84 to 94 percent of the pollinating agents on cabbage were honey bees. Radchenko (*1966*) reported that honey bees comprised 85 to 100 percent of the pollinators on cabbage, increased the seed crop by 300 percent over plants not freely visited, and that this visitation also considerably enhanced the seed quality. Sakharov (*1958*) showed that cabbage seeds from flowers receiving adequate bee visits were three times as large as those from flowers not visited by bees. Atkinson and Constable (*1937*) stated that the intense and repeated pollination that takes place within a cage when honey bees are enclosed results in more fruit set with more seeds per fruit than occurs in the open.

Pollination Recommendations and Practices

Many publications on the production of cole crop seed give little or no consideration to the value of insect pollinators (Griffiths et al. *1946**), or these insects are considered only from the standpoint of varietal contamination (Bateman *1947–48*, Knott *1949*, Natl. Inst. Agr. Bot. *1942*, Priestley *1954*, Watts *1968*).

The excellent United Nations (FAO) report (*1961*) stated that to insure good seed set of *Brassicas*, insect pollination of all the flowers is necessary. To accomplish this, they recommended placing colonies of bees near the larger fields but did not indicate how many colonies. Skirm (*1971*) said that bees were essential. Sakharov (*1956*) showed the following interesting relationship

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between a high density of bees and seed production and quality as follows:

Explanation	Method of pollination used		
	Saturated pollination by bees	Free pollination	Self-pollination
Average seed yield per plant	46.6	0.9	0.1
Weight of 1,000 seed . . . . . grams	4.8	2.0	(1)
Germination . . percent	96	64	0

[1] "Puny."

Eckert (*1959**), without supporting data, recommended two colonies per acre of all vegetable seed. Odland and Noll (*1950*) stated that a colony of bees located by their plots increased the seed yields. Oldham (*1948*) stated that having "a few colonies of bees dotted around the field" was a distinct advantage. When more than 5 or 10 acres are involved, the chances are good that the local supply of wild bees is inadequate for maximum flower visitation and seed set. If this is likely to be the case, the grower should arrange for the placement of strong colonies of honey bees in or adjacent to his field during flowering.

The number of colonies needed will doubtless vary with their strength, the size of the field, and the competing plants that might lure the bees from his field. Under some conditions, two colonies—as recommended by Eckert (*1959**)—might be adequate. Under other conditions where the grower is striving for maximum seed production, twice as many or more may be needed. In any case, where seeds of cole crops are produced commercially, the grower should take steps to assure the presence of the maximum population of insect pollinators.

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CORIANDER

Coriandrum sativum L., family Umbelliferae

Coriander is a minor crop grown for its aromatic seeds and oil, which are used in the flavoring of food, in certain drinks and in medicine. It is extensively cultivated in India and grown to some extent in Europe and Brazil, with only a few acres in the United States.

Plant

The plant is a strong-smelling annual, 1 to 3 feet high, and is cultivated somewhat like carrots. Yields of 2,000 to 3,000 pounds of dried seed per acre are obtained in India (Purseglove *1968**).

Inflorescence

The coriander flower has five irregular-shaped petals, five stamens, five sepals, and two styles. The white to pinkish flowers are in umbels. The first umbels to bloom have hermaphrodite flowers, with possibly a few staminate ones (fig. 86). The later umbels have only staminate flowers. The hermaphrodite flowers are completely protandrous, so that selfing is impossible. After the pollen is gone, the stigmas become receptive and are liable to crossing with other plants; however, the umbels of staminate flowers may develop in such a way that they are right over the receptive stigmas of later flowers. When these anthers dehisce, the pollen is thrown out and falls to the stigmas below in crumbling masses. In this way, some of the stigmas may be pollinated even if an insect has not brought pollen from another flower (Kerner *1897** p. 325).

Pollen is produced in the pinkish anthers. Nectar is freely secreted on the ovary. The blossoms are highly attractive to both pollen-collecting and nectar-collecting insects (Glukhov *1955*), and honey bees "go a bit frantic" over them (Pellett *1947**).

Pollination Requirements

Although the coriander plant is partially self-fertile, bees are beneficial to it. Glukhov (*1955, p. 216*) reported that when they were excluded only 49.4

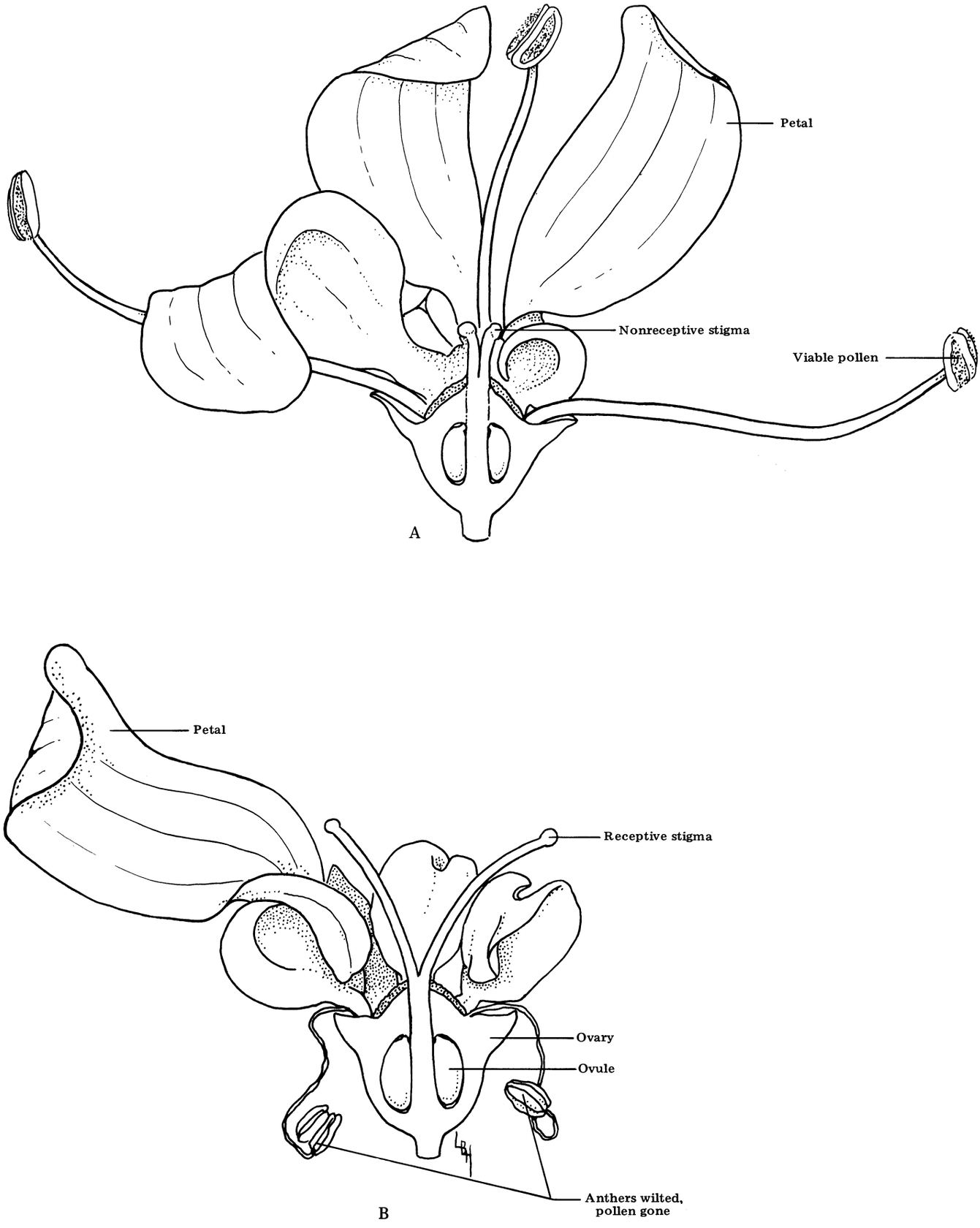

FIGURE 86.—Longitudinal section of coriander flower, × 40. *A*, Staminate stage; *B*, pistillate stage.

percent of the seeds set, but when they were present 68.3 percent of the seeds set. With the possible yield of 2,000 to 3,000 lb/acre, the above bee effect would be of significance. Bogoyavlenskii and Akimenko (*1966*) associated seed yields with greater insect visitation.

Pollinators

Honey bees are apparently ideal pollinators of Coriander.

Pollination Recommendations and Practices

None.

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COTTON

Gossypium spp., family Malvaceae

Cotton is grown primarily for its lint, although the seed, valued at about one-fifth that of the lint, is also used for planting or is crushed, a food oil recovered, and the residue used as a livestock food.

Cotton was naturally dispersed throughout much of the warmer parts of the world even before 3,000 B.C., when its lint was spun and woven into cloth (Gulati and Turner *1928*). Only four of the numerous species of *Gossypium* are cultivated for their spinnable fibers. These are the two diploid Asiatic species, *G. arboreum* L. and *G. herbaceum* L., and the two amphidiploid species, *G. barbadense* L. and *G. hirsutum* L. The first two are confined primarily to the Old World. The last two are grown both in the New World and abroad. *G. hirsutum*, known as upland or short staple cotton, is grown most extensively. *G. barbadense*, known in the United States as American Pima, or Pima, and sometimes called extra-long staple cotton, is grown in long-season areas, such as our Southwestern States.

The crop is grown from Virginia southward and westward to California, in an area often referred to as the Cotton Belt. The more important cultivars[24] of upland cotton planted in 1971 included 'Deltapine 45', which accounted for 25 percent of the total acreage, 'Stoneville 213', which accounted for 18 percent, and 'Acala SJ-1', which accounted for 10 percent. Other major cultivars and their percentages included: 'Lankart LX 571', 7; 'Coker 201', 4; and 'Paymaster 111', 'Stoneville 7A', and 'Stripper 31', each 3 percent (USDA *1971*).

Texas, California, Mississippi, and Arkansas were the leading cotton producing States in 1970. The value of the entire U.S. crop was approximately $1.2 billion. The leading cotton producing countries of the world in 1970 are shown in table 12.

The lint percentage of cotton varies from 30 to 40 percent, more often in the high 30's for upland and the low 30's for Pima.

[24] In cotton, a cultivar, or "variety," is neither a clone, a pure line, nor a primary mixture of pure lines. It is usually a progeny row selection, bulked and mass multiplied, during which time insect pollination may have played a major or insignificant role, depending upon the pollinator population present during the flowering season.

TABLE 12.—Leading cotton producing countries of the world in 1970[1]

Country	Millions of acres	Pounds of lint per acre	Millions of bales of lint[2]
India	19.0	111	4.4
China (mainland)	12.5	268	7.0
United States	[3]11.2	437	10.3
Russia	6.8	761	10.8
Brazil	6.0	183	2.3
Pakistan	4.3	271	2.4
United Arab Republic	1.7	664	2.3
Turkey	1.3	676	1.8
Sudan	1.3	406	1.1
Mexico	1.0	692	1.4

[1] Source: Anonymous *1972*.
[2] An average bale weighs 480 pounds.
[3] Includes about 77,600 acres of Pima.

Recognizing the variation in cotton due to natural speciation, breeder manipulation, the wide distribution, and the conditions under which it is grown, the following discussion will be largely confined to upland cotton. Pima and, to a much lesser degree, the other two species, will also be mentioned. Because of some lack of agreement on the pollination requirements of cotton, more than the usual amount of space is devoted herein to this crop.

Plant

The cotton plant is a broad-leaved perennial, 2 to 5 feet tall, that is treated as an annual under much of its growing conditions in the United States. It becomes a perennial if the ground in which it grows does not freeze during the winter. The plants will grow and be productive on a wide variety of soils. It is most productive on fertile soil under hot weather and irrigated conditions if rainfall is deficient. The seeds are usually planted 4 to 8 inches apart in about 3-foot rows after all danger of frost is past in the spring. Flowering on the first of its lower branches begins in about 2 months and may continue on succeeding branches and growth another 2 months at about which time the first ripe fruit (bolls) begin to open and expose the mature lint-covered seed

(fig. 87). Most of this raw cotton is currently machine-harvested then transported to a cotton gin where the lint is separated from the seed then pressed into bales.

Flowering and fruiting on the plant follows a spiral course from the innermost bud on the oldest and lowest fruiting branch, and ends on the latest growth toward the tip of the plant.

Pima cotton is usually more robust than upland cotton, with waxy-green leaves and smaller bolls. Fruiting on the plant begins later in the season, which tends to restrict its culture to the area with the longest growing season, such as the extreme southwestern United States.

Only about half as much lint per acre is normally produced on Pima cotton as is produced on upland cotton; however, the grower receives about twice as much for the more desirable lint, so the net profit from the two types of cotton is similar. The lint can be removed from the seed with the same type of gin saws that are used on upland cotton, but the quality of the lint is better if it is removed with a roller gin.

Inflorescence

The 2- to 4-inch-long by 2-inch-broad cotton blossom is subtended by three green leafy bracts, each an inch or more across, and a green calyx that fits snugly around the base of the ovary. The five-petal corolla of upland cotton is cream colored when it opens in the morning shortly after sunup, but turns pink in the afternoon and closes toward nightfall never to reopen (fig. 88). On the second day, the color of the petals is a watermelon-red. The typical corolla of Pima cotton is yellow, with a maroon throat or petal spot, and the color changes little with age. The corolla and staminal column usually fall on the second day.

The staminal column surrounds the 1- to 2-inch-long style leading from the ovary and terminating in the ¼- to ½-inch-long stigma (fig. 89). The ovary contains 5 to 10 ovules in each of three to five sections, carpels, or locules. The staminal sheath, enclosing most of the style, bears numerous stamens ¼ to ½ inch long, each terminating in an anther that normally produces an abundance of viable self-fertile pollen, 45,000 grains per flower (Tsyganov *1953*). The grains are large, 81 to 143 microns (Kaziev *1964*), and coated with a viscid material that causes them to adhere to each other; therefore, cotton pollen is not transported by wind. Each section of the oval, 1-inch boll that develops from

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FIGURE 87.—Open bolls of cotton.

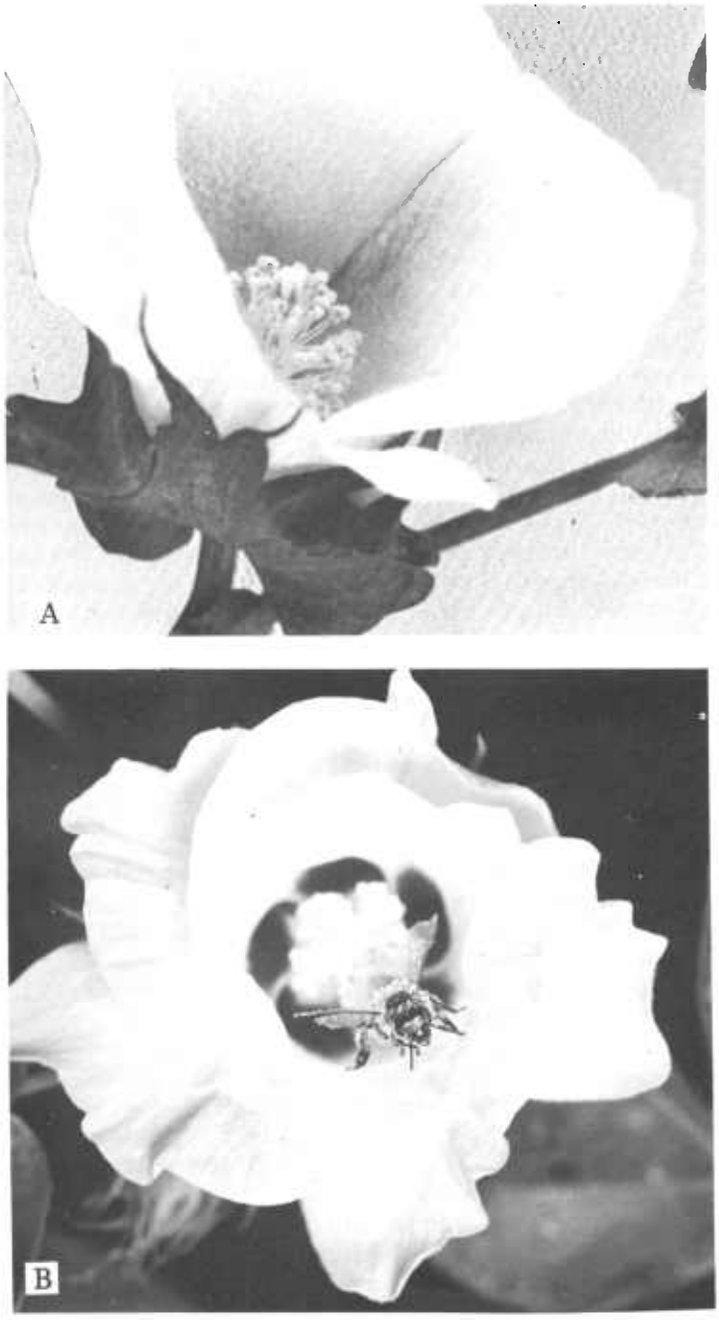

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FIGURE 88.—Cotton flower, showing general corolla shape and proximity of anthers to stigma. *A*, Upland cotton flower with flared, cream-colored corolla, and stigma protruding only slightly above the anthers; *B*, Pima cotton flower, with tubular shaped yellowish corolla and dark "petal spot" toward base. Stigma extends well above the anthers.

the ovary may produce a "lock," a distinct group of lint-entangled seed. These locks are exposed at maturity in the open three- to five-sectioned "burr."

The number of flowers on a cotton plant are determined by numerous factors including the available plant food, water supply, variety, and density of the plant population. Usually, about half of the flowers produce mature bolls (Brown *1938*, Buie *1928*, Dunlap *1945*, McNamara et al. *1940*, Sen and Afzal *1937*). Flowering reaches its peak at about four flowers per plant per day. Between 225 and 400 bolls are usually required to produce a pound of lint.

NECTARIES AND NECTAR SECRETION OF COTTON

Nectar is normally produced in five different areas on the cotton plant, although the reason why the nectar is secreted is not clear. Trelease (*1879*) made a detailed

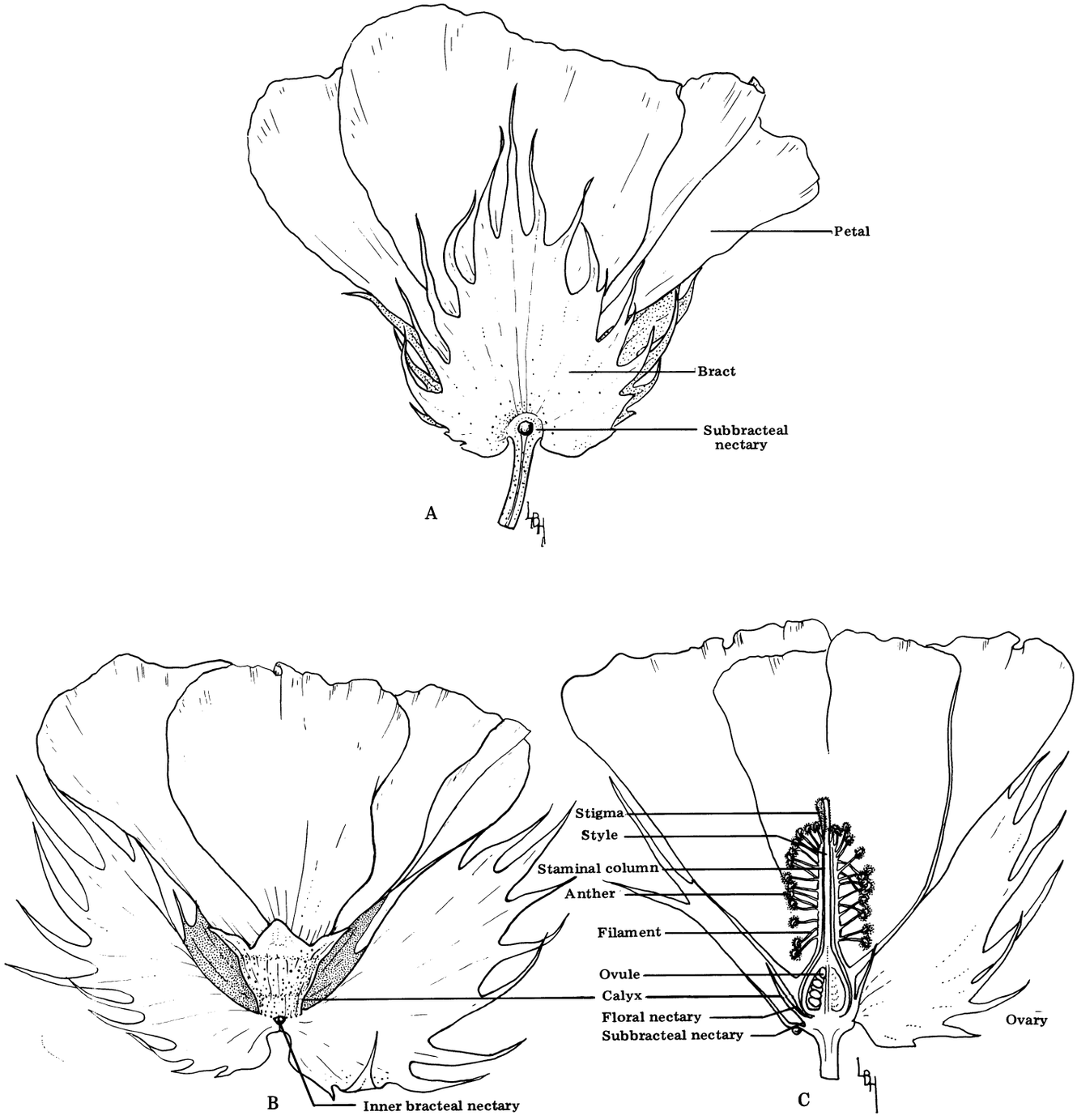

FIGURE 89.—Flower of 'Deltapine' upland cotton, ×1.5. *A*, Side view, showing one of the 3 subbracteal nectaries; *B*, bracts slightly spread to show one of the 3 inner bracteal nectaries; *C*, longitudinal section.

report on cotton nectar secretion and its possible purposes (although he stated "Glover, Agricultural Report 1855, p. 234, mentions these glands—and their secretion of a sweet substance, which ants, bees, wasps, and plant bugs avail themselves of as food"). Kaziev (*1964*) stated that Delpino, in 1900, was the first to characterize the floral and foliar nectaries of cotton.

The different areas of nectar secretion are (1) floral, (2) inner or circumbracteal, (3) outer or subbracteal, (4) foliar or leaf, and (5) unipapillate (microscopic) areas on the flower peduncles and young leaf petioles (Mound *1962*) (fig. 90). These unipapillate nectaries are rarely visited by pollinating insects, contribute nothing to pollination and little or nothing to the welfare of pollinating agents, and will not be further discussed. Trelease (*1879*) believed that the floral nectaries were associated with pollination but that extra-floral nectaries were associated with attracting harmful insects away from the delicate flower parts. Kottur (*1921*) believed that the nectar and pollen in the flower invited natural crossing.

In addition to the secretion from the nectaries, there is a saccharine exudation of certain aphids, white flies, and thrips on cotton, known in the Sudan as "asal" (Bedford *1921*). When this material is present in abundance, it supports growth of a sooty fungus, causing a detrimental blackening of the cotton leaves. At times, the sticky material becomes mixed with the lint with damaging effects (Hadwich *1961*). When honey bees are present in sufficient numbers, they collect this material as food, and by removing it they become beneficial in a sense other than as pollinators.

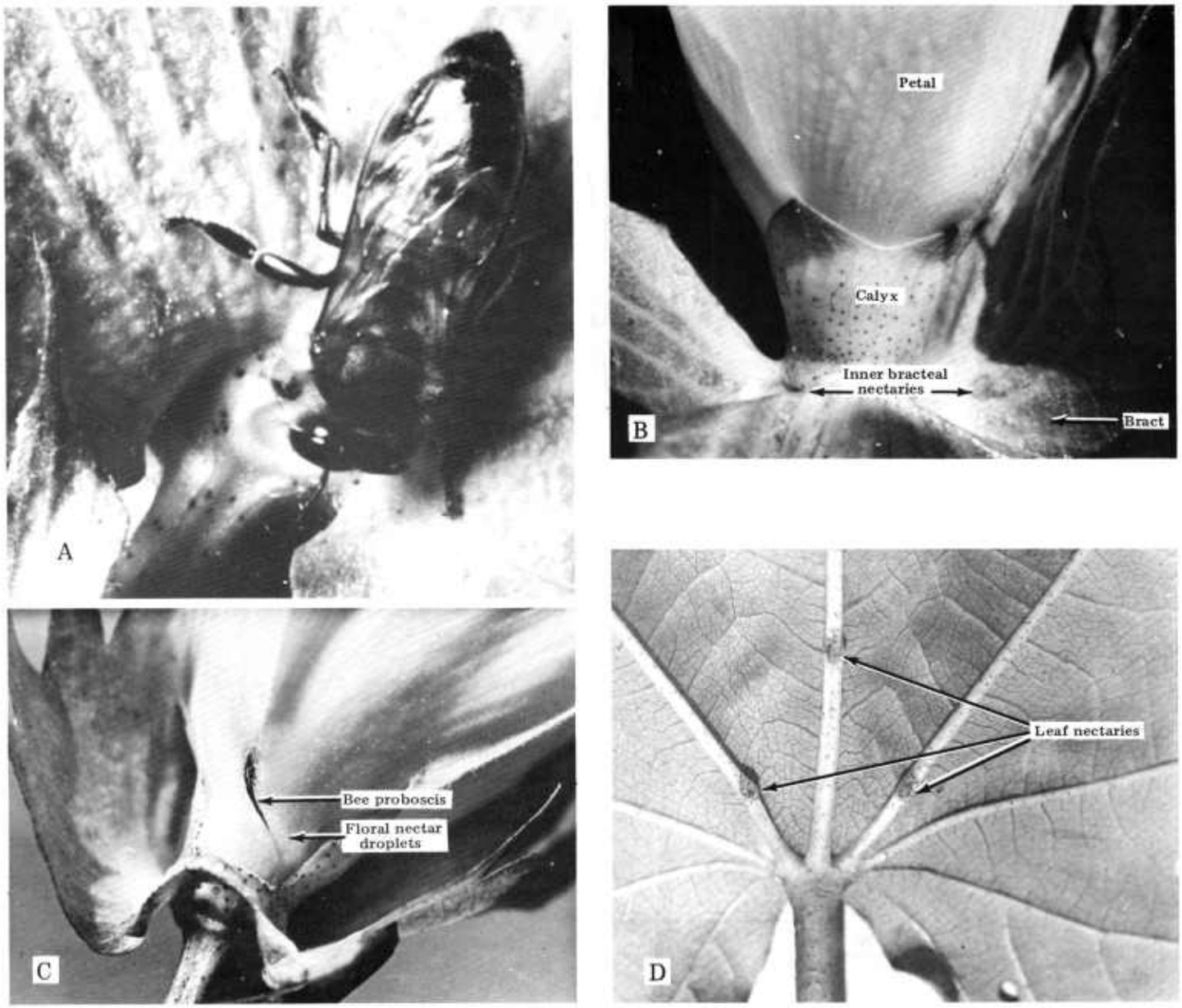

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FIGURE 90.—Nectaries of cotton plant. *A*, Honey bee collecting nectar from a subbracteal nectary; *B*, inner bracteal nectaries; *C*, section of calyx removed to show proboscis (tongue) of bee (while bee is inside flower) reaching for floral nectar droplets; *D*, underside of leaf, showing location of leaf nectaries.

FLORAL NECTARIES

Within the flower, the nectar exudes from a ring of papilliform cells at the base of the inner side of the calyx (Tyler *1908*). Secretion may begin a few hours to a few days before the flower opens, but, because of its unavailability to pollinators until the flower opens, this possible early secretion is of no consequence. The nectar reaches its maximum accumulation by midafternoon, the amount depending upon climatic factors, soil fertility, water, and cultivar involved (Kaziev *1959a, b, 1967*), and ceases when the petal color begins to change, an indication, according to Kaziev (*1964*) and Mel'nichenko (*1963*) that pollination has occurred.

NECTAR COMPOSITION IN RELATION TO ATTRACTIVENESS TO BEES

At times, honey bees appear to be noticeably reluctant to visit cotton blossoms, even though much nectar and pollen are present. Wykes (*1952*) studied the preference of honey bees for solutions of various sugars and found that preferences were shown for solutions of single sugars in the following descending order: Sucrose, glucose, maltose, and fructose, and that mixtures of equal parts of all these sugars was the most attractive combination. Vansell (*1944a, b*) studied the composition of sugars in orange and cotton floral nectar and found the percentages shown in table 13.

TABLE 13.—*Percentage of sugars and moisture content of cotton and orange nectars*

Plant	Levulose	Dextrose	Sucrose	Approximate Moisture
Cotton:				
'Acala'	14.27	13.06	0.71	70
'Pima'	10.36	9.25	.35	80
Orange:				
'Washington Navel'	6.46	5.42	12.87	75
'Valencia'	6.08	5.06	12.38	77

Butler et al. (*1972*) collected nectar from leaf, floral, and extra-floral nectaries of 'Hopicala', 'Deltapine Smooth-leaf', 'Deltapine 16', and 'Pima S-2' near Tucson, Ariz., and analyzed it by gas chromatography for its sugars. They also found low sucrose percentages in nectar from floral and subbracteal nectaries.

Ivanova-Paroiskaya (*1950*) showed the fructose–glucose–sucrose percentages of floral nectar of *G. barbadense* cotton, cv. '35–1', to be 39.78–37.50–1.63, and for upland cotton, cv. '36–7 M', to be 37.85–35.65–6.89. Kaziev (*1964*) showed that the range of the sucrose content of cotton nectars was from 2.3 to 7.6 percent, with the total mono-sugars ranging from 21.2 to 46.9 percent. All samples were taken during midseason flowering. Whether the percentages change with the season has never been determined.

Numerous observations have shown a relatively low percentage of honey bee visits to flowers of cotton during midseason and a high percentage toward the beginning and the end of the season. For example, in August 1952 (unpublished data), at Tucson, Ariz., eight blossoms of 'Pima S-1' were observed constantly from 8:45 until 11:30 a.m. During that time, they received visits from one honey bee, one *Bombus* spp., 100 *Melissodes* spp., and five unidentified pollen-collecting bees. In the same plot, on October 10 between 7 a.m. and noon, three blossoms of 'Pima S-1' were visited by 363 honey bees and seven *Melissodes* bees. The reason for this extreme difference in the number of bee visitors is unknown.

The volume of nectar in the blossoms of Pima cotton is greater than that in upland cotton, but the sugar concentration is lower. As much as 0.1 ml of nectar has been collected at one time from the former but never more than half this amount from upland. The sugar concentration of upland cotton floral nectar is greater (reaching a maximum of about 69 percent) than that of Pima nectar (a maximum of only 34 percent (fig. 91). The volume of floral nectar of both cottons exceeds the volume of extrafloral nectar, but, as previously stated, the floral nectar is less attractive to honey bees.

Nectar secretion of cotton is strongly influenced by soil fertility, as various tests made in Russia have shown. For example, superphosphate increased nectar secretion by 170 percent and potassium by 130 percent (Monokova and Chebotnikova *1955*). Extensive studies by Kaziev (*1964*) showed that nitrogen had no effect on nectar production, but the greatest increases resulted from application to the soil of cattle manure alone or with complete fertilizers.

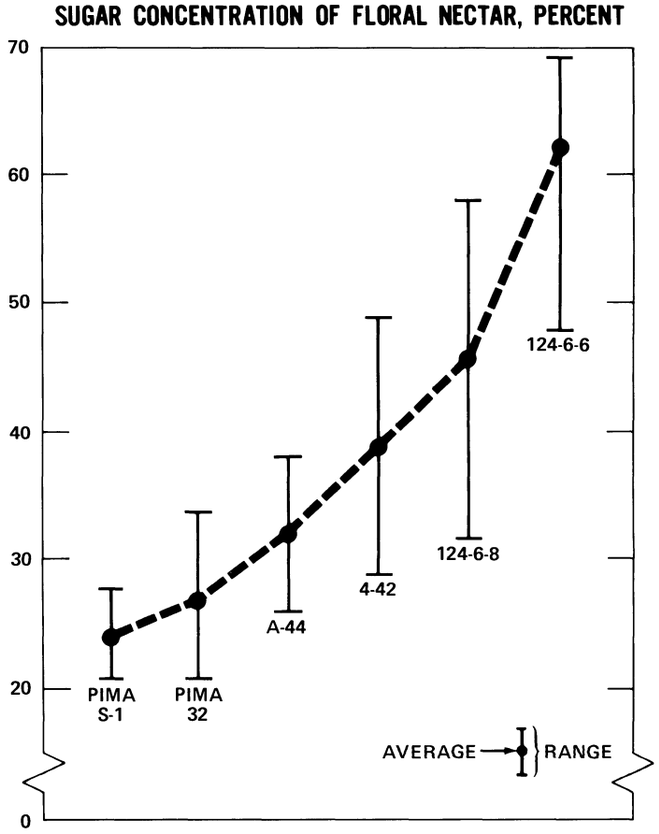

FIGURE 91.—Average and range, in percent, of sugar (soluble solids) of floral nectar of 6 different cotton cultivars grown at the USDA Cotton Research Center, Phoenix, Ariz., August 1957.

NECTARIES OUTSIDE THE COROLLA (INVOLUCRAL NECTARIES)

There are usually three nectaries just below the sepals at the union of the three bracts, and three others just below the base of the bracts. These have variously been referred to as calyceal and subbracteal, inner and outer involucral, extrafloral internal and extrafloral external, and bracteal nectaries. They begin to function several days before the flower opens, but the day before opening they secrete nectar in copious amounts and this secretion may then continue from several days to 2 to 3 weeks after flowering. When beekeepers report good honey flows from cotton, the bees are usually working these involucral nectaries more intensively than the other nectaries of cotton. Kaziev (*1964*) also showed that these involucral nectaries were highly attractive to bees. Some upland cotton plants may not have all of these nectaries.

In Hawaiian cotton (*G. tomentosum* Nutt. ex Seem.), the nectaries are entirely absent. This characteristic has been transferred to some commercial selections to provide a nectariless cotton (Meyer and Meyer *1961*). These selections are studied to determine the effect of nectar deprivation on harmful lepidopterious insects on cotton (Lukefahr and Martin *1964*, Lukefahr and Rhyne *1960*). The nectariless characteristic has been suggested in connection with proposed production of hybrid cotton, the theory being that if only floral nectar were present the bees would visit the flowers more frequently. The opposite, however, may be true, that is, the bees may be attracted to the field by the extrafloral nectaries and then discover the floral ones. Research in this area is requisite for a successful hybrid cotton program if pollinating insects are used.

FOLIAR OR LEAF NECTARIES

Nectar is also produced on the underside of the leaf in usually one nectary on the primary vein near the blade and petiole juncture. Occasionally, there are two additional nectaries, one on a vein on either side of the primary vein. The leaf nectary begins to function before the leaf reaches full size and may function for 2 or 3 weeks. Leaf nectar secretion on the plant begins when the first flower is in the early bud, or "square", stage and may continue as long as the plant is producing new leaves (Kaziev *1964*). The structure of cotton leaf nectaries was described by Reed (*1917*).

Honey bees show preference for all of the extrafloral nectaries over floral nectar but under certain conditions collect nectar from all. Ivanova-Paroiskaya (*1956*) showed the following relative number of honey bee visits to the nectaries: Floral 32, calycular 219, subbracteal 580, and leaf 389. Many other insect species show a preference for the floral nectary of cotton.

COTTON AS A HONEY PLANT

In many of the areas where cotton is grown it is considered a major honey plant (Benton *1937*, Kuliev *1958*, Minkov *1957*, Parks *1921*). It does not produce as much honey per acre per day as alfalfa, clover, or many other sources (Butler et al. *1972*) but because of its longer flowering period, excellent crops of honey can be obtained. Pima cotton is recognized by beekeepers as a better honey source than upland cotton. Vansell (*1944a*) calculated that 1 acre of Pima cotton was equal to 30 acres of Acala in the production of nectar. Ivanova-Paroiskaya (*1950*) reported honey crops of 300 kg/ha (267 lb/acre) for *G. barbadense* compared to 75 to 90 kg/ha (66 to 80 lb/acre) for upland. Normally, when bees are working cotton blossoms, there is a steady, but not spectacular, storage of the high-quality cotton honey. Unfortunately, highly toxic insecticides, frequently used on cotton during the flowering period, kill many bees and prevent the harvest of a honey crop.

Pollination Requirements

Cotton is usually referred to as a partially cross-pollinated crop, although many breeders have treated it as a completely self-fertile and self-pollinating crop except for accidental and unwanted cross-pollination caused by pollinating insects. Cross-pollination has been referred to as "natural crossing," and is considered detrimental because of the introduction of off-type plants into the progeny. Its impact on production has not been given much consideration. Breeders know that a cotton blossom isolated by any one of several techniques will usually develop a mature boll with viable seed. Breeders also know that they seldom obtain by this method quite as many seed or as much lint from such bolls as they obtain from open-pollinated ones (Stephens *1956*). Because this difference can be altered to the benefit of the grower by the activity of pollinating insects, and because of the association of pollinating insects with natural crossing and resultant undesirable cotton types, the subject of natural crossing is reviewed.

NATURAL CROSSING

The term "natural crossing" is freely used in cotton literature, but not always precisely defined. The generally accepted meaning appears to be "the amount of cross-pollination effected by insects, as opposed to hand cross-pollination, that can be detected in breeding lines." Fryxell (*1957*) defined natural crossing as "that which occurs between individuals within a population." He stated that the two phenomena (intra- and inter-population crossing) are related, but the distinction is not always made clear. Simpson (*1954a*) stated that cross-pollination is not readily detected in cotton unless distinctive marker characters are present in the parental lines. For this reason, the extent of natural crossing in open-pollinated fields has been consistently underestimated by some cotton breeders. Natural crossing is usually associated with insect pollination of plants but seldom with its benefit to the cotton plant.

Various breeders have reported the percentage of natural crossing in their area and commented upon its detrimental effect. Balls (*1912*) reported 13.3 percent natural crossing of cotton in Egypt, and proposed the isolation of plants under mosquito netting to exclude bees. He noted, however, that some strains "resent this treatment and refuse to hold their bolls," a possible indication that he might have been unknowingly dealing with a degree of self-sterility in the plants, although shading of the plants might also have contributed.

Webber (*1903*) also reported 5 to 10 percent natural crossing between varieties of upland cotton grown in adjacent rows in the United States and concluded that absolute prevention of crossing would require isolation of cotton by 5 to 10 miles from other cotton. Ricks and Brown (*1916*) reported 2.8 to 18.5 percent in alternate hills in alternate rows. The type or preponderance of insect pollinators responsible for this cross-pollination was not given.

Cook (*1921*) stated that natural cross-fertilization in the field is one of the major causes of "running out" of varieties. Later, Cook (*1932*) stated that maintaining the seed stock of superior strains rather than creation of new ones was the essential breeding problem. To maintain good seed stocks, he stressed complete isolation from other varieties to prevent contamination by natural crossing. Peebles (*1942*) considered 1 mile as a sufficient isolation distance.

Ware (*1927*) stated that the amount of natural crossing, providing all other factors were the same, would be in direct proportion to the number of insects capable of carrying pollen. He made observations on the cross-pollination of cotton in two areas—at Scott, Ark., where the cotton acreage was large, and at Fayetteville, Ark., where there was little cotton in the vicinity other than the breeding plots. Honey bee colonies were fewer at Scott than at Fayetteville, the number of pollinating insects visiting the cotton flowers was much smaller, and less than 1 percent hybrids were obtained, compared to 40.9 percent hybrids at Fayetteville. Ware (*1927*) concluded that there was a close association between the presence of honey bees and other pollinating insects and the amount of cross-pollination obtained. Afzal and Khan (*1950*) reported 2 percent natural crossing with seven or eight visits per flower by insects daily, principally *Apis dorsata* Fab., *Anthophora confusa* Smith, and *Elis thoracica* Lepeletier.

Stephens and Finkner (*1953*), considering the beneficial effect of insect cross-pollination in the possible production of hybrid cotton, indicated that cross-pollination in different areas ranged from 5 to 50 percent or more, which they associated with differences in the effective bee population. They concluded that even in the area where the higher percentage of crossing occurred, the number of bees did not keep pace with the number of flowers available, so that the flowers were worked less effectively during the peak. Their proposed solution was the provision of a supplementary source of bees during the flowering period.

Simpson (*1954a*) made a survey of the natural crossing across the Cotton Belt and stated that the cooperators in the experiment were "in general agreement concerning the following factors that influence the amount of natural crossing: (1) cotton pollen is relatively heavy and wind is not an agent in pollen dispersal; (2) therefore, the amount of natural crossing in cotton is determined by the number of insect pollinators present in relation to the number of cotton flowers; and (3) intercrossing may be affected by the flowering habits of the varieties grown, by the abundance of unlike pollen, by location of the fields in relation to insect habitats, by flowering periods of other plants attractive to insect pollinators, by distance between unlike varieties, by topography and barrier crops, and by other environmental, climatic and biotic factors."

Further in the same paper, he stated that natural crossing had heretofore been considered a handicap in breeding programs and a hazard to be avoided, but that a beneficial intermingling of unlike genotypes could be obtained by increasing the population of insect pollinators. This was supported earlier by Brown (*1927*). Conversely, Harland (*1943*) proposed that a completely self-fertile cotton might be grown, a direction that some breeders seem to seek, but which is unlikely to result in the most productive type.

Simpson (*1954a*) also stated: "Cotton is a partially cross-pollinated plant, thus some degree of heterozygosity is maintained indefinitely when open pollinated seeds from an original F_1 population is continued on through F_2, and F_3, and subsequent generations. The relative proportions of selfing and outcrossing determine the amount of hybrid vigor retained in later generations." He hinted that this relationship could be utilized advantageously in current breeding programs. Kalyanaraman and Santhanam (*1957*) also hinted that breeding programs such as the mass pedigree method (Harland *1949a,b*) should be modified to allow increased genetic plasticity through open pollination and bulk methods of breeding.

Knight and Rose (*1954*) proposed that one stage of the cotton breeding program be conducted in an area of "high natural crossing" for improvement of the variety. This proposal has not been adopted in the United States, although it and the other statements would indicate that in current cotton breeding systems the breeders should strive for a high bee population in their seed increase fields. Somewhat similar usage of pollinating insects has been suggested by Simpson (*1954a*) and Turner and Miravalle (*1961*). The absolute dependence on pollinating insects for success in the Knight and Rose (*1954*) method was stressed by Bhat (*1955*), who concluded that natural crossing could result in deterioration of the variety, "not as a result of cross-pollination as is often fallaciously argued but because of its inadequacy." Al-Jibouri (*1960*) seemed to agree, for after reporting an average of only 0.47 percent crossing in Iraq, he concluded that this inbreeding could result in deterioration of the variety.

It stands to reason that the grower would want to preserve heterosis through favorable gene combinations, or crossing of proper types, and refrain from allowing crossing with inferior or unwanted types.

Many cotton breeders seem to believe that the natural crossing in an area, once established, does not vary from year to year. Thus, they speak of areas of high natural crossing without considering that the factors responsible for crossing may be considerably altered from season to season or even within the season. Humbert and Mogford (*1927*) stated that cross-fertilization in cotton will vary from 2 to 20 percent and will not average over 15 percent under normal conditions. The "normal" conditions were not described. Fikry (*1931*) also indicated that natural crossing was a rather fixed 4 percent. Sappenfield (*1963*) reported a range of 1.0 to 32.2 percent (average, 13.6 percent) natural crossing in

Missouri; Simpson (*1950*)[25], a range of 3.3 to 90 percent in his Cotton Belt survey; while Thomson (*1966*) reported 1 to 2 percent natural crossing in the Ord Valley of northwest Australia. He noted that there were no honey bees in the valley and that insecticides were applied weekly or more often, which, he stated, undoubtedly suppressed any wild bee activity.

Natural crossing, once considered a hazard to be avoided, now is being presented as a tool to be utilized in the development of superior varieties. Also, with the high degree of efficient transportation of apiaries by beekeepers from one area or crop to another, there is no longer assurance that a location will have the same pollinator population from year to year or even throughout the season. This alteration in pollinator population is further accentuated by applications of toxic pesticidess to crops, which may damage, destroy, or cause removal of the majority of the pollinators in a given area.

In the "natural pollination" studies made by cotton breeders, none have indicated the relative number of pollinators or visits responsible for the crossing.

MOTES IN COTTON AND THEIR SIGNIFICANCE

Cotton ovules that fail to develop into seeds with well-developed ginnable fibers are termed "motes." The motes in a cotton crop represent a loss in yield. If 15 to 20 percent or more of the ovules fail to produce seeds with ginnable fibers, the potential yield is lowered just that much (Pearson *1949a*). Some structures at the base of certain locks of cotton have the appearance of motes, but they are not derived from ovules. They are termed "false motes." The failure to recognize them as false motes can contribute to an error in estimating the potential seeds that fail to mature (Pearson *1949b*). Rea (*1928*) reported 6.5 percent motes at the apex of the locks of 'Anton' (upland) cotton and 25.3 at the base, with 11.1 and 38.5 percent, respectively, in 'Bolton' cv. He concluded that this difference might be due to incomplete fertilization. Afzal and Trought (*1934*) also concluded that mote formation may be due to defective pollination.

Rea (*1929*) found that the higher the percentage of motes, the smaller the boll and the lower the yield of cotton. Hughes (*1968*) studied motes in 'Bar 14/25', and concluded that most of the motes occurred near the base of the lock in ovary positions 1 and 2. Porter (*1936*) stated, "To the extent that motes represent unfertilized ovules, it is natural that fewer motes would be found near the apex of the lock, as the ovules near the top of the ovary are favored in fertilization, being reached first by the pollen tubes. If the quantity of pollen deposited on the stigmas is scanty, or much of it defective, there would be a correspondingly small chance of the lower ovules being fertilized." Pearson (*1949a*) also noted that the number of motes increased with the number of ovules, again an indication of inadequate pollination.

Not only does inadequate pollination contribute to reduced yield through failure of ovules to develop, but mote formation could result in another type of loss. It is easily demonstrated that when a ripe lock of cotton is pulled from the burr, the lock is most likely to break at the location of a mote, and when two motes are adjacent to each other, a break is almost certain. If such a break should occur in the mechanical harvesting of cotton, the remaining portion of the lock would likely be missed by the machine and either lost or only salvaged later at reduced quality during complete destruction of the burr.

The preponderance of bolls with motes in commercial fields indicates the loss of yield being experienced. If the plant "makes up" for motes by setting more bolls, harvest is delayed. The quality of late-developing lint is likely to be inferior to earlier lint.

SHEDDING

The cotton plant frequently sheds half or more of its fruit. Some of this shedding occurs in the bud stage, but the peak occurs about 5 or 6 days after flowering, then tapers off toward the full-grown boll stage. Many factors contribute to shedding, including humidity, temperature, soil-water conditions, genetic factors, diseases, insects, mechanical injury, and inadequate pollination (Beckett and Hubbard *1932*, Brown *1938*, Eaton and Ergle *1953*, and Lloyd *1920*). Rainfall during the day the flower is open can damage the pollen and cause shedding although the amount of shedding from this factor is minor. Kearney (*1923*) doubted that deficient pollination and fertilization were the primary reasons for boll-shedding in Pima cotton at Sacaton, Ariz. However, Kaziev (*1964*) showed that bee pollination caused a decrease in the shedding of five common cultivars of upland cotton. McGregor et al. (*1955*) also reported reduced shedding of 'Pima S-1' cotton visited by bees as compared to plants caged to exclude bees. Occasionally, during periods of extremely hot weather, the cotton flower will fail to produce or dehisce viable pollen. When this occurs, the flower sheds unless pollen is brought to it from another flower by insects.

Many factors, therefore, contribute to shedding by cotton, one of which is inadequate pollination.

NEED FOR POLLEN TRANSFER WITHIN OR BETWEEN PLANTS

When the cotton pollen grains contact the stigma, they germinate tubes that grow down the "conducting tissue" in the center of the style (Arutiunova *1940*). When a tube reaches the ovary, the sperm enters and fertilizes an ovule. About 50 ovules must be fertilized if a full complement of seeds is produced; therefore, at least 50 viable pollen grains must contact the stigma. The stigma is normally receptive to the pollen by the time the flower opens or before (Loden et al. *1950*), but receptivity drops sharply after about noon (Janki et al. *1968*). Because of this limited timespan, most hand pollination in cotton breeding work is made during the forenoon.

The majority of the flowers on a cotton plant are largely self-fertile and, to varying degrees, self-pollinating (Ewing *1918*, Kearney and Harrison *1932*). The method, time, and type of pollination of the stigma

[25] SIMPSON, D. M. MEMO TO: COOPERATORS IN NATURAL CROSSING TESTS (RESULTS OF 1949 TESTS). Tenn. Agr. Expt. Sta. and U.S. Cotton Field Sta., Knoxville, 3 pp. 1950. [Mimeographed.]

influence the degree of self-pollination. Flowers that receive pollen on the whole surface of the stigma yield more seeds per boll than those pollinated at the base of the stigma (Kearney *1926*). The base of the stigma affords less favorable condition for pollen germination or growth than the apex (Iyengar *1938*, Kearney *1923*). Pollen from anthers on the lower part of the staminal column is best (Trushkin *1956*). Repeated applications of pollen to the stigma, such as repeated bee visits, are also helpful (Finkner *1954*). Therefore, for best pollination of the stigma, repeated applications with an abundance of pollen from the basal anthers on the tip of the stigma insures the highest percentage of fruit set and maximum cotton production.

The pollen-laden anthers that touch the stigma, resulting in self-fertilization, usually contact only the base of the stigma. When this occurs, self-pollination is assured, but maximum fertilization within the ovary of that boll is not usually accomplished. Arutiunova and Gubanov (*1950*) indicated that "pollen seems to stimulate pollen" so that increased amounts of it on the stigma increased the percentage of germinating pollen tubes, further insuring ovule fertilization.

Rose and Hughes (*1955*) increased yield of 'Bar 7/8.2' by 11 percent over naturally pollinated flowers by brush pollination of stigmas. The increase resulted from more bolls set. Kohel (*1968*) also obtained more seeds per lock and per boll from unbagged open flowers, or hand-pollinated open flowers than from bagged or emasculated flowers. Guseinov and Muktarov (*1963*) showed that cross-pollination within the variety resulted in increased production.

Some pollens are too weak to compete with self-pollen. For example, when McGregor et al. (*1955*) grew equal numbers of 'A-44' and 'Red Acala' plants in cages with honey bees, only 2.31 percent of the offspring of 'A-44' were hybrids, whereas 44.0 percent of the 'Red Acala' offspring were hybrids.

As the pollen tube grows down the style, its nucleus moves a few microns ahead of the sperm (Jensen and Fisher *1968*). The sperm and contents are discharged into the germ sac of the ovule in 16 to 32 hours (Gore *1932*, Kearney *1923*, Saakyan *1962*). Surplus pollen tubes that penetrate the ovary are eventually assimilated without damage (Linskens *1964*), so there is no damage from surplus pollen on the stigma.

According to Arutiunova (*1940*), the pollen tube begins to form more quickly if the pollen grain is from a genetically different cultivar. For example, tubes in cross-pollinated flowers were visible within 5 to 10 minutes after the pollen was placed on the stigma, but tubes from self pollen did not appear until after 60 to 150 minutes. Also, tubes from pollen placed on the tip of the stigma grew faster than those from pollen placed on the base of the stigma.

Arutiunova (*1940*) also studied the effect of the number of pollen grains and the kinds of intravarietal pollen on pollen tube growth in both upland and *G. barbadense* cottons and reported that in the *G. barbadense* cottons twice as many tubes reach the ovary with cross-fertilization as with selfed flowers. Except for one cultivar, pollen of upland cottons grew better on its own stigma than on others. In many of the selfed flowers, no pollen tubes developed, but in crossed flowers this failure was rare.

This means that more self pollen must be deposited on the stigma than mixed or cross pollen. The sooner the tube reaches the ovary and fertilizes an ovule, the less the likelihood that the fruit will shed. Arutiunova and Gubanov (*1950*) also concluded that an increased number of pollen grains on the stigma increased the percentage of germinating grains and tube development. Arutiunova and Kanas (*1955*) concluded that cross-pollination within the cultivar insures the best seed development. In other words, a well cross-fertilized stigma tip is most likely to result in the best fertilization of the ovules in the ovary.

There seems to be constant warfare within the plant between setting and shedding of fruit. Anything that can be done to influence the battle in favor of fruit setting tends to increase production. The earliest possible thorough application of pollen on the tip of the stigma to insure speediest arrival of the tubes in abundance within the ovary would insure maximum set.

BENEFITS DERIVED FROM INSECT POLLINATION OF COTTON

The benefits derived by cotton from insect pollination have been cited by numerous workers, largely in Russia, where much attention has been given to this subject, but also in Egypt, India, and the United States. Meade (*1918*) was the first to call attention to the fact that cotton at San Antonio, Tex., should benefit from insect pollination. He applied supplementary pollen by hand to open flowers that may or may not have been visited by pollinating insects and increased the set of 'Durango' cotton flowers by 10.96 percent and 'Acala' flowers by 5.31 percent. His results convinced him that pollination of cotton by honey bees should increase production.

Kearney (*1921*) was stimulated by Meade's work to compare naturally pollinated Pima flowers with flowers that received supplementary pollination by hand. At Sacaton, Ariz., where the cotton was relatively isolated and insect pollinators were prevalent, he obtained no significant increase in set of flowers or seed produced. However, at Phoenix, in a large cotton-growing area, he obtained only 1,157 seeds per 100 naturally pollinated flowers, but 1,526 seeds per 100 flowers that received supplementary pollination. As a result, he, too, recommended the keeping of bees in cotton fields for their pollination service. Later, Kearney (*1923*) concluded that Pima cotton production in the Salt River Valley of Arizona could be substantially increased (about 32 percent) if honey bees were kept around the cotton fields.

The rather comprehensive and convincing research by Shishikin (*1946*, *1952*) apparently awakened his countrymen to the value of bees to cotton. His work was followed by that of numerous workers but especially certain leaders in this work: Kaziev (*1955*, *1956a*, *b*, *1958*, *1959a*, *b*, *1960*, *1961a*, *b*, *1963*, *1964*, *1967*), Kuliev (*1958*), Minkov (*1953a*, *b*), Radoev (*1963*, *1965*), Radoev and Bozhinov (*1961*), Skrebtsov (*1964*), and Trushkin (*1956*, *1960a*, *b*).

In Peru, Mercado Mesa (*1956*) concluded that insect

pollination was of no value to 'Tanguis' cotton (*G. barbadense*). In a more thorough test Dulanto Bartra (*1958*) showed that 51.7 percent of the flowers shed if they were not visited by the bee *Melitoma euglossoides* Lepeletier and Serville compared to only 32.2 percent of flowers visited by this bee.

Shishikin (*1946*) was the first to use the term "saturation pollination"—the uniform distribution of colonies of honey bees among cotton fields. He showed that saturation pollination, at the rate of one-half colony per acre, increased production of cotton 19.5 percent more than areas dependent upon only local pollinators. The increase over cotton grown in cages, excluding all insects, was 43 percent. In his more complete report, Shishikin (*1952*) stated that 4,130 to 5,000 colonies were used, at the rate of one colony per hectare, and distributed in groups 1 km apart. The tests dealt with "the old variety, '114', and the new variety '1298'." During the tests, the natural crossing caused by the honey bees varied from 26 to 43 percent. He concluded that the wild pollinators were "far from being able to assure cross-pollination of cotton plants."

In a sense, Babadzhanov (*1953*) duplicated the test by Kearney (*1923*) and obtained a similar benefit from supplemental pollination. He reported that it increased the boll set of cultivar '108–F' by 30 percent, the raw cotton per boll by 5 to 10 percent, the seed germination from 93 percent in selfed seed to 98 percent in cross-pollinated seed, and decreased the motes by 12.5 percent. Ter-Avanesyan (*1952*) showed that crossing within the cultivar varied with the cultivar tested: 8.4 percent in 'Sreder', 14.4 in '8582', and 22 percent in '915'.

These tests were supported in theory by Miravalle (*1964*), who compared the effects of bulked pollen from several plants with pollen from one flower of the same selection. He found that 76 percent of the bolls set, with 34.47 viable seeds per boll, when the flowers were pollinated with bulked pollen, but only 70 percent set, with only 27.07 seeds per boll, when the flowers were pollinated with pollen from one flower of the same plant.

McGregor et al. (*1955*) studied the effect of bee pollination upon upland and Pima cotton in cages, some of which contained a colony of honey bees (figs. 92, 93). In their test, 'Pima S-1' produced 24.5 percent more cotton in cages with bees than in cages without bees. This increase was caused by the set of more bolls, with more seeds per boll. The presence of bees did not

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FIGURE 92.—Pollination studies involving honey bees on caged cotton plants.

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FIGURE 93.—Author taking data for pollination studies on tagged Pima cotton flowers.

increase total production of upland 'A-33' or 'A-44', but the crop set earlier. In an area with a short season, this effect would doubtless be reflected in a greater total yield. Also, the cotton was handpicked, with extreme care taken to collect every seed. If machine harvesting had been used, doubtless more cotton would have been collected where there were fewest motes—in the bee cages. The lock usually breaks if motes are prevalent, and the remaining lint remains unharvested in the base of the burr.

In this test and others, McGregor and Todd (*1955, 1956*) noted that a decided difference developed before the end of day in the appearance of the petals of the upland cotton flowers visited by bees as compared to those not visited. By midafternoon, the visited ones began to change color and wilt, and the petals formed a tight cylindrical roll; whereas, in those flowers not visited by bees, the petals stayed white and open until sunset then became limp and adhered to each other like pieces of wet paper (fig. 94).

Mahadevan and Chandy (*1959*), using cultivars 'M.U.I.' and 'M.C.U.2' in India, obtained 23 to 34 percent and 40 to 53 percent, respectively, more cotton in open plots than in plots caged to exclude bees. They did not have plots caged with pollinating insects. This leaves unexplained the possible effect of the caging on the plant. Sidhu and Singh (*1962*), also in India, compared production in cages with *Apis indica [cerana]* and *A. florea* and in cages without pollinators and obtained an increase of 17.45 to 18.98 percent in favor of the pollinating insects. The increase was attributed to more and larger bolls.

In the United Arab Republic, Wafa and Ibrahim (*1960*) also obtained 22.4 percent more 'Ashmouni' cotton with honey bee pollination.

Skrebtsov (*1964*) obtained 33 percent increase in raw cotton by cross-pollination within the variety with honey bees, and showed that the bees improved hybrid vigor.

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FIGURE 94.—Effect of insect pollination on cotton flowers. Photograph taken 4:30 p.m. of the day these 2 flowers opened. Flower on left was in a bee cage. Its petals had changed from cream to pink and tightened into a tubular shape. Flower on right was in a no-bee cage. Its petals remained cream-colored and flared until sunset.

Radoev and Bozhinov (*1961*) obtained 10.6 to 24.4 percent greater yield from flowers freely visited by bees than from flowers tied to exclude insects during flowering. There were 0.5 more seeds per boll, fewer motes, and better seed germination. Radoev (*1963*) stated that freely pollinated plants set 11.04 percent more cotton than isolated plants, with more sound seed and better germination. Radoev (*1965*) concluded that the honey bee is the most important insect in Russia in the pollination of cotton, even though only 18 percent of the floral visits contribute to pollination.

Minkov (*1953b*) studied the effect of pollination on Russian cultivars '611–b' and '108–F', which were visited primarily by wild bees. He found that exclusion of pollinators increased the number of motes.

These tests indicate that the value of insect pollination is not limited to any particular area, species, or cultivar.

The material in the reports by the various authors previously mentioned as well as numerous others, leaves little doubt that cotton is benefited by bees in terms of greater lint and seed production, earliness of harvest, fewer motes, better lint, better germination, and improved qualities in the offspring.

Trushkin (*1960a*) concluded that the use of bees on cotton must be considered not only possible but expedient. Trushkin (*1960b*) stated, "The time has come to fully exploit [utilize] honey bees for purposes of obtaining high cotton yields and improving seed quality . . . ."

HYBRID VIGOR IN COTTON

The accentuated effect of cross-fertilization is referred to as heterosis or hybrid vigor. It can result from interspecific (between species), intraspecific (within species), or intervarietal crossing. The possible utilization of hybrid vigor in cotton has been of considerable interest to cotton breeders since Mell (*1894*) showed that some cotton hybrids exceeded their parents in certain characteristics. Although Kottur (*1928*) concluded that selfing of *G. herbaceum* plants for 12 generations had no injurious effect, and Harland (*1943*) proposed the breeding of a cotton immune from natural crossing, Brown (*1942*) and O'Kelly (*1942*) independently concluded that inbreeding of upland cotton reduced production and caused fewer flowers and smaller bolls. Simpson and Duncan (*1953*) also showed that cultivars selfed for 10 years produced 15 percent less cotton than the original plants. As a result, breeders now generally agree that too much inbreeding is detrimental. Instead, they strive for or desire some degree of outcrossing but, so far, have not been able to control it. The subject of hybrid vigor in cotton was thoroughly reviewed by Loden and Richmond (*1951*).

Hybrid vigor in cotton has been observed in interspecific crosses as well as in crosses between varieties within the species. Fryxell et al. (*1958*), Hutchinson et al. (*1938*), Marani (*1967*), Stroman (*1961*), and Ware (*1931*) in particular showed that crosses between *G. barbadense* and *G. hirsutum* were much more productive than either parent. Because of the differences in the characteristics of the lint of the two species, it frequently has objectionable qualities in the hybrid. This problem is less likely to arise in intraspecific hybrids where considerable hybrid vigor has also been shown.

Kime and Tilley (*1947*) made numerous crosses of commercial cultivars of upland cotton and showed an increase in production of the F_1 ranging from 7 to 20 percent. They doubted that hand cross-pollination to produce the hybrid seed was practical but considered production feasible in areas where "a high percentage of crossing normally occurs." Kohel and Richmond (*1969*) showed that significant heterosis could be obtained in areas of high natural crossing. Patel and Patel (*1952*) indicated that in India hand-pollination might be practical. Thakar and Sheth (*1955*) proposed that the government subsidize hybrid cotton seed production. Simpson (*1948*) obtained increases in yield from crosses of upland cultivars ranging from 5.7 to 44.2 percent. He, like Meade (*1918*) and Kearney (*1923*), also recommended that honey bee colonies be placed around the fields, knowing that hybrid seed could only be produced in quantity with pollinating insects (natural crossing) (Simpson *1954b*).

Hybrid vigor has been shown within upland cotton by numerous workers (Barnes and Staten *1961*, Christidis *1955*, Galal et al. *1966*, Hawkins et al. *1962*, Lee et al. *1967*, and Turner *1953a*, *b*).

Miller and Lee (*1964*) reported larger bolls with higher lint yields. Muramoto (*1958*) showed increases in yield, lint percentage, lint index, and seeds per boll. Ter-Avanesyan and Lalaev (*1954*) reported yield increase, bolls ripening 5 to 6 days earlier, and some resistance to *Verticillium* wilt. Trushkin and Truskina (*1964*) also reported that supplementary pollination by bees increased resistance to wilt, fungal root rot, and *Xanthomonas malvacearum*. Kaziev (*1961b*) reported earlier germination of hybrid seed and wilt resistance.

Wanjura et al. (*1969*) showed the importance of early emergence of the seed to plant survival and yield. For plants emerging on the fifth, eight, and 12th days, the survival was 87, 70, and 30 percent, and the relative yield of the plants was 100, 46, and 29 percent respectively.

The value of the hybrids is not in the mere mixing of

plant types in the field, such as might occur in certain breeding programs without insect pollination. Richmond and Lewis (*1951*) showed that from the standpoint of yield nothing was gained by growing a mixture of seed types in a pure stand although such a mixture, they indicated, might supply a mixture of fibers not obtainable from a lone commercial cultivar.

A method tried by Peebles (*1956*) consisted of planting alternate rows of 'Pima 32' and 'Pima S-1' and the use of saturation pollination by honey bees. He showed the economic feasibility of this method, but it was not accepted by the industry. An attempt was made by a commercial company (DeKalb Agricultural Association, Inc. *1961*) to produce hybrid cotton, but their supply of pollinating insects was apparently inadequate. Instead of attempting to increase the local supply, they concluded that hybrid cotton seed must be produced "in marginal cotton growing areas where bee activity is great." Turner (*1959*) proposed the planting of appropriate male-sterile and normal-functioning flower seed mixtures, then reaping the benefit of the hybrid vigor caused by thorough cross-pollination between the plants by a high population of honey bees.

One method frequently proposed (Christidis and Harrison *1955*) for utilizing hybrid vigor involved male-sterile plants. Allison and Fisher (*1964*), Fisher (*1961*), Justus and Leinweber (*1960*), Justus et al. (*1963*), Meyer and Meyer (*1965*), Turner (*1948*), and Weaver and Ashley (*1971*) have reported the presence of male sterility in cotton. At one time, the creation of male-sterile plants with a chemical "gametocide" (Sodium 2, 3-dichloroisobutyrate) looked promising (Eaton *1957*, McGregor *1958*, Meyer et al. *1958*, and Rohm and Haas *1958*); however, subsequent testing failed to establish its reliability. It also created some female sterility; therefore, its use was discontinued.

Stith proposed (*1970*) the use of cytoplasmic male-sterile stocks and restorer genes in cotton cross-pollinated by bees. Kohel and Richmond (*1962*) showed that bees should function satisfactorily in the production of cotton on male-sterile plants. Meyer (*1969*), commenting on the progress made with cytoplasmic male sterility, stated that the basic plant work has been done, but the bee breeders and their bees still have a lot of work to do. She concluded that the most critical problem in the production of hybrid cotton appeared to be in finding some way to get the male-sterile flowers pollinated.

Hybrid vigor in cotton offers possibilities for increasing cotton production to a new plateau, if insects can be used as the cross-pollinators. Tests mentioned herein show this is possible. The problem is to find the proper cotton combiners and the best utilization of pollinating insects.

Pollinators

There is agreement that cotton is not wind pollinated (Balls *1915*), that all pollen transport outside of the flower requires an active vector, and that "bees" are the best pollinators of cotton. Tsyganov (*1953*) stated that "bees on the cotton flower are not guests but thoroughly adapted symbionts because they feed and rear their young on the products gathered from the flowers."

The bees most frequently mentioned are the bumble bees (*Bombus* spp.), honey bees (*Apis dorsata*, *A. florea*, *A. indica [cerana]*, and, most frequently, *A. mellifera*), and the solitary groundnesting *Melissodes* spp. Other hymenoptera sometimes mentioned include *Anthophora* spp., *Elis thoracica* Lepeletier, *Halictus* spp., *Megachile* spp., *Melitoma euglossoides* Lepeletier and Serville, and *Nomia* spp. Numerous species from several other orders of insects sometimes find their way into cotton flowers, but as Simpson and Duncan (*1956*) stated, pollen distribution is essentially a "put and take" procedure, and unless the insect consistently visits large numbers of cotton flowers it is relatively ineffective as a pollinator.

In the United States, the bumble bee, honey bee, and *Melissodes* bees are considered most important as pollinators of cotton (Allard *1910*, *1911a*, *b*, Butler et al. *1960*, Kearney *1923*, McGregor *1959*, McMillian *1959*, Stephens and Finkner *1953*, Theis *1953*). In Russia, the honey bee is undisputedly considered the most important. In India, *Apis* spp., *Elis thoracica*, and *Anthophora* spp. have been mentioned (Sidhu and Singh *1961*, Khan and Afzal *1950*). In Egypt, the honey bee is most commonly seen (Wafa and Ibrahim *1957*, *1959*).

BUMBLE BEES

Brown (*1927*) stated: "Large lubberly bumble bees that get pollen all over their bodies and rub against the stigma of every flower they meet are doubtless the best." With this there is no disagreement. Many of the cotton researchers concerned about insect visitation to cotton flowers in the Cotton Belt east of the Brazos River consider the bumble bee most important (Allard *1910*, *1911a*, Loden and Richmond *1951*, Stephens and Finkner *1953*, Theis *1953*).

The visits to the plant by bumble bees are predominantly within the flower. Because of its size, the bumble bee can scarcely enter the flower without depositing pollen on the stigma and picking up more from the anthers. Because the nest is provisioned with both nectar and pollen, the bumble bee makes numerous collecting trips to the flowers. Also, bumble bees are colonial and under favorable conditions the population within the nest may increase so that numerous individuals from one nest will be foraging simultaneously in a field.

In isolated cotton test plots in North Carolina, it is not unusual to find a bumble bee on every plant and at times in every flower. Under such conditions, their effectiveness as pollinators could not be surpassed. Incidentally, Dulanto Bartra (*1958*) reported up to three or four *Melitoma euglossoides* in a single flower near the nesting sites, but they were very scarce farther away. By contrast, in the western half of the Cotton Belt, an entire day might be spent in a large cottonfield without seeing a bumble bee. Here, they are of no importance whatever as pollinators of cotton.

Bumble bees are colonial only through the active season. The nest is abandoned in the fall, the males die, and the females go into hibernation. Each female that survives hibernation establishes a new nest in the spring. Nests are only established if suitable nesting sites can be found. The colony in the nest then faces numerous hazards throughout the season, such as lack of a

continuous source of fresh nectar and pollen, diseases, pests, pesticides, and other environmental factors or agricultural practices. For these reasons, bumble bees are not always present in adequate numbers when desired, and their numbers cannot be increased as desired. The culture of bumble bees for the pollination of cotton holds little promise.

MELISSODES BEES

The *Melissodes* bee frequently constructs its nest in the soil in the cottonfield. It visits cotton flowers as a preferred host plant and rarely if ever visits extrafloral nectaries. It provisions each cell of its nest with a ⅕-inch pellet of pollen and nectar. The female spends the night in her subterranean nest. She rapidly visits blossom after blossom of either upland or Pima cotton and will cross over from the one to the other on a single trip. Under natural conditions, a single bee may make as many as 200 floral visits in a day (Butler et al. *1960*).

Melissodes bees are quite seasonal, therefore, they may be plentiful during one part of the flowering season but rare later in the same season. They are adversely affected by pesticides applied during the daytime, but the females may escape damage from nighttime applications. Little is known about the adverse effects on them of insecticides, soil cultivation, irrigation, or crop rotation. No way is known to increase these bees when desired.

HONEY BEES

In contrast to bumble bees and *Melissodes* bees, honey bees show a preference for the extra-floral nectaries of cotton and often seem reluctant to enter the cotton flower. When a honey bee enters a cotton flower, it may emerge coated with pollen, then alight on a leaf, and comb much of the pollen off without attempting to pack it in the pollen baskets on the hind legs. However, all of this pollen is not removed, and a familiar sight, where bees are working cotton, is their incoming at the hive entrance coated with cotton pollen. Radoev (*1965*), in Russia, stated: "The honey bee is the most important insect in the pollination of cotton." As shown in other places herein, its value in the United States would appear to be in proportion to its use and concentration on the cotton.

At times, honey bees collect small amounts of cotton pollen and transport it to the hive (fig. 95). This usually occurs only when no other pollen is available for the bees. Minkov (*1956*) concluded that honey bees can collect cotton pollen but seldom do so. On the other hand, Kaziev (*1956a, 1964*) stated that 15 to 25 percent of the bees were collecting pollen when the average colony was storing 2 to 5 pounds of honey per day. The bees were collecting the pollen from 8 a.m. to 4 p.m. Whether he referred to their actually collecting the pollen in their pollen baskets or whether they were merely entering the hive with pollen on their bodies, indicating that they had been inside the cotton flowers, is not clear.

Pollen collection is not always dictated by supply and demand. Honey bee colonies have been observed in Arizona by the author (unpublished data) and Grout (*1955*) showing every evidence of pollen deficiency,

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FIGURE 95.— Honey bee collecting cotton pollen.

although these colonies were surrounded by hundreds of acres of both species of cotton in flower. Later in the season, the bees in the same location collected cotton pollen freely. No reason could be determined for this strange behavior. At all times, the honey bees which were concentrated at the rate of one colony for each acre of cotton, were collecting both floral and extra-floral nectar.

In 1957 (unpublished data), I counted the honey bees in cotton flowers on each of five farms at Shafter, Calif., and four farms near Mettler Station, about 50 miles to the south. In both areas, the only cotton grown was 'Acala 4-42', and in both areas cultivation was large scale and dependent on irrigation water. Near Shafter, water was plentiful, and much of the land was devoted to cotton and alfalfa hay production. There were few apiaries near Shafter. Near Mettler Station, the water supply was acute; therefore, the growers devoted some of their land to alfalfa seed production, which required less water than cotton. The alfalfa seed fields and cotton fields were interspersed. About 50,000 colonies of honey bees had been transported into the Mettler area to pollinate about 20,000 acres of alfalfa seed. In the Shafter cotton fields, only 13 honey bees were observed in 1,000 cotton flowers (1.3 bees per 100 flowers), but at Mettler Station 158 were counted (15.8 bees per 100 flowers). One unidentified wild bee was seen.

All cotton fields within one-quarter mile of the alfalfa fields had 20 or more honey bees per 100 flowers. This proved that honey bee populations can be built up to provide "saturation pollination" or the "10 bees per 100 flowers" shown by McGregor (*1959*) to be sufficient to provide thorough coverage of the stigma with pollen.

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In an 80-acre 'Pima S-1' cottonfield at midseason in Arizona, Johansson (*1959*) dusted fluorescent pigmented particles in a single, newly opened flower. The following day he recorded the percentage of day-old (closed) flowers showing the presence of such particles (brought the previous day) in relation to distance from the treated flower. There were 212 colonies of honey bees within or along the borders of this field (fig. 96), but few other pollinating insects were active where the test was conducted. His results were: 0 to 50 feet (40.5 percent), 50 to 100 feet (14.0 percent), 100 to 150 feet (3.5 percent), and 150 to 200 feet (1.6 percent). This showed that when honey bees are present in sufficient numbers, they can effectively distribute such particles (and pollen grains) from flower to flower.

Kohel and Richmond (*1962*) concluded that a single insect visit to a cotton flower is not enough for complete pollination. Ter Avanesyan (1959) showed that 600 to 1,000 pollen grains on the stigma is the minimal "norm" quantity of pollen required. Shoemaker (*1911*) and Minkov (*1953b*) mentioned the commonly observed characteristic of the honey bee in alighting on the corolla rim, after which it crawls down the petal with its back to the anthers, rarely touching the stigma. However, when there is sufficient honey bee traffic into the cotton flower some of the individuals "get careless" and alight upon or crawl over the stigma, giving it a liberal coating of pollen in the process. The secret of successful pollination of cotton with honey bees seems to be in having sufficient visitation so that the bees are "forced" to visit the flowers, and considerable bee traffic into and out of the flower results.

Pollinating bees are an obstacle to most cotton breeders attempting to develop pure lines. Each cotton blossom from which the breeder desires seed must be enclosed or isolated in some way, otherwise the pollinating insect may dilute the line by bringing pollen to it from another type of cotton plant. This is particularly true if the breeder is using the *individual* plant selection method where he breeds offspring from a single plant. However, Brown (*1942*) and Simpson and Duncan (*1953*) have shown that continual inbreeding causes a decrease in productiveness not fully compensated by gains in other properties. As a result, Harland (*1949a*) proposed his mass pedigree selection system in which outcrossing within the mass is permitted, and Knight and Rose (*1954*) proposed a modification in which there is the initial selfing generation, then a selection of progeny rows, the seeds from which are bulked and grown in an isolated area with the highest pollinator population that can be obtained.

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FIGURE 96.— Honey bee colonies beside cotton field.

Thus, the pollinating insect changes from a "harmful" insect in the development of the plant selection to a "beneficial" insect in the later stages of the program, but there still remains within the minds of many cotton specialists an aura of animosity toward these insects. This has been coupled with the fact that bees are not "necessary" in the production of cotton. The evidence strongly indicates that for the best interest of the grower the pollinating insects should be protected and their presence encouraged in breeding and seed increase programs and in the production of bulk cotton.

Although the use of honey bees for systematic or saturation pollination of cottonfields is practiced to a considerable extent in Russia, resulting in increased and/or improved productivity, the American grower has tended to strive for his increased production through the use of pesticides and other agronomic practices and has given little heed to the beneficial insects. Some growers, after observing that areas near apiaries are frequently more productive, feel that bees are of some value. Others, fearing that their pesticide program might damage the bees and result in legal action by the beekeeper, discourage the keeping of bees near their cottonfields. The request for or the rental of bees to pollinate cotton in the United States is extremely rare.

The cotton plant may flower for 2 months or more; however, Buie (*1928*) showed that the majority of the flowers that set fruit appeared within 3 to 4 weeks. If the bees were concentrated on the cotton for this period with the use of harmful pesticides curtailed, the bees could perform their pollination service and escape pesticide damage.

Pollination Recommendations and Practices

Meade (*1918*), Kearney (*1923*), and Stephens and Finkner (*1953*) recommended the keeping of honey bees near cottonfields, but no ratio of bees per flower or colonies per area was indicated. Shishikin (*1952*), who studied the effect of bees on about 5,000 acres of cotton in Russia, recommended one colony per acre, with the colonies grouped about 0.6 mile apart. McGregor and Todd (*1955*) suggested one colony per acre. Avetisyan (*1965, ch. 5, pp. 209–248*) suggested 0.5 to 1.0 colony per hectare (one colony per 2.5 to 5.0 acres). Glushkov and Skrebtsov (*1960*) stated that with 4.9 and 6.6 colonies per hectare (2.0 to 2.5 colonies per acre) the cotton production was increased 20.9 and 45.5 percent, respectively, over the control areas.

The colonies-per-acre ratio (from one-fifth of a colony to five colonies per acre have been suggested) is doubtless influenced by the acreage involved, competing crops, and colony strength. The ratio of 10 bees per 100 flowers suggested by McGregor (*1959*) is a more realistic ratio than colonies per acre. Quite probably, a low population of honey bees contributes little or nothing to pollination. A method of maintaining a high population should be considered when honey bees are used. Although not an ideal pollinator of cotton, the honey bee is the only pollinator that can be manipulated on cotton.

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COWPEA

Vigna sinensis Savi (L.) ex Hassk., family Leguminosae

The cowpeas inculde the blackeyes, cream, crowders, purplehull, and some other less common types. They are grown primarily in the South and in California. Production of cowpeas decreased from 899,000 acres in 1954 to 93,000 acres in 1967 when the USDA ceased including the crop in the annual Agricultural Statistics report. The farm value also decreased from $8,600,000 in 1954 to $3,150,000 in 1967.

Plant

Cowpeas may be prostrate, erect, or climbing to about 3 feet. They are sensitive to cold and are killed by frost, but are tolerant to heat and drought conditions. The seeds are planted after all danger of frost is past. The plants flower in midsummer, and the seeds or forage are harvested before frost. The trifoliate leaves, 2 to 5 inches across, form a dense canopy that covers the ground. The seeds are in slender pods 8 to 10 inches long with eight to 20 seeds; vary in size (2 to 12 mm), shape (globular to kidney shaped), texture (smooth or wrinkled), and color (white, green, buff, red, brown, or black; and are variously speckled, mottled, blotched, or eyed). The type of cultivar grown depends upon whether it is to be used to produce forage, green pods, or the dry seeds as a pulse crop.

Inflorescence

The inflorescence consists of two to eight whitish, yellowish, or violet papilionaceous flowers in pairs crowded together on the tip of a slender peducle or stem, 1 inch to 6 inches long. The ¾- to 1-inch flower has a bent style, bearded on the inner curve immediately below the oblique stigma, and uniform anthers in two fused groups around the style (fig. 97).

The flower has a single ovary with eight to 20 ovules. Extrafloral nectaries are located at the base of the corolla. Whether floral nectar is secreted is not clear, but most likely it is.

The flower is attractive to bumble bees and various other insects that forage upon both the nectar and pollen.

Pollination Requirements

Purseglove (*1968**) stated that the flowers open early in the morning and close before noon of the same day. Warnock and Hagedorn (*1954*) stated that the stigma is receptive only one day at 68° to 72° F but slightly longer at 60°. Robbins (*1931*) stated that the cowpea is capable of self-fertilization, and this is probably the common occurrence, although the flowers are often visited by honey bees or bumble bees, attracted chiefly by the extrafloral nectar. However, Warnock and Hagedorn (*1954*), after detailed study of the stigma of the cowpea, learned that receptivity is limited to only the very tip of the stigma, which in appearance somewhat resembles the sensitive end of the trunk of the elephant. They also found that from 14 pollinations made in the greenhouse, 59 seeds set when pollen was placed on the end of the stigma but only seven set when pollen was

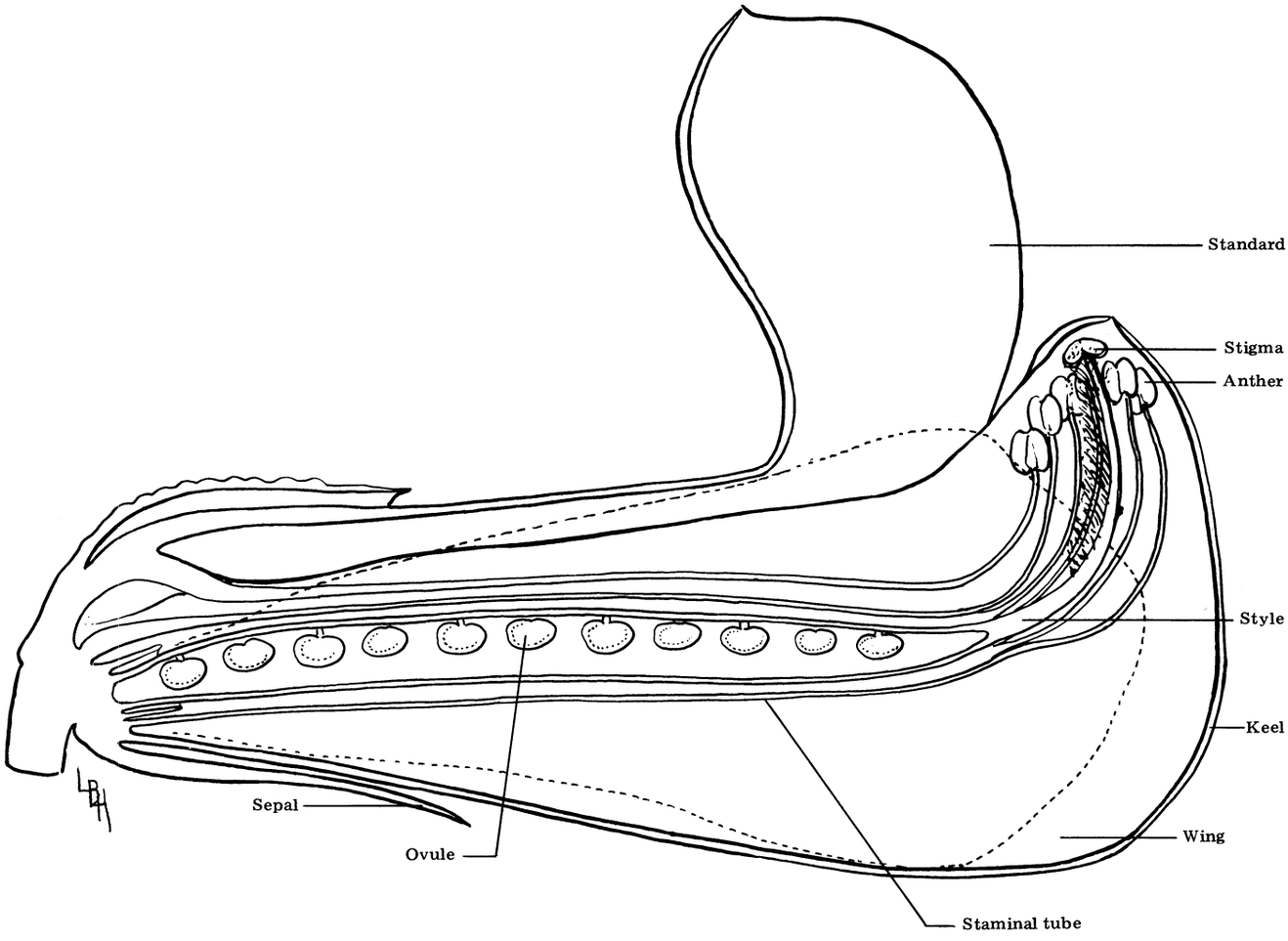

FIGURE 97.—Longitudinal section of blackeye cowpea flower, ×7.

rubbed on the style. It was interesting that they never got more than an average of 5.4 seeds per pollination when pods normally produce eight to 20 seeds, which would indicate that their method was not as efficient as the natural method.

Pollinators

Purseglove (*1968**) stated that a heavy insect is required to depress the wings of the flower and expose the stamens and stigma. The pollen is sticky and heavy, indicating that the plant is not wind-pollinated (Mackie *1946*). Cross-pollination seems to be associated with areas where bumble bees are numerous. Mackie and Smith (*1935*) stated that bumble bees are the primary pollinators.

The actual value of frequent visitation by pollinating insects to blossoms of cowpeas has not been determined; however, the study by Warnock and Hagedorn (*1954*) would indicate that such activity is beneficial in increasing the number of pod set, the number of seeds per pod, or both.

A male-sterile mutant cowpea has been reported (Sen and Bhowal *1962*). It has not been utilized in hybrid seed production, but if such a mutant were used, since cowpeas are not wind pollinated, insects large enough to operate the floral mechanism would be required to carry pollen from fertile to male-sterile plants.

Pollination Recommendations and Practices

There are no recommendations for the use of pollinating insects on cowpeas.

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CRABAPPLE

Malus spp., family Rosaceae

A crabapple is basically a small apple. Hedrick (*1938**) concluded that the most common crabapples are hybrids of the common apple and the Siberian crabapple (*Malus sylvestris* Mill. × *M. baccata* (L.) Borkh. He listed and described 23 cultivars, and Bailey (*1949**) listed eight species. Jefferson (*1966*) stated that there were more than 200 species and cultivars in the National Arboretum. Wyman (*1965*) stated that there were 250 cultivars in the Arnold Arboretum. The USDA (*1967*) listed 19 popular cultivars including six hybrids. Van Dersal (*1938*) listed 10 species of crabapples of value in erosion control and of value to wildlife.

The crabapple fruit is not an important crop. The plants are grown primarily as ornamentals, although a few growers produce the fruit commercially. The fruit is preserved or pickled or it is used in making jellies. No production data are available on the quantity of fruit that is used commercially.

Plant

Most crabapples are grown for their ornamental value, and cultivars are chosen because of their beautiful flowers, foliage, or fruit. The general appearance is similar to a small bearing apple tree. Culture is also similar to the culture of apple trees.

Inflorescence

The flower is similar to that of the apple. Nectar secretion and pollen production has not been studied in detail. Bees freely visit the flowers, for both nectar and pollen (fig. 98).

Pollination Requirements

Like the apple, the crabapple appears to require cross-pollination between cultivars by insects. Bradford and Bradford (*1949*) and Crandall (*1928*) concluded that all native crabapples are self-sterile. Pammell (*1920*) stated that self-pollination is impossible and that pollinating insects are absolutely needed. Cook (*1891*) covered 200 blossoms, which set no fruit, the same number not covered set three fruits. Jefferson (*1968*) discussed a new crabapple cultivar called "Fugi" whose anthers are generally sterile.

Pollinators

Little is known about which insect pollinators are of most value to crabapples. Pammel and King (*p. 239, 1930**) noted that the often cultivated Iowa wild crabapple was freely visited by honey bees. Considering that the only difference between the crabapple and the apple is fruit size, the deduction would appear reasonable that the most effective pollinator of apples, the honey bee, should be equally effective on the crabapple. Although the evidence is meager, it indicates that pollinating insects are essential for crabapple fruit production.

Pollination Recommendations and Practices

Individual or dooryard plantings usually are likely to receive ample insect pollination. If commercial fruit production is anticipated, and crabapple trees are grown along with other fruit trees in commercial orchards,

there is a likelihood that additional pollinating insects will be required. If the grower is providing bees for his other fruits, then he should provide enough for crabapples also.

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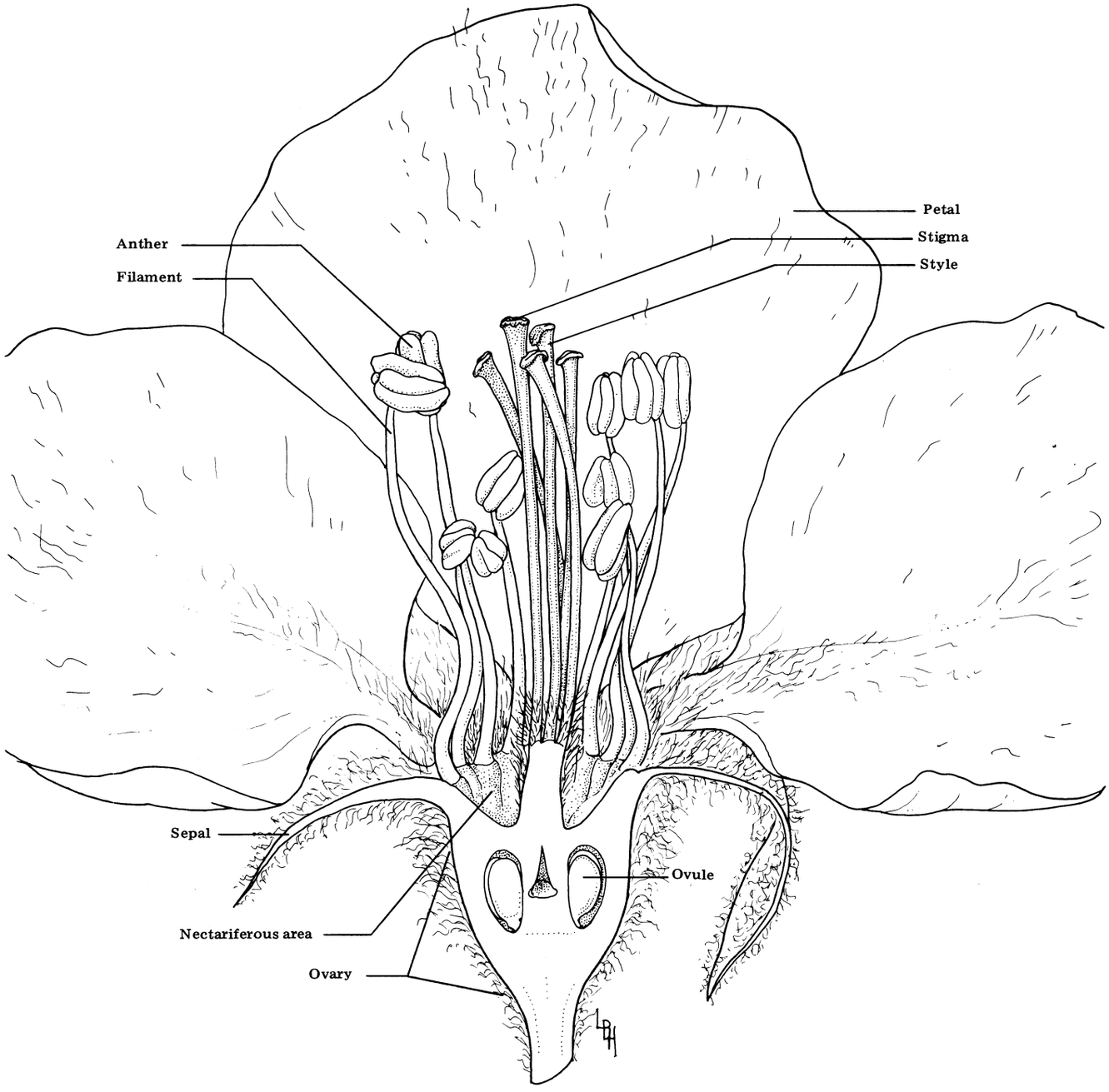

FIGURE 98.—Longitudinal section of 'Transcendent' crabapple flower, × 6.

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CRANBERRY

Vaccinium macrocarpon Ait., family Ericaceae

The large or commercial cranberry of the United States is grown only in Massachusetts, New Jersey, Oregon, Washington, and Wisconsin. Practically all cranberries are grown commercially, as compared to many fruits and vegetables that are also produced in dooryard plantings. In 1970, 21,445 acres produced 2,038,600 barrels of cranberries, for which the growers received $23.6 million. Massachusetts led with 10,900 acres. Other producing States were Wisconsin with 5,700 acres; New Jersey, 3,100 acres; Washington, 1,000 acres; and Oregon, 745 acres.

Plant

The cranberry plant is a low, creeping, semievergreen perennial that roots freely along the runners to form a mat. The runner sends up many slender, fruiting branches 6 to 18 inches high. Its leaves are oblong and ⅓ to ½ inch long. Flowers on the 1-year-old shoots (uprights or fruiting spurs) eventually produce a red globular fruit, a true berry, ¼ to ½ inch in size. There may be five or six blossoms per shoot, but one to three full-sized berries per shoot (fig. 99) may result in an excellent harvest (Sibert *1967*), depending upon the density of the uprights. The crop is confined to cool, moist, natural, or artificial bogs that can be flooded or drained as desired. A bog may remain productive for many successive years. Some bogs in New Jersey and on Cape Cod have been productive for more than 75 years (fig. 100).

Inflorescence

The cranberry flower in silhouette resembles the neck and head of a crane, hence the name "craneberry," which became contracted to "cranberry" (Marucci *1967a*). The tiny blossom, ¼ to ⅓ inch in size, begins to open in the morning and is fully open in 2 hours. As it expands in opening, the petals spring spart suddenly and visibly, and within a few minutes they curl back on themselves, leaving the sexual parts of the flower, the stamens and style, exposed. The petals of newly opened flowers are white or only slightly pink. If the flower is not pollinated, these petals may hang on the vine for 2 or 3 weeks, during which time they change to a rosy pink.

The five to eight individual brownish stamens fit so closely together they form a tube (Cross *1953*, Darrow et al. *1924*, and Franklin *1940*). As the anthers in the stamen mature, they release the dry pollen which falls out the tip of this tube. The pollen is relatively heavy and is not wind blown, nor is it likely to come in contact with its own stigma. The grain is a tetrad, or a four-part grain, apparently capable of germinating into four functional pollen tubes (Roberts and Struckmeyer *1942*). For this reason, not a lot of pollen is needed to fertilize the two to three dozen ovules in the four-carpel ovary.

PN-3807

FIGURE 99.— Cranberry plant with mature fruit.

PN-3808

FIGURE 100.— Harvesting cranberries from a large bog.

Marucci and Filmer (*1964*) and Marucci (*1966*) also found that flowers receiving pollen from other cultivars produced more berries per stem, and larger berries with more seed than selfed flowers. This indicated that mixed lines in the bog might be more productive than a single line. Where insect pollinators were excluded, Filmer et al. (*1958*) found that the berries that set had only 2.7 seeds, were small, and not uniform.

Just inside the base of the stamens is a ring of nectaries (fig. 101), surrounding the base of the style. At opening, the style is slightly shorter than the stamens. When the pollen is shed, the stigma is dry. The next day, the style lengthens so the stigma extends about 1/16 inch beyond the no-longer functioning stamens, and it becomes moist and sticky. It is not receptive to pollen until 24 to 36 hours after pollen shedding begins (Rigby and Dana, *1972*).

When the bee thrusts its head and proboscis or "tongue" into the staminal tube to reach the nectar, the pollen rains down upon the bee. Then when another more advanced flower with a receptive stigma is visited, the pollen is accidentally transferred, and fertilization is accomplished. As previously stated, if the flower is not fertilized, it may hang on for 2 or 3 weeks, and the petals will take on a rosy hue. A key to identification of inadequate pollination is the presence of this pinkish cast in the field. Prompt pollination causes the petals to shed and fruit development to proceed before this can occur. The fruit ripens in a couple of months.

The production of pollen and nectar of cranberries, vital in the pollination and fruit-set of the crop, seems to vary with conditions and location. Caswell (*1962*) stated that the blossom secreted little nectar, in some locations practically none, but produced generous quantities of pollen. This seems to be the general rule. Bergman (*1954*) found that cold injury further reduced or even stopped nectar secretion. Marucci (*1967a*) stated that cranberry blossoms are apparently poor producers of nectar and pollen, and honey bees do not eagerly work them. Stricker (*1953*) stated that bees work cranberries in New Jersey only for pollen. However, Gates (*1911*) reported that nectar from cranberries produces a superior grade of honey. Caswell (*1962*) and Oertel (*1967*) list cranberries as a nectar and pollen source. Beekeepers occasionally obtain a reddish honey they associate with bee activity on cranberries. There seems little doubt that the plant is more attractive to honey bees for its pollen than its nectar, but if bees visited it solely for its pollen, which is available before the stigma is receptive, little pollination would occur. Shimanuki et al. (*1967*) showed that some colonies consistently collect more pollen from cranberries than other seemingly similar colonies. This may lead to the development of specially selected bees for cranberry pollination.

Cranberry breeders might benefit the industry by selecting plant strains that produce more nectar or that have more attractive nectar for pollinating insects.

Pollination Requirements

Earlier publications (Eastwood *1866*) made no mention of pollination of cranberries. However, Gates (*1911*) recommended that growers keep bees for this purpose, and Franklin (*1911*) concluded that bees were beneficial and he recommended the placing of colonies of honey bees near cranberry bogs at blossoming time. Later, he (*1912*) reported that the area from which the bees were excluded bore at least a half crop of berries, this exclusion of bees had no effect on production from the plots the following year (*1914*). Darrow (*1924*) reported that many growers in Massachusetts kept apiaries, and even though Wisconsin growers did not consider bees essential they did consider them of value in hastening pollination which resulted in more even maturity. Roberts and Struckmeyer (*1942*) believed that pollination was affected by wind, but this has been discounted by the various tests, which showed that plants caged to exclude bees were unproductive (Filmer and Doehlert *1955*). Hutson (*1924*, *1925*, *1926*, *1927*) devoted considerable time to cranberry pollination studies and concluded that in most instances there were sufficient wild bees in New Jersey cranberry fields, but as insurance against those years when there were insufficient wild bees, the grower should rent colonies of honey bees.

Farrar and Bain (*1946*, *1947*) and Bain (*1946*) did the best work on cranberry pollination from the standpoint of showing the value of honey bees. They showed that one cage with bees produced berries at the rate of 171 barrels (bbl) per acre, whereas another cage in the same field without bees produced none. In another less productive field, the cage with bees produced 64 bbl/acre, whereas the beeless cage produced 3 bbl/acre. They recommended that the grower use one strong colony for each 2 acres of this crop.

Filmer (*1949*) studied the effect of four-tenths of a colony per acre on two bogs and learned that bee distribution was not uniform over the bogs. In bogs 400 feet wide, pollination decreased toward the center. He recommended that colonies be placed around, or on roadways in the middle of any bog 400 feet or more across. Later, Filmer and Doehlert (*1952*) showed that only 15 berries per square foot set where bees were excluded, but 90 to 152 berries set where bees were plentiful. Even at the then current rental price of $5 to $7 (with one colony per 5 acres recommended), the bees were quite profitable. One berry per square foot produces about 1 bbl/acre. Filmer and Doehlert (*1959*) recommended one colony for each 2 or 3 acres "if the population of wild pollinators is near normal." Filmer (*1953*) showed that increasing the number of colonies from one-half to one per acre increased cranberry production 12 to 34 bbl/acre.

Swenson (*1958*) concluded that "no bees" meant "no cranberries" and reported that by adding one colony per acre the yield was increased 50 percent, and when the population was doubled the yield increased another 60 percent.

Sibert (*1967*) stated that bog owners were renting about one colony per acre. Although the national average production is about 60 bbl/acre, he stated that a well-managed bog should produce 150 bbl/acre. When such high production occurred, he stated that the ground at harvest time is solid red with berries.

The data establish that bees are essential to cranberry

production; in most areas there are not enough bumble bees so honey bees at the rate of one colony per acre or more should be used to supplement the native bees. Pollination must be accomplished during a 3- to 4-week period, and rain, wind, or cold almost always interferes with insect activity during this period.

Pollinators

There is little doubt that bumble bees are excellent pollinators of cranberries; 3 per rod[2] are considered sufficient. Johansen and Hutt (*1963*) recommended the placement of bumble bee hives or other nesting domiciles around cranberry bogs, for the queens to occupy. They also recommended the planting of flowering plants nearby for bumble bees to forage on, protected from pesticides, as a means of increasing the bumble bee population. Unfortunately, bumble bee populations continue to decrease in most areas, but their activity can be supplemented with honey bees. Various other wild

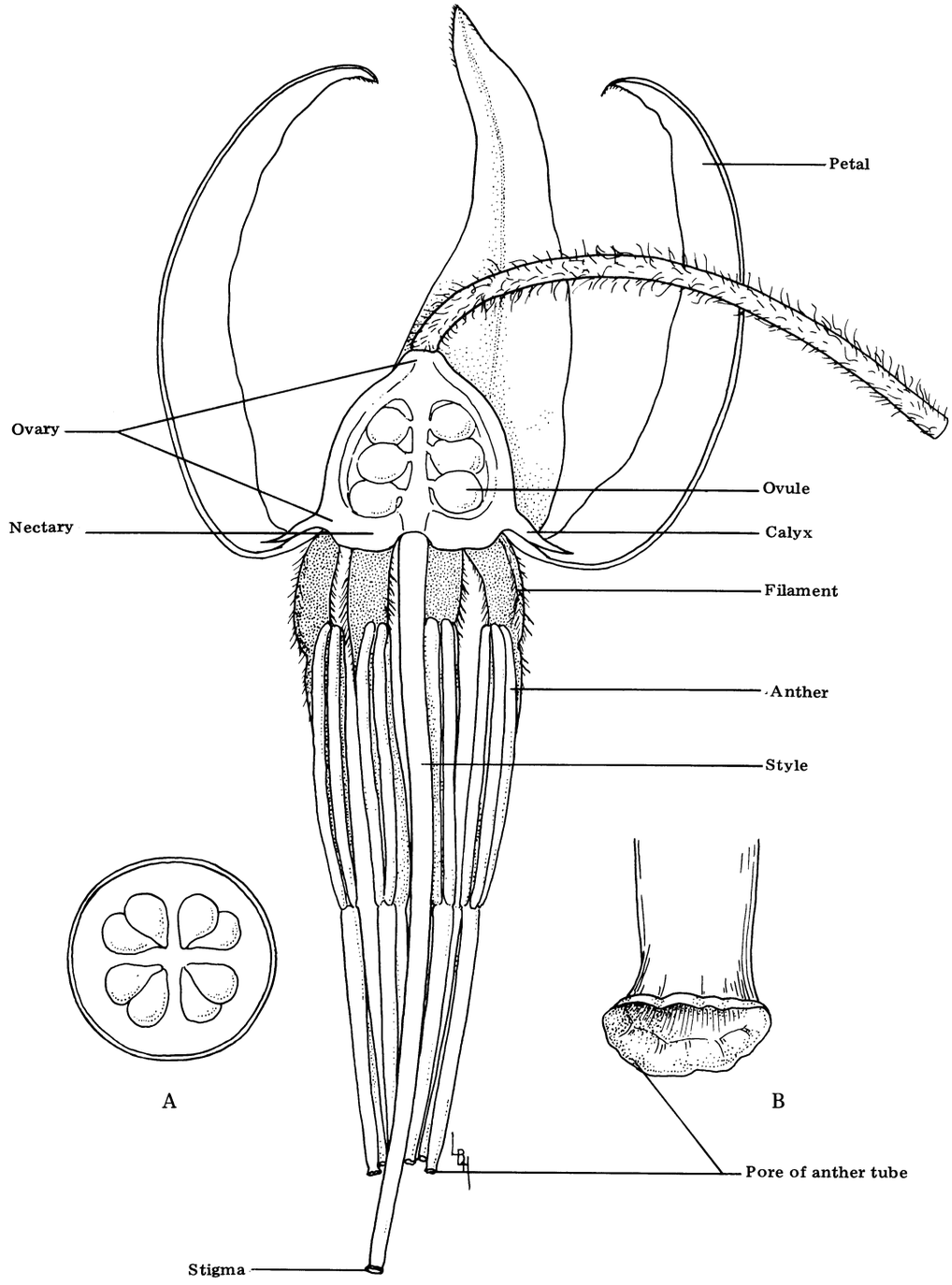

FIGURE 101.—Longitudinal section of a 'Searles' cranberry flower, ×16. *A*, Cross section of ovary, ×16; *B*, pore of anther tube, greatly magnified.

bees have been reported from time to time on cranberries in different locations, but none of them can be depended on as a stable source of pollinators. Because cranberries are not highly attractive to honey bees, the bee population should overflood or saturate the competing plants so the bees will visit the cranberry flowers.

Marucci (*1967b*) stated that flowers that do not set but remain on the plant are called "blasts," and he noted that high bee concentrations reduced the number of blasts present.

Pollination Recommendations and Practices

The pollination recommendations for cranberries lean constantly toward the use of more colonies of honey bees per acre. Earlier recommendations called for one colony per 5 acres (Doehlert *1940*), one colony per 2 to 3 acres (Filmer and Doehlert *1959*), one colony per 2 acres (Cross *1953*, *1966*), one colony per 1 or 2 acres (Filmer *1953*), and one colony per acre (Swenson *1958*). Farrar and Bain (*1946*) stated that one strong colony per 2 acres was satisfactory, if weather conditions are favorable, but under unfavorable conditions 5 to 10 colonies per acre might be needed. Stewart (*1970*) and Stewart and Marucci (*1970*) recommended one colony per acre. In general, one strong colony per acre is currently used. Usually, by the time cranberries bloom, the honey bee colonies have become populous so that strong colonies are common.

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CRIMSON CLOVER[26]

Trifolium incarnatum L., family Leguminosae

Crimson clover is an important and colorful winter annual legume in the South and is grown to some extent on the Pacific coast, where winters are mild. It is also grown in some Northern States as a summer annual. Alabama, Georgia, and Tennessee, in that order, were the leading producers of crimson clover seed, but most of it is now produced in Oregon. More than 2.5 million pounds were produced in 1970.

Compared to other clovers, crimson clover is a heavy producer of seed. Yields of 300 to 600 pounds per acre are common, and yields of 1,000 to 1,200 pounds have been obtained (Wheeler and Hill *1957**).

Plant

Crimson clover grows erect to about 2 feet tall, and is easily recognized by its crimson flowers that are about 2 inches long by 1 inch wide. It resembles red clover, but its leaves have a more rounded tip, and both the stems and leaves have more hair on them than does red clover. It is usually sown and develops a crown of growth in the fall. In the spring, fresh stems form, then terminate in the long, pointed flower head. Flowering in the South occurs in April. The seeds develop, then with the coming of summer weather, the plant dies.

The plant is widely used as forage, pasture, green manure, and an erosion control plant. It has the advantage of producing large quantities of seed that can be easily harvested and planted without the use of expensive equipment (Hollowell *1938*).

Inflorescence

The 65 to 125 crimson florets that make up the colorful crimson clover head are typically *Trifolium* and roughly ⅝ inch long by ⅛ inch wide. Weaver and Ford (*1953*) recorded 96 florets per flower head and estimated roughly 2 million flower heads per acre. Amos (*1950*) estimated 200 million florets per acre.

Knight and Green (*1957*) stated that although honey bees are attracted to crimson clover they have difficulty in forcing their mouth parts into the floret. The bee trips the floret whether nectar or pollen is collected. Knight (*1969*) found that an apetalous male-sterile selection was unattractive to bees.

Girardeau (*1958*), Lovell (*1926*), and Pellett (*1947**) rated crimson clover high as a honey plant. The quality of honey produced is excellent. Girardeau (*1954*) stated that when bees forage on crimson clover they do not crowd their broodnest with honey. Girardeau (*1958*) observed that bees collected nectar from crimson clover primarily in the mornings and pollen in the afternoons. This is exceptional because most plants that attract bees for pollen do so in the forenoons. The pollen is collected in large amounts and this, also, is unusual for leguminous plants. Girardeau (*1958*) also noticed that cells filled with crimson clover pollen were scattered throughout the honey storage area instead of being concentrated around the broodnest, and that colonies foraging on this crop swarmed excessively. No reasons were determined for these behaviorial differences.

Pollination Requirements

The crimson clover floret is self-fertile but is not self-tripping (USDA *1967*), therefore pollinating insects are required for profitable seed production (Pieters and Hollowell *1934*). The flower is easily tripped. After tripping and release of pressure on the keel petal by the bee, the staminal column returns to its original position. No data have been obtained on the value of repeated bee visits to a floret. If the floret is pollinated, it withers within a day's time; but if not pollinated, it will remain fresh-looking for about 2 weeks. This characteristic contributes to the flower-garden appearance of a poorly pollinated field and the dull appearance of a well-pollinated field (Knight and Green *1957*).

[26] See "Clovers, General."

Pollinators

There seems little doubt that honey bees are the primary pollinators of crimson clover. Knight and Green (*1957*) stated that wild bees, such as bumble bees, do not pollinate much crimson clover. They accredited wind and rain with 13 to 20 percent of the pollination in the open. Scullen (*1956**) observed that the flowers were attractive to bumble bees and some species of wild bees in Oregon, but in general he indicated that they alone were insufficient. Girardeau (*1958*) found that because of the early flowering of crimson clover in the spring in Georgia, few bees other than honey bees were active in the field. Beckham and Girardeau (*1954*) reported that about 2 percent of the bees in the field were bumble bees, the rest honey bees.

Weaver and Ford (*1953*) stated that virtually all of the pollination seemed to have been performed by honey bees. Blake (*1955*) reported that pods containing seeds and seed yields were always higher near apiaries. Hollowell (*1947*) stated that bees were effective as tripping agents and in the transfer of pollen from flower to flower, with a consequent increase in the number of seeds per head. Wheeler and Hill (*1957**) stated that placing colonies of bees near fields has increased yields in some cases up to 1,000 to 1,200 lb/acre.

The effect of honey bees as pollinators has also been established with cage tests. Amos (*1950, 1951*) obtained only 2.64 g of seed from 50 crimson clover heads caged under 2-, 4-, or 16-mesh per inch screen to exclude various types of bees, but harvested 6.36 g per 50 heads exposed to one colony of honey bees per acre. Scullen (*1956**) obtained five seeds per head excluded from bees, but 69 seeds per head available to bees. Beckham and Girardeau (*1954*) harvested 130 lb/acre from caged plots but 491 lb/acre from open fields supplied with one colony per acre. Blake (*1958*) obtained 1,019 lb/acre with three colonies per acre and best agronomic practices, a gain of more than 800 pounds over production where bees were excluded. Killinger and Haynie (*1952*) harvested only 3 lb/acre in cages where bees were excluded, 64 lb/acre from cages with bees, and 105 lb/acre from open plots. Weaver and Ford (*1953*) harvested 59 lb/acre from cages where bees were excluded, 233 lb/acre from bee cages, and 297 lb/acre in open plots. (Eight colonies of bees were one-half mile from the 4-acre experimental plot.)

Johnson and Nettles *(1953)* obtained 37 pounds of seed per acre in caged plots but 375 lb/acre in the open field where there were 2.5 colonies of honey bees per acre. Vansell[27] reported that he obtained 5.08 seeds per head on caged crimson clover plots in Oregon and 69.2 seeds per head in the open field. He stated that a 144-acre field in Hanford, Calif., supplied with three colonies of honey bees per acre produced 1,100 pounds of seed per acre.

Pollination Recommendations and Practices

The need for honey bees as pollinators in the production of crimson clover seed is firmly established. The number of bees required is less firm. In Texas, Weaver and Ford (*1953*) calculated that one colony of honey bees per acre should be sufficient to saturate any field of crimson clover, providing there was not too much competition from other sources of pollen and nectar. Pedersen et al. (*1961*) and Girardeau (*1958*) also recommended one colony per acre. Killinger and Haynie (*1952*) recommended one colony per acre, but they stated that some increase in seed production was obtained with up to five colonies per acre. Blake (*1958*) recommended two colonies per acre in Alabama, and, when three colonies per acre were used, the exceptionally good yield of 1,019 lb/acre was obtained. Hollowell and Knight (*1962*) recommended the placement of the colonies of honey bees in or adjacent to the field, and they stated that, with good clover stands and good pollination, yields of 1,000 to 1,200 pounds of seed per acre could be obtained.

Weaver and Ford (*1953*) stated, "The clover itself gives a reliable indication of whether there are adequate numbers of pollinating insects in the field. When the blossoms are not pollinated they remain open for about 2 weeks before they wither. Blossoms which are pollinated, however, wither within a day. In the cages from which all insects are excluded, the blossoms open in successive whorls from the bottom, and remain open until the entire flower head is a solid mass of beautiful open florets. When adequate pollinating insects are present, however, there is a narrow whorl of open blossoms with buds above and withered flowers below. A field with some pollinating insects, but in inadequate numbers, has an "intermediate, or rather spotted appearance."

Knight and Green (*1957*) stated that close proximity of a field to honey bee colonies does not guarantee good pollination because of possible competition by other plants. They offered a much better method of estimating pollinator populations—bee visitors on the clover flowers. They believed that from two to three bees per 100 flower heads was an adequate population for good pollination. The counts should be made between 10 a.m. and 3 p.m., on a warm day with the clover in full bloom. They warned that "Since the peak of blooming and pollination is so short, it is often too late to get more bees when their need is discovered and the counts may be of value only for the next year." The grower might be wise to assure himself of a higher bee population in the field before peak bloom to insure adequate pollination at that time. By doing this, his field would never become a flower garden but would yield the maximum crop of seed.

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CROTALARIA

Crotalaria spp., family Leguminosae

The genus *Crotalaria* contains some 325 species, recognizable by their papilionaceous flowers, smooth leaves, erect growth, roundish pods, and yellow, brownish-yellow, blue, or purple flowers (Bailey *1949**). McKee and Enlow (*1931*) stated that *C. mucronata* Desv. [*C. striata* DC.] was the only one of commercial importance in the United States. Ritchey et al. (*1941*) tested 11 species for forage, and McKee et al. (*1946*) stated that four species (*C. intermedia* Kotschy, *C. lanceolata* E. Mey., *C. mucronata*, and *C. spectabilis* Roth) were extensively grown, primarily in the South (fig. 102). Wheeler and Hill (*1957**) listed only two species—*C. mucronata* and *C. spectabilis.* Their justification for the growing of crotalaria was that it—

- Makes excellent growth on light sandy soil, where it is sown for cover and green manure crops.
- Does not harbor nematodes or rootknot.
- Is well nodulated with nitrogen-fixing bacteria.
- Is an annual (except in nonfreezing areas).
- Sets seed in abundance.

The drawbacks to the cultivation of crotalaria are that it—

- Contains an alkaloid that is poisonous to livestock or poultry (particularly the showy *C. spectabilis*).
- Has a tendency to harbor certain insects harmful to citrus and pecans.
- Has hard seeds that tend to germinate and come up years later and contaminate other crops.

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FIGURE 102.—*Crotalaria spectabilis* pods ready for harvest.

• Is treated as a noxious weed in at least one State if the seeds are harvested with corn or soybeans.

Because of these drawbacks and their significance at present, the crop is not being planted and the seed is almost unavailable.

Inflorescence

Free (*1970**), referring to work by Howard et al. (*1919*), stated that the large showy flowers of *C. juncea* L. occur in inflorescences, each flower having 10 stamens, five with short filaments and long narrow anthers, and five with long filaments and small round anthers. The long anthers dehisce in the bud, then the filaments of the round anthers elongate and push the pollen to the orifice of the keel. When a heavy insect alights on the wings, the pressure forces the style forward, and a ribbon of pollen is pushed out the orifice and onto the insect's abdomen. When the pressure is released, the style retracts through the mass of pollen, and another ribbon of pollen is extruded on the next insect's visit.

Roberts (*1939*) stated that crotalaria was a source of some nectar and an abundance of pollen. He did not explain how the bee collects the nectar. Pellett (*1947**) stated that a colony of honey bees near Winter Haven, Fla., stored 50 pounds of dark and poor quality honey from *C. mucronata* and that the bees worked *C. spectabilis* to some extent. The effects of these visits on the flowers was not mentioned.

Pollination Requirements

The pollination requirements of crotalaria are not too well understood. Todd (*1957**) listed crotalaria as largely self-pollinated. Free (*1970**) in discussing *C. juncea* stated that "When flowers are not visited by insects the continual elongation of the filaments presses the pollen masses onto the stigma so that self-pollination is possible. However, self-fertilization does not occur unless the stigmatic surface is rubbed against an insect's body, and lack of pollinators probably helps to explain why in parts of India few flowers set seed." A study of the effect of pollinating insects on the volume of seed produced by the different species of crotalaria and also on the germination of the seed would be of interest.

Pollinators

Honey bees seem to be suitable pollinators.

Pollination Recommendations and Practices

None

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CROWNVETCH

Coronilla varia L., family Leguminosae

Plant

Crownvetch is a spreading, long-lived, winter-hardy, drought-tolerant, herbaceous legume with angular stems that grow to a height of 2 to 3 feet during the blooming period, after which the plant forms a dense mat about a foot deep. It will grow at fertility levels so low that few other plants will normally survive. Its principal use is for erosion control, soil building, and ground cover (Hawk *1955*, Musser et al. *1954*, Richardson and Diseker *1963*, and Richardson et al. *1963*). It is especially valuable for holding banks along highways. The stand improves with age and gradually chokes out other weeds. It is also used for its ornamental value on steep banks and hillsides (Grau *1962*). The plant can be established from seeds or crowns (Wheeler and Hill *1957**).

Inflorescence

Crownvetch produces attractive rose, white, or pinkish-white flowers from June to September. The inflorescence is a contracted raceme, and its flowers are a source of both nectar and pollen, which bees gather. The nectar is not secreted in the usual place but on the outside of the fleshy calyx, where it is sought out by bees (Müller *1883**). They alight upon the petals in the normal manner and probe with their proboscis between the bases of the petals to the outside of the flower for the nectar on the calyx (Knuth *1908**, *p. 313*, and Müller *1883**). Anderson *(1958)* stated that the honey bee has to learn how to trip crownvetch blossoms to obtain pollen, the primary attractiveness of the flowers, and, incidentally, to pollinate the blossoms.

The bee straddles the lower section of the flower with its head facing the center of the blossom; then with its two rear legs, the bee pushes the two sides of the blossom outward. This pressure causes the cup of the flower to shorten and the anthers and stigma to snap out where the pollen is available to the bee, and the stigma is exposed to pollination. Anderson also stated (personal correspondence, 1970) that bees have been known to starve on large acreages of crownvetch located in wooded areas of Pennsylvania.

Coronilla, meaning "little crown," is derived from the

characteristic crownlike shape of the cluster of blossoms. The specific name, *varia*, refers to variations in flower color as well as growth habits (Ruffner and Hall *1963*).

Pollination Requirements

Knuth (*1908*, p. 313*) indicated that crownvetch might not be self-pollinating. However, Todd (*1957**) listed it as largely self-pollinated. Grace and Grau (*1952*) talked of the problem of low seed yields but did not mention pollination. Cope and Rawlings (*1970*) stated that it is almost completely cross-pollinated, and Al-Tikrity (*1969*) stated that it is entirely dependent upon insect pollination. Anderson (*1958*) showed that plants caged to exclude bees produced no seed, while similar plants caged with honey bees produced seed. He stated that a flower head consists of 12 fingerlets with 10 potential seeds in each fingerlet or 120 seeds per head. Eighty seeds per head is considered a good set. In the cage with bees, he obtained only 10 seeds per head, and in the open with few bees present he obtained 18 seeds. He attributed part of the low seed set in the cages to reduced light, but proved that crownvetch is self-sterile and that honey bees can and do pollinate it.

The following year, Anderson (*1959*) used plastic cages and more bees, and obtained 21.1 seeds per head in the cage and 24.6 seeds per head in the open despite the fact that weather was far less favorable for pollinator activity the second season. He also made repeated counts of pollinating insects in 8- by 50-foot plots, and recorded an average of 14 honey bees and 1.6 bumble bees. Other bees were negligible. Bumble bees visited 2.4 times as many blosoms per minute as did honey bees.

Henson (*1963*) compared seed production from bagged flowers tripped by hand, rolled, or untouched. The tripped flowers set twice as many seed as the rolled flowers and eight times as many as the untouched flowers. He showed that tripping increased seed production, but even this was low compared to the set obtained by Anderson (*1959*) when bees were used. Al-Tikrity (*1969*) reported 150 to 466 lb/acre.

Pollinators

The observations by Anderson (*1958, 1959*) showed that although crownvetch is not a good source of nectar for honey bees, they are its primary pollinators. Bumble bees visit 2.4 times as many blossoms per minute, but because of the scarcity of these bees they are far less effective and important than honey bees.

Pollination Recommendations and Practices

Because it requires cross-pollination by insects, and because it is not overly attractive as a nectar source, probably a large number of colonies per acre would be required to provide a heavy bee population within the field. Anderson (*1959*), with 18 colonies of honey bees on 90 acres of crownvetch, obtained only 14 bees per 400 ft^2—about one-third bee per square yard and 24.6 seeds per blossom head (80 seeds per head is considered a good set). This would indicate that many more bees were needed, probably more than one per square yard, or more than one colony for each acre of crownvetch.

Al-Tikrity et al. (*1970*) suggested that three to four colonies per acre, arranged singly or in groups in rows 200 to 240 yards apart, would provide maximum pollination and result in high seed yields. Later, Al-Tikrity et al. (*1972*) suggested the moving of honey bees at the start of bloom, then additional colonies as blooming progressed. Sharp (*1964*) noted that when a good seed crop is being set, the field has a brownish cast. This could be an important factor in judging the effectiveness of the pollinating insects and possible needs for an increase in pollinator population.

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CUCUMBER AND GHERKIN

Cucumis sativus L., family Cucurbitaceae

Cucumbers and gherkins are grown in most of the States to some extent but over half of the 179,400 acres devoted to this crop in 1969 was in five States: North Carolina (34,100), Michigan (23,100), Wisconsin (13,900), Florida (16,400), and Texas (10,900). The 1969 crop was valued at $78 million, of which $32 million was derived from cucumbers marketed in the fresh state and $46 million from processed cucumbers.

The so-called gherkin of American commerce is a small-fruited cucumber type processed in a special way. The true gherkin, or West Indian gherkin, is another species (*C. anguria* L.). It is grown primarily in Brazil and occasionally in the West Indies. Its fruit is somewhat oval rather than oblong like the cucumber (Purseglove *1968**).

Plant

The cucumber is a trailing or climbing, normally monoecious, annual herb, with vines 2 to 10 feet long covered with stiff bristly hairs. The roughly triangular leaves are 3 to 10 inches across, and they are supported on 3- to 7-inch petioles or stems, which permit the leaves to overshadow the prostrate branches, flowers, and fruit (Whitaker and Davis *1962**).

Chao-Shan and Humphries (*1969*) studied fruit setting on the vines of three cultivars in North Carolina, and found that 75 to 90 percent of the fruit set within 20 inches, and the bulk with 12 inches, of the crown.

Two main types of fruit are grown commercially in the United States—the slicing- or salad-type cucumber and the pickling cucumber. The two types have been developed for their specific uses and differ in production methods.

The fruit is pendulous and oblong and has a relatively large stem. Particularly when young, its skin has spiny, wortlike tubercles. It has a characteristic odor and taste that make it not too palatable alone, but delicious in salads. The majority of the fruit is consumed as processed pickles.

The plant requires warm weather but not as hot as that required by watermelons. Some crops of salad-type cucumbers are grown under glass in cold countries to supply off-season demands for the fresh fruits. Greenhouse cucumbers are usually more uniform than field-grown ones, primarily because of better control of plant growth and environmental conditions including insect pollination. An estimated 20 percent of the pickling cucumbers were machine harvested in 1967, and the percentage is increasing (Zahara and Sims *1966*, Sims and Zahara *1968*).

In Europe, and to some extent in the United States, a special slicing cucumber sets fruit parthenocarpically (without pollination) (Strong *1931*, Whitaker and Jagger *1937*). It sets no seed unless pollinated. If seeds are produced they detract from its eating quality (Kettner *1967*). In some areas in Europe where this cucumber is grown, beekeepers are required to remove their bees from the area during the flowering period (Milne *1941*, van Berkel *1960*, van Berkel and Vriend *1957*, van Koot *1960*). In such areas, the planting of phacelia is recommended so that it flowers simultaneously with this cucumber and lures the bees from the cucumber flowers (Proefstation Voor de Groentenen Fruitteelt onder Glaste Naaldwijk *1958*).

Inflorescence

Cucumber flowers are axillate and quite similar to those of muskmelons. The staminate ones are borne in clusters, each flower on a slender peduncle or stem. The pistillate ones are usually borne solitary on a stout peduncle. As in other cucurbits, the pistillate flower is easily recognized by the large ovary at the base of the flower. In the muskmelon, the ovary is covered with soft hairs, but in the cucumber it is sparsely covered with spiny wortlike growths. The yellow, wrinkled petals are similar in size and shape to those of the muskmelon. The pistillate flower has three thick stigma lobes atop a short broad style (Heimlich *1927*). Normal cucumber types have staminate and pistillate flowers in varying proportions depending on plant growth, vigor, and environmental conditions.

The staminate flowers (fig. 103) usually appear about 10 days before the first pistillate flowers appear (Judson *1929*). They normally out-number the pistillate flowers about 10 to 1 (Alex *1957*), but this ratio has been known to reach 100 to 1, and there are seasonal variations in the ratio (Currence *1932*, Edmond *1931*). This ratio can be altered also by the application of certain pheromone chemicals (McMurray and Miller *1968*, Robinson et al. *1968*, Sims and Gledhill *1969*).

In the recently developed "gynoecious" plants, the flowers are predominantly pistillate (Peterson *1960*, Peterson and Anhder *1960*, Peterson and de Zeeux *1963*, Peterson and Weigle *1958*).

Pollination Requirements

The need for insect pollination of cucumbers has been known for years. Before the turn of the century, honey bees were used to pollinate cucumbers grown under glass (McIntosh *1855*, Root *1886*, Pieters *1896*, Hunn and Craig *1905*, Corbett *1906*, Lyon *1906*). Later tests experimentally confirmed this need (Markov and Romanchuk *1959*). The need for bees on fieldgrown cucumbers was also recognized (Jones and Rosa *1928**), and growers in localities where bees were scarce were

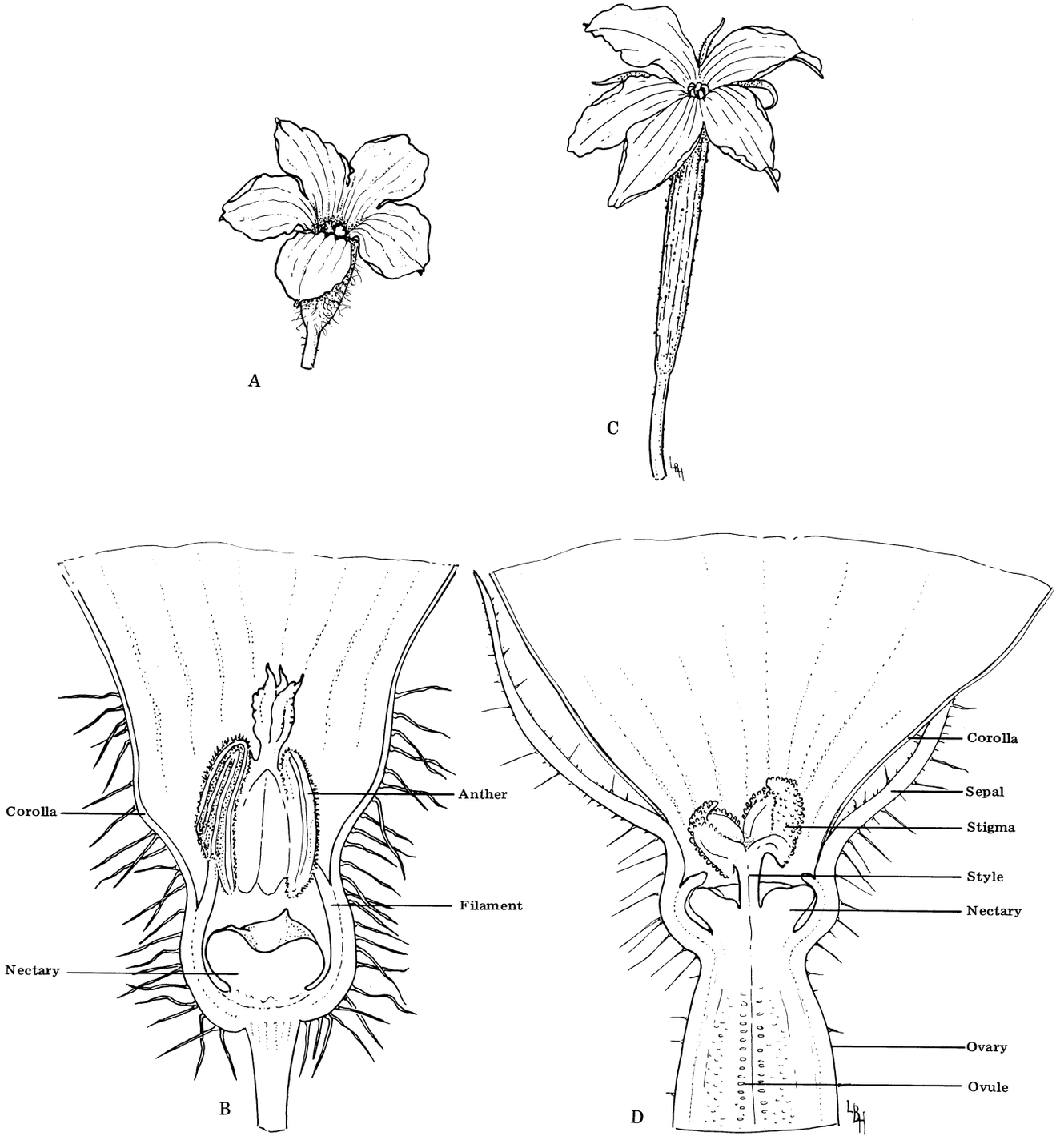

FIGURE 103.—Flowers of 'Tosca' cucumber. *A*, Staminate, or male, ×1; *B*, longitudinal section of male, ×4; *C*, pistillate, or female, ×1; *D*, longitudinal section of a portion of female, ×4.

advised to keep honey bees to insure fruit set (Beattie *1928*, Seaton et al. *1936*). More recent tests have verified earlier ones (Alex *1959*, Beattie *1935*, Connor and Martin *1969a*, *b*, *1970*, Martin and Collison).[28]

[28] MARTIN, E. C., and COLLISON, C. HONEY BEE POLLINATION OF PICKLING CUCUMBERS—THEORY AND PRACTICE. 3 pp. Mich. Pickle Growers' Mtg., August 13, 1970. [Processed.]

Edgecombe (*1946a*, *b*) also reported that he used bees in the field for the transfer of pollen between cultivars for the production of hybrid cucumber seed. Numerous tests have shown that all present varieties of cucumber are inter-fertile, but the pollen must be transferred to the stigma by a pollinating agent, usually honey bees.

The exception is the previously mentioned partheno-

carpic slicing cultivars. McCollum (*1934*) showed that the setting of fruit on these cultivars does not produce the inhibiting effect on plant growth comparable to that caused by fertilized fruit.

The relative time of anthesis in staminate and pistillate cucumber flower was determined by Atsmon et al. (*1965*). Connor (*1969*) found that the best time of day for effective cucumber pollination in Michigan was from 10 a.m. to 3 p.m. He also found that pollination was about equally effective whether the pollen was placed on one lobe of the stigma or on all the lobes. Seaton et al. *(1936)* also stated the stigma is receptive throughout the day but most receptive in the early morning and that several hundred pollen grains should reach the stigma for most effective pollination.

The pollination requirements of pickling cucumbers vary greatly with the variety used, the method of production, and the geographic area. Traditionally, pickling cucumbers have been produced on monoecious vines, planted at the rate of about 5,000 to 15,000 plants per acre. The first one or two fruits on each vine are handpicked when they reach the desired size, usually a few days after flowering. The vine continues to grow and set fruit, which is harvested in a succession of handpickings throughout the season, but the trend is toward machine harvesting (Stout et al. *1964*).

During the 1960's the introduction of gynoecious cucumbers and the development of harvesting machines launched a new era in pickle production. The machine usually destroys the plant as it harvests the fruit so there is only one harvest, commonly called a destructive harvest of the crop, although nondestructive or "multiple-pick" harvesting machines are also available. Yield somewhat comparable to a succession of handpickings is obtainable by planting 50,000 to 150,000 (that is, about 10 times as many) plants per acre and carrying out one machine harvest averaging one or two cucumbers per vine.

The gynoecious characteristic was an innovation designed to provide pistillate flowers in rapid succession. Staminate flowers are provided by blending in about 10 percent seed of a monoecious type. With adequate pollination, fruit forms quickly and, under favorable weather conditions, grows uniformly to an optimum size for machine harvesting. These revolutionary changes in pickling cucumber production have greatly increased the need for timely and adequate pollination because of the greater concentration of pistillate flowers and the need for more rapid, uniform fruit set necessary for a single machine harvest.

Pollinators

Although cucumber flowers are attractive to bees, the crop is not considered a major source of nectar or pollen. Individual flowers produce relatively large amounts of nectar, but the number of flowers per acre is low relative to that of our major honey plants. Pellett (*1947**) stated that in numerous localities cucumbers are of some importance to bees. Stephen (*1970a*) stated that bees get little pollen from cucumbers, and that pistillate and staminate flowers are about equally attractive. Connor (*1969*) and Martin (*1970*) stated that even when honey bees visit staminate flowers, the primary objective is to collect nectar, and that cucumbers are visited for pollen largely when other sources of pollen are absent. Shemetkov (*1960b*) in Russia and Amaral et al. (*1963*) in Brazil reported that bees collected cucumber pollen heavily from 8 to 10 a.m. and nectar from 10 a.m. to noon. Bees work the blossoms later in the day in springtime or cooler climates than in summer or warmer climates. Nemirovich-Danchenko (*1964*) reported that nectar secretion was greatest 3 to 4 hours after the flower opens. Skrebtsova (*1960*) stated that pistillate flowers produce more nectar sugar than staminate ones. Amaral et al. (*1963*) concluded that bees show no preference for staminate over pistillate flowers.

Connor and Martin *(1969a, b)* stated that in Michigan "native bees cannot and should not be relied upon as pollinators. The honey bee is the primary and only dependable pollinator of cucumbers." Tsyganov (*1953*) considered one bee equal in value to 11,000 thrips as pollinators of cucumbers. Skrebtsova (*1964*) stated that honey bees represented 84 to 96 percent of the insect pollinators on cucumbers. In many U.S. fields, they are the only pollinators present. Szabo and Smith (*1970*) reported that the leafcutter bee, *Megachile pacifica*, worked cucumbers in a greenhouse if the temperature remained at 30° C. Stephen (*1970b*) reported that honey bees failed to work effectively in plastic greenhouses, apparently because of the reduction in ultraviolet light.

Shemetkov (*1957, 1960a*) showed that a cucumber flower should be visited 8 to 10 times for satisfactory fruit set, but the number of seeds and weight of fruit increases up to 40 to 50 visits. Connor (*1969*) also found that as many as eight visits per flower were necessary for maximum set, and seed production was significantly greater with 20 or more visits than with 10 visits. Anderson (*1941*) stated that "nubbins," "balls," and "crooks" were the result of poor pollination resulting from too few bee visits per flower. Seaton (*1937*) reported that uniform fruits weighed 626 g and had 314 seeds, but constricted fruits weighed only half as much and had only 150 seeds.

Knysh (*1958*) removed and tested the viability of pollen from bees flying 250, 500, 750, and 1,000 m to the hive. He found that 38 percent of pollen grains taken from bees flying 250 m were viable but only 18 percent from bees flying 500 m. He found no viability in pollen grains that were carried greater distances. This indicates that the pollen grains exposed on the bee have a relatively short lifespan. Seyman et al. (*1969*) reported the importance of honey bees in cucumber production by obtaining increased fruit yield with increased exposure to bee activity. Shemetkov (*1960a*) calculated that one colony of bees was equal to 300 man-days in pollination of cucumbers.

In Michigan, one colony to 2 or 3 acres have been used to pollinate monoecious type cucumbers for handpicking. The flowers are attractive to bees, and even though the number of flowers per acre is low, bees continue to visit and pollinate the blossoms as they mature. The gynoecious hybrids grown for machine harvest present a different picture. Here the current

Michigan recommendation is one colony to each 50,000 plants, or one to three colonies per acre (Martin *1970*).

Connor and Martin (*1970*) using highly gynoecious cultivars showed that preventing the pollination of cucumber flowers for periods up to 11 days after the appearance of the first pistillate flowers resulted in higher yields of more uniform pickles. Unfortunately, this cannot yet be duplicated on a field basis because commercially developed gynoecious hybrids have not so far been able to maintain the gynoecious characteristic at a sufficiently high level to delay pollination. That is, present gynoecious hybrids produce some staminate flowers, so pollen is available as soon as pistillate flowers are produced. If fully gynoecious hybrids become available, growers may interplant a few rows of monoecious plants with gynoecious hybrids in such a way that staminate flowers appear later than pistillate flowers. Pollination could thus be delayed until the gynoecious plants attained better growth and capacity to produce a higher yield of more desirably shaped fruit. This points out that pollination studies coordinated with studies of other cultural practices including plant breeding may have broader application than has been fully appreciated to date.

Pollination Recommendations and Practices

The literature leaves little doubt that insect pollination of cucumbers in the United States is essential to profitable production, and that honey bees are the primary pollinating agents. The question of the number of pollinators per unit area (acres or flowers) is not completely resolved. Recommendations have varied from "fields no farther than one-fourth mile from one or more swarms," to "a few stands [colonies] in or near the field," or from one colony per 10 acres to one strong colony per acre (Anonymous *1959;* Alex *1959;* Conner *1969;* Conner and Martin *1969a, b;* Davis and Hall *1958;* Eckert *1959*;* Martin *1970;* Peto *1951;* Seyman et al. *1969;* Sims and Zahara *1968;* Steinhauer *1970, 1971;* Warren *1961, 1967*). Hughes (*1971*) recommended 30 to 40 bees within a 30-foot circle. The University of Arizona *(1970)* recommended one bee per 100 flowers.

Recommendations should differ between monoecious, handpicked, low plant population, and gynoecious, single-machine-harvest, high plant population. Many of the recommendations that have been made are mere statements without supporting data, and, as might be expected, they vary considerably. The most thorough study of cucumber pollination has been made in Michigan (Connor *1969*, Connor and Martin *1969a, 1970*, Martin and Collison *1970*). It is of interest to note that although one strong colony per acre is recommended (Connor *1969*, Connor and Martin *1969a, b*) or "one colony per acre 2 or 3 might pay off" (Martin and Collison *1970*), the data by Connor and Martin (*1970*) leave little doubt that production with three colonies per acre was significantly below their bee saturation (cage) population. In Michigan, more than three colonies per acre were required for maximum cucumber production when gynoecious hybrids were grown for machine harvest. Davis et al. (*1970*) indicated that honey bees were more effective if they were moved to the cucumber field after flowering had started. This was supported by Martin (*1970*) who showed that delayed pollination improved yield and fruit shape. Enzie (*1934*) stated that when bees are scarce it may be necessary to distribute hives among the larger plantings.

Hughes (*1971*) gave the most practical recommendation. He stated that, on a clear day walk into the cucumber field. If you cannot count 30 to 40 bees in a 30-foot diameter (within 15 feet) or cannot hear a very noticeable hum you probably need to bring in more bees. He generally recommended one colony per acre as essential, with two or more as desirable, or one bee per 100 flowers.

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CURRANT

Ribes spp., family Saxifragaceae

Bailey (*1949**) listed the following species of currants:

R. americanum Mill.	American black currant
R. aureum Pursh.	golden (black) currant
R. nigrum L.	European black currant
R. odoratum Wendl.	Missouri or buffalo (black) currant
R. rubrum L.	northern red currant
R. sativum (Reichenb.) Syme	common or garden (red or white) currant

Red currants are more common in the United States, whereas black currants are produced primarily in Canada, England, and Russia. Shoemaker (*1955*) stated that production of currants and gooseberry in the United States amounted to about 4 million quarts from about 4,000 acres. The majority of this was currants, of which New York produced about half the total amount. The 1964 U.S. Census of Agriculture showed only about 600 commercial acres of red and golden currants, which produced 2.5 million quarts and valued at about one-half million dollars. Yields of 100 to 400 bushels per acre were obtained.

The fruit, a berry that ripens in late summer, is used primarily in jellies, jam, juice, and canning or is eaten

fresh. The fruit may be from ⅓ to ⅔ inch in size, oval, soft, and juicy and may contain many seeds.

This crop should not be confused with the dried currants of commerce, which is a seedless grape (Hedrick *1938**).

Plant

The currant is a stout, woody, usually spineless deciduous shrub, 4 to 7 feet tall unless trimmed to a lower height for ease of fruit harvest. Some of the species are fragrant, but *R. nigrum* emits a strong unpleasant odor. The fruit (fig. 104) varies in color from black to purple and scarlet with hues and stripes of yellows, greens, and white (Bailey *1914*, v. 2, pp. 603–1200, v. 5, pp. 2423–3041*). The plants are native in comparatively cold climates and are the hardiest of fruits from the standpoint of resistance to cold or changing temperatures. They do not thrive in hot or dry climates.

The growing of these crops has been prohibited in some areas because the plant serves as a host for white pine blister rust (Slate *1933*).

Cultivated red currants are set about 5 feet apart in the row; black currants, 6 to 7 feet apart, with the rows 8 to 10 feet apart (Strong *1944*).

Inflorescence

The small flowers of the black and red currants are saucerlike (open-campanulate) and whitish or greenish. The yellow flowers of *R. odoratum* are tubular, about one-half inch long, with the calyx tube about twice as long as the sepals. Nectar, produced in the base of the flower, and pollen, produced on the half dozen or less anthers (Thayer *1923*), are both highly attractive to bees (Pellett *1947**). Zakharov (*1958*) stated that those cultivars with higher sugar concentration in the nectar were visited more frequently than those with low-sugar concentration. The flowers are in few- to many-flowered racemes, and the minute petals are smaller than the sepals. The extremely short stamens arise on the base of the petals and incline slightly toward the style. Style and stigma are roughly the same length on most species (Thayer *1923*); however, at least in some cultivars the stigma extends beyond the anthers (Strong *1944*). Apparently, the stigma is receptive about the time pollen becomes available. Some plants are dioecious.

PN-3810

FIGURE 104.— A well-laden currant branch.

Pollination Requirements

Fraser (*1927*), apparently referring to American-grown species, stated that currants are self-fertile, thus single cultivars could be planted in a block, even though two or more are usually planted together to extend the season. Apparently, he did not distinguish between the receptivity of the plant to its own pollen and the ability of the flower to fertilize itself without the aid of an outside agency. Philp (*1933*) and Strong (*1944*) recognized this difference for they stated that currants are self-fruitful but that they require insect application of the pollen to the stigmas. Smith and Bradt (*1967**) also stated that some cultivars require transfer of pollen by an outside agency.

Much more research on the black currant (*R. nigrum*) has been conducted in Europe and Russia than elsewhere. Free (*1970**) reviewed the pollination information on this crop, including his own work (Free *1968a*). He (Free *1968a*) showed that both yield and quality of black currants were improved by cross-pollination by insects. He was supported by Hughes (*1966*), Glushkov (*1958*), Williams and Child (*1963*), and Zakharov (*1960a, b*). The fruit drop of black currants 7 to 10 days after flowering was associated by Zakharov (*1958*) with lack of adequate insect pollination. Wellington et al. (*1921*), according to Free (*1970**), associated fruit drop with lack of pollination. Teaotia and Luckwill (*1956*) concluded that seeds per berry was the main cause for variation in size of fruit and the percentage of drop of the fruit.

Pollinators

Frequently, when currants bloom, there are few native insects to visit the flowers in numbers sufficient to adequately account for the pollination required in the production of a commercial crop. In general, the honey bee is the only insect present in numbers sufficient to be of economic importance, although at times and in certain locations bumble bees are also of value (Free *1968b*). Although, as Free (*1970**) indicated, a certain amount of pollen may be transferred from anthers to stigma by swaying of the plant in the wind, in general, insects, specifically bees, are necessary on most cultivars of currants. Free (*1968a*) showed that self-incompatibility was not a factor in black currants, but transfer is necessary of pollen to the stigma within the flowers of most cultivars. Glushkov (*1958*) showed that the 'Laxton' black currant set only 2.2 percent of seed (0.08 kg fruit per bush) when isolated from bees but when pollinated by bees it set 46.0 percent of the seed (1.9 kg fruit per bush).

Hughes (*1966*) showed a significant increase in black currant production from the presence of bees, and

Zakharov (*1960a*) concluded that the heavy fruit drop 7 to 10 days after the end of blooming is because of a lack of adequate pollination by honey bees. Pollination by bees was always more effective than hand pollination (Zakharov *1960b*). Schanderl (*1956*) obtained 10.9 to 17.3 times as much fruit from open bee-visited plants of *R. nigrum* as from those covered with a gauze screen cage, even though this species is considered self-fertile.

Although information is far from complete on the pollination of currants, it indicates that some cultivars require insect transfer of pollen within the cultivar. Most cultivars are materially benefitted by an adequate supply of pollinating honey bees or related bees, which can cause fruit to set and to be larger.

Pollination Recommendations and Practices

Only Skrebtsova (*1959*) has studied the relation of insect populations to set of currants. He found that with 0.5 to 0.7 colonies per hectare, only 53 to 59 percent of the fruit set; with three colonies per hectare, the set of black currants was 88.3 percent. An increase to nine colonies per hectare, increased bee visitation but not seed set, primarily because the plants could not support additional fruit due to lack of fertility.

The demand for supplemental pollination of our crop of currants would not be great under any conceivable need; however, the evidence indicates that if maximum production is desired, maximum insect pollination should be provided. If local pollinators are insufficient, they should be supplemented with colonies of honey bees placed in or adjacent to the plantings.

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DATE

Phoenix dactylifera L., family Palmaceae

Dates are grown on about 4,600 acres in southern California and about 300 acres in southwestern Arizona. The value of the crop is about $4 million (Henderson and Swedberg *1970*, Nixon *1959*). The plants prosper in hot, arid climate with ample subsurface moisture.

Plant

The date palm may reach 50 feet in height but has only a single bud or growing point, the leaf-crowned tip. The leaf may be 10 to 20 feet long, and it has a normal lifespan of 3 to 7 years. Leaves do not shed but are removed under cultivation after drooping in death. Palms are grown entirely under cultivation and irrigation. The trees are usually spaced 60 feet apart in the grove.

Inflorescence

The date is normally dioecious, although occasional trees may be bisexual at times. The 2- to 4-foot staminate inflorescence is a branching axillary spadix with numerous racemes and hundreds of flowers, each flower having three petals and usually six stamens, all in a protecting sheath or spathe (Nixon *1959*). The less numerous pistillate flowers have three petals and also three ovaries but only one ovary develops into a seed. They occur on a slightly smaller branching spadix in a protecting spathe, that opens upon maturity of the flowers.

Pollen is produced in abundance on the staminate trees and is eagerly sought after by bees. If nectar is produced by date flowers it is not mentioned in the literature.

Pollination Requirements

Pollen must be transferred from staminate trees to pistillate ones if fruit is produced. Leding (*1928*) showed that delay in placement of pollen on pistillate flowers reduced production to 89 percent by the second day, to 70 percent by the fourth day, to 54 percent by the sixth day, to 46 percent by the eighth day, and to 23 percent by the eleventh day. Nixon (*1928*) showed that the source of pollen affected the date of ripening (as much as 10 days), the shape of seed, and the size of the seed. Later, he (*1935a, b, 1956*) showed that pollen not only affects the seed but also the fruit pulp, which he termed "metaxenia." Nixon (*1959*) stated that pollination of 50 to 80 percent of the pistillate flowers is sufficient for a full crop.

Pollinators

If sufficient staminate or "male" trees are near the pistillate or "female" ones, wind and sometimes insects will transfer sufficient pollen for adequate fruit set (Knuth *1908*, p. 487*). However, the grower keeps male trees to a minimum inasmuch as they yield no fruit and he distributes the pollen manually. Meeuse (*1961**) stated that man was hand-pollinating dates before 800 B.C.; it is the oldest known means of controlled pollination of crops.

Pollination Recommendations and Practices

For best set of fruit, the most common method of pollination is to cut strands of the staminate flowers from a freshly opened inflorescence and invert two or three pieces, 3 to 6 inches long, between the strands of pistillate flowers during the first three days after opening. Twine should be tied around the cluster to hold the flowers in place during the pollination process. Also the dried pollen taken from mature anthers may be dusted onto a 1- to 2-inch ball of cotton, which is then tied into the pistillate strands, or the pollen may be placed into a clean insecticide dust gun and dusted into the flowers. Aircraft have also been tried for distributing pollen (Brown *1966*), but such use is economically questionable.

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DILL

Anethum graveolens L., family Umbelliferae

Dill is grown primarily for its seeds and herbage used in seasoning of foods. The best known food product is dill pickles. According to Hawthorn and Pollard (*1954**), only about 100 acres is devoted to the production of dill seed in the United States. Martin and Leonard (*1949**) stated that 500 to 700 pounds of seed are produced per acre, yielding 20 pounds oil. Production is limited to the north central United States and the Pacific northwest (Rosengarten *1969**).

Plant

Dill is a glabrous annual or biennial herb, 2 to 4 feet tall, usually grown in rows 30 inches apart, with the plants 6 inches apart in the row (fig. 105).

FIGURE 105.— Branch of dill, showing typical arrangement of florets and seed.

Inflorescence

Unlike the flowers of most other umbelliferous crops, the small yellow dill flowers contain little nectar, although they have a strong odor. They are visited by many insects, chiefly flies and bees. Knuth (*1908**, *p. 462*) stated that the flowers are homogamous and hermaphrodite—the primary umbels bearing hermaphrodite flowers, the secondary and tertiary ones bearing hermaphrodite ones on the margins and staminate ones in the center, similar to coriander. On the plant from which the flower illustrated in figure 106 was taken, some of the flowers were entirely pistillate (female), some staminate (male), and a few were hermaphrodite.

The ovary of the 5-mm pistillate flower normally contains two ovules, although in numerous pistillate flowers examined, one or both had aborted. Nectar is visible on staminate flowers, but there is little or none in pistillate flowers. The 2-mm yellow staminate flower has five stamens that are about 1 mm long when extended and dehiscing pollen. The strongly incurved petals never completely straighten out. The stamens arise between the petals.

Pollination Requirements

Flemion and Waterbury (*1941*) and Flemion and Uhlmann (*1946*) found an average of 16 percent of the seed embryoless or with immature embryos in the Umbelliferae, including dill. No correlation was found between embryolessness and plant spacing, seed size, yield, temperature, rainfall, fertilizers, or seed from different areas. However, when Flemion and Henrickson (*1949*) confined nine dill plants in insect-free cages during the flowering period, only 59 seeds per primary unbel were obtained, but when nine plants were caged with houseflies present, 1,001 seeds per primary umbel were obtained, showing that insect pollination is essential to good seed set.

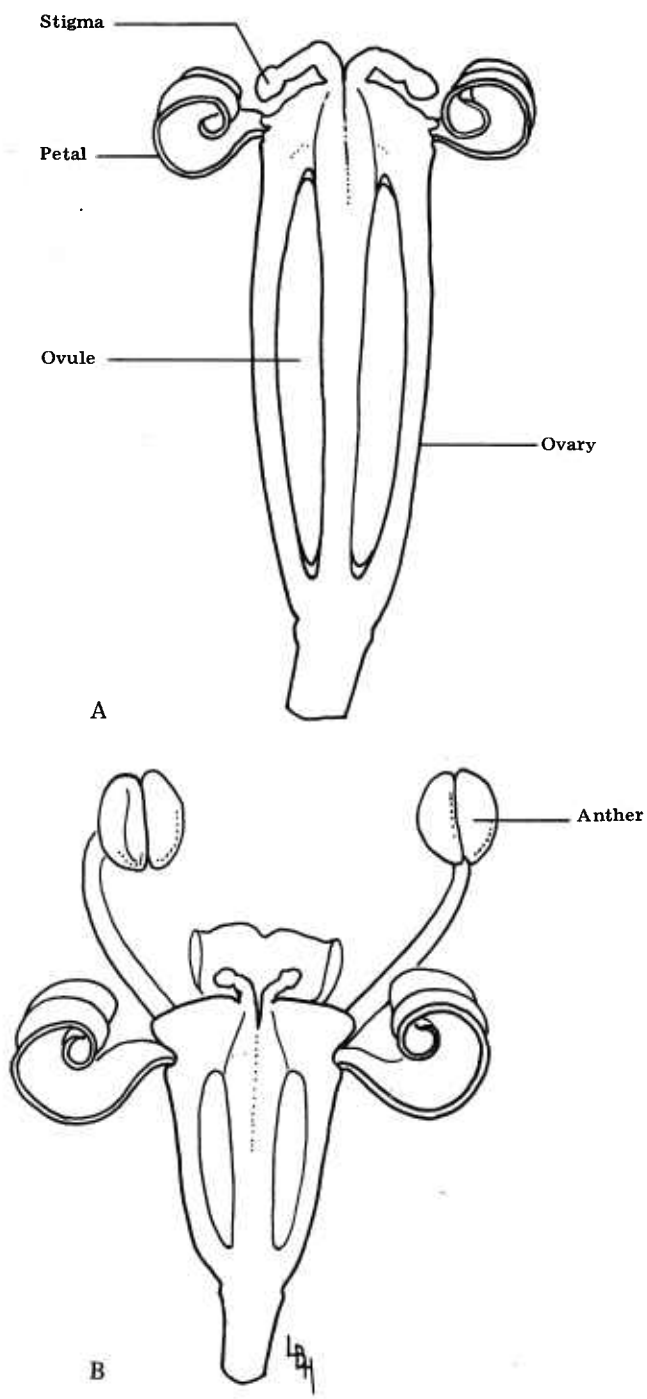

FIGURE 106.—Longitudinal section of dill flower, ×20. *A*, Female; *B*, male.

Pollinators

Both flies and bees have been mentioned as pollinators of dill. If seed is grown commercially, there are probably not enough flies in the vicinity to pollinate all the flowers. Honey bees can be moved to the field, and doubtless this should be done if the highest seed production is desired.

Pollination Recommendations and Practices

None. If maximum seed production is desired the meager evidence indicates that a heavy population of honey bees should be created in the field.

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DRUG PLANTS

Mention should be made of drug plants, many of which are cultivated. Usually, these plants are produced only in gardens or similar-sized lots, but some are harvested in the wild state. Krochmal et al. (*1954*) listed 60 useful drug plants native to the American southwestern desert, and Krochmal (*1968*) about 125 species in the Appalachian region. Sievers (*1948*) listed more than 200 species and varieties of drug and condiment plants.

Many of the above plants doubtless depend upon insect pollination. Youngken (*1950*) studied bee activity on more than 50 drug plants and concluded that bee pollination was a major factor in drug plant culture. Later he (*1956*) reported on more than 250 species of drug plants in the Drug Plant Garden and Laboratory in Seattle, Wash., and concluded that beekeeping should be encouraged near drug plants for maximum production.

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EGGPLANT

Solanum melongena L., family Solanaceae

The eggplant is a minor cooked vegetable crop in the United States. Florida with 2,350 acres and New Jersey with 1,400 acres in 1969 accounted for the bulk of the acreage, which was valued at $4,112,000. However, the plant is grown in home gardens in most areas of the country where there is a long, warm growing season. The average planting in Florida was 42 acres with a yield per acre of 565 bushels, for which the grower obtained an average of $1,310 per acre (Brooke *1970*). The value of the 1969 crop in the U.S. was estimated by Brooke (*1970*) at $5.5 million.

Plant

The eggplant is a much-branched, gray-green annual 20 to 50 inches high and appears somewhat like the pepper plant but is much coarser. The simple, thick, 6- to 15-inch leaves, are more or less oval, with the underneath portion covered with thick, white woolly, sometimes spiny hairs. It is grown in rows and cultivated in a manner similar to that for peppers and tomatoes. The egg-shaped, purple fruit is usually harvested when near full size, 3 to 6 inches in diameter (fig. 107).

A fruit may have as many as 2,500 seeds (Odland and

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FIGURE 107.— Eggplant, showing flower buds and fruit almost ready for harvest.

Noll *1948*). Fruits are sometimes produced with few or no seeds, but they are hard and undesirable.

Inflorescence

The 1 ½- to 2-inch violet flowers of the eggplant are in two- or three- (rarely five) flowered cymes. They may be perfect (Sambandam *1964*) or hermaphrodite (Jones and Rosa *1928**). They develop opposite or near opposite the leaves instead of in the leaf axils as in most plants. The six to 20 anthers form a conelike tube around the style (fig. 108), and they dehisce at the terminal pores in a manner similar to that of the tomato

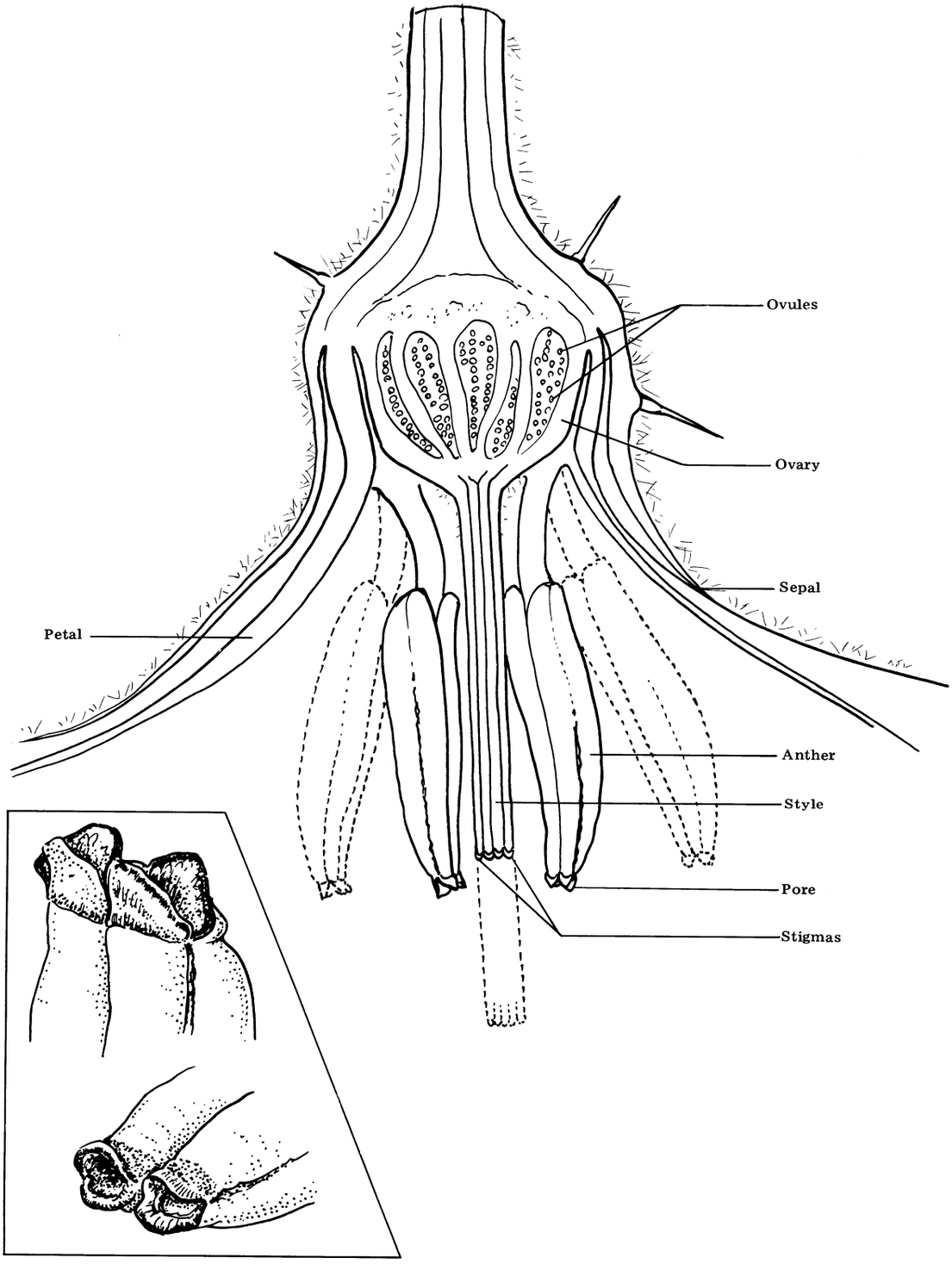

FIGURE 108.— Longitudinal section of eggplant flower, × 6. Dotted areas indicate variation in length of style and in positions of stamens. Inset shows pores of anther tubes enlarged.

flower, which favors self-pollination (Kakizaki *1924*). However, the stigma ultimately projects beyond the anthers, where pollinating insects are more likely to contact it. This position affords ample opportunity for cross-pollination (Hawthorn and Pollard *1954**). The flower remains open 2 to 3 days without closing at night (Kakizaki *1924*). It is visited by pollinating insects largely, if not exclusively, for pollen. Smith (*1931*) found that single flowers are less likely to shed than those on multiple cymes. Whether this is associated with pollination or some other factor is not clear.

Pollination Requirements

Bailey (*1891*) noted that artificial pollination always resulted in fewer seeds than natural pollination even when an excess of pollen was applied. He stated that with hand pollination a few seeds were produced at the apex of the fruit, but most of the ovules remained undeveloped. Jones and Rosa (*1928**) reported that plants grown in a screened house isolated from insects were nonfruitful, and that flowers emasculated and left to natural pollination rarely set fruit. This indicated that the plant is not self-fruitful, that wind is not a factor in fruit set but that insects are required to transfer the pollen to the stigma in appropriate amounts and at the right time. The relative time period of pollen transfer for most effective fertilization of a flower has not been determined.

Jasmin (*1954*) reported that male-sterile plants have been found, in which the anthers do not dehisce. Such plants must be insect pollinated and might be used in the production of hybrid plants. Capinpin and Alviar (*1949*) reported that hybrids fruited earlier than the parents. Baha-Eldin et al. (*1968*) concluded that hybrid vigor was strongly manifested in total yield and number of fruit per plant, which would justify the utilization of heterosis in eggplant. Kakizaki (*1931*) reported that in most of his crosses the first harvesttime was earlier, and production exceeded the best parent by 17 percent. Hybrid eggplants are now being produced commercially by the use of this male sterility factor.

Pollinators

Wind is not a factor in eggplant pollination, and vibration of the blossom will not cause a sufficient deposit of pollen on the stigma. The eggplant does not self without the aid of bees or man (Kakizaki *1924*). The pollinating insects on eggplant have never been studied. Pammel and King (*p. 606, 1930**) reported that bumble bees were common on the flowers at Ames, Iowa, but no honey bees came to the flowers. Workers dealing with this crop have tended to overlook the insect visitors, but the amount of crossing recorded by different ones indicates that insect visitation occurs in relative abundance. Sambandam (*1964*), for example, stated that 30 to 40 percent of the fruit set is attributed to pollination by contact, gravity, and wind, the rest to insects, and he reported that crossing on the same plant (in India) ranged from 0.7 to 15 percent, but he made no mention of the insect pollinators responsible for the set or crossing. Kakizaki (*1924*) reported 0.2 to 46.8 percent cross-pollination. Pal and Taller (*1969*) likewise discussed pollination of eggplant, and stated that within the variety the number of seeds per fruit is higher in cross-pollinated than in selfed plants, but substantially lower than in open-pollinated plants. No mention is made of the pollinating insects responsible for the better effect on the open-pollinated flowers.

Kakizaki (*1924*) concluded that bees or man are necessary in the pollination of eggplants.

Pollination Recommendations and Practices

If male-sterile plants are grown for the production of hybrids, the pollinating insects are essential and should probably be present in relatively large quantities. Even if fertile varieties are grown for fruit production, the meager evidence available strongly indicates that a goodly supply of pollinating insects should be available in the field.

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ENDIVE

Cichorium endivia L., family Compositae

Endive is a green leafy vegetable crop cultivated in the United States on a few thousand acres. It is biennial in seed production characteristics. Most of the seed is produced in California (Hawthorn and Pollard *1954**).

Plant

Endive forms a large taproot and a rosette of leaves before producing the seedstalk, which elongates the second year. As a vegetable, the leaves are harvested when tender and are used primarily in fresh salads. Culture is similar to that of lettuce; the seeds are planted in the fall, and seeds are harvested the following early summer. As in lettuce, the seed heads on the plant do not mature uniformly so some shattering occurs when the seeds are harvested. Seed yields of 200 to 600 lb/acre for the smooth cultivars, 30 percent less for the curled cultivars can be expected (Griffiths et al. *1946**, Hawthorn and Pollard *1954**, Jones and Rosa *1928**).

Inflorescence

The composite flower head is 1.0 to 1.5 inches across and is made up of 18 to 20 pale blue florets. The head opens early in the morning and closes before noon (similar to chicory). Numerous flower heads occur on the somewhat branched seedstalk.

Pollination Requirements

Jones and Rosa (*1928**) stated that the flowers of endive are perfect and mostly self-pollinated. Rick (*1953*) said that the flower is self-compatible. However, Anderlini (*1956*) reported that better results were obtained in producing seed from cross-pollination of flowers than by self-pollination, which indicates that cross-pollination would at least be beneficial in seed production.

Pollinators

No attention has been given to the pollinators of endive flowers. Considering the relatively few hours the flower is open, if insect pollination is utilized, the population of the pollinators on the flowers should be high.

Pollination Recommendations and Practices

None.

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FEIJOA

Feijoa sellowiana Berg., family Myrtaceae

Feijoa is a subtropical plant native to South America but grown to a limited extent in Florida and California with occasional plantings of 1 to 2 acres (Schroeder *1949*). Feijoa prefers a mild temperature with 30 to 40 inches of rain a year (Bailey *1952*). Its product is the delectable fruit that is eaten fresh, out of hand, stewed, or processed into jam or jelly. Clark (*1926*) reported that 9-year-old plants were producing fruit at the rate of 10,000 lb/acre and had not reached maximum production.

Plant

The evergreen plant reaches 15 to 18 feet with various shapes. The fruit is round, oval or oblong, 1 to 3 inches long, and dull green with a whitish bloom. The thin skin covers a whitish granular flesh about ¼-inch thick around a translucent jellylike pulp in which 20 to 30 minute seeds are embedded. The flavor suggests pineapple or strawberry, and the aroma is delightful. The fruit is sometimes called pineapple guava.

The plants are generally spaced 15 to 18 feet apart. Irrigation is necessary for best production in California (Popenoe *1920*).

Inflorescence

The handsome flower, as described by Popenoe (*1920*), is 1½ inches across with edible fleshy cupped petals that are white on the outside and purplish within. The long, stiff stamens form a conspicuous crimson tuft in the center, with the one stigma extending above the stamens (fig. 109).

Pollination Requirements

Popenoe (*1912*, *1920*) stated that some plants are self-sterile, whereas others are self-fertile, but even the self-fertile ones were not self-pollinating. Ryerson (*1914*) found in a preliminary test that six different seedling plants were self-sterile. Clark (*1926*) found one cultivar that apparently did not need cross-pollination, but transfer of pollen within the flower was necessary. Ryerson (*1933*) again stated that the feijoa tends toward self-sterility.

Pollinators

Popenoe (*1920*) and later Ryerson (*1933*) stated that birds feeding upon the edible petals in their native habitat became dusted with pollen from the tuft of anthers then when they visited another flower they affected cross-pollination. Schroeder (*1953*) believed that transfer of pollen between plants either by insects or man was required.

Clark (*1926*) reported that honey bees were the only insects that visited the flowers, and they gathered no nectar, only pollen. Plants screened to keep bees off set only 9 percent of the flowers while those visited by bees set 40 percent of their flowers.

Schroeder (*1947*) conducted a thorough test on five cultivars under cheesecloth in Los Angeles during 1945 and 1946. He found that open pollinated flowers set about 16 times as well as comparable flowers under cage. He then and later (*1953*) concluded that the feijoa is pollinated by insects, primarily by bees, and that most cultivars "show markedly improved fruit-set when cross-pollinated."

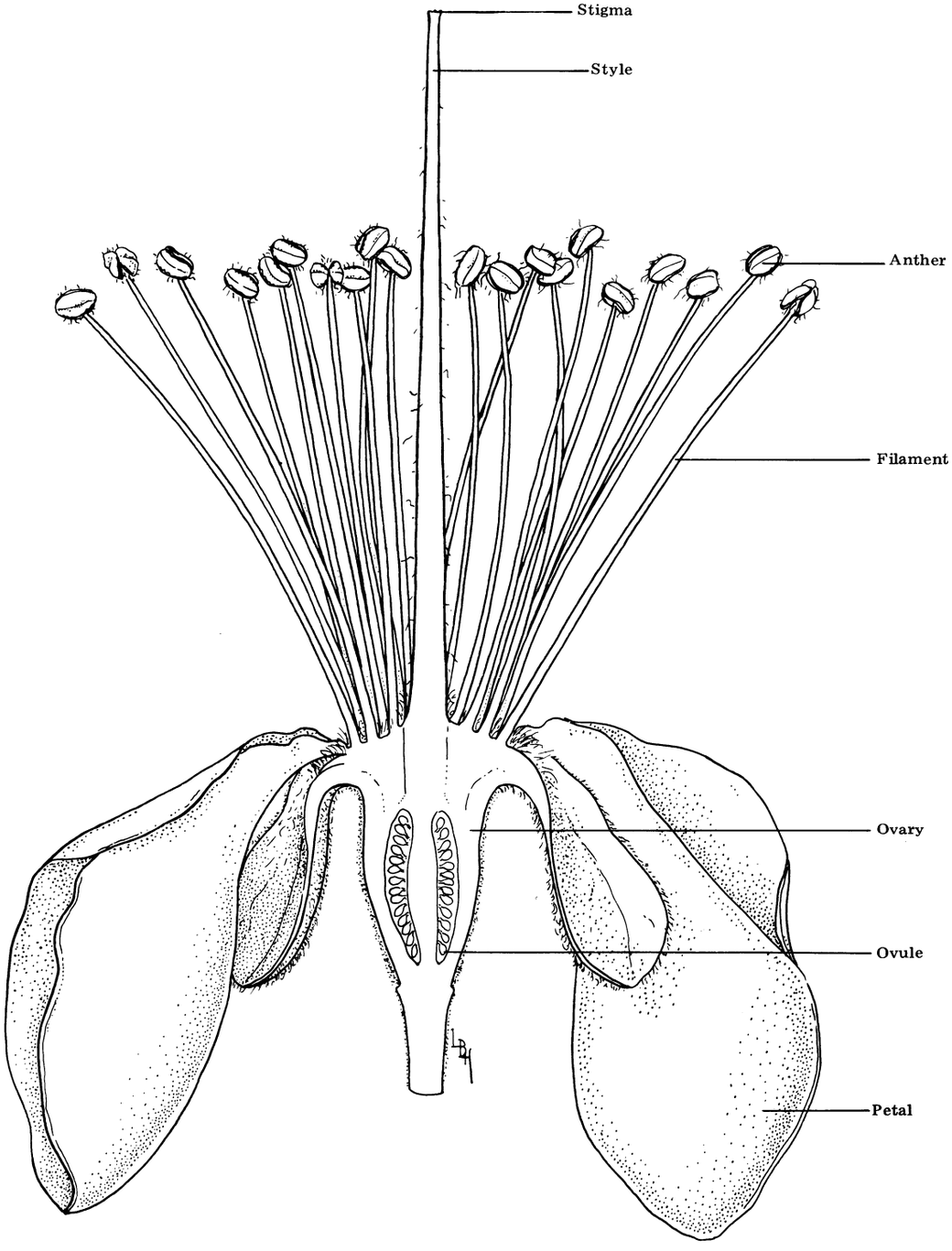

FIGURE 109.—Longitudinal section of feijoa flower, × 4.

Pollination Recommendations and Practices

The evidence indicates that the plants must be pollinated by bees unless the proper species of birds are available. No recommendations on methods of using bees have been made. Should the acreage increase the proper usage of bees would doubtless be necessary.

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FENNEL

Foeniculum vulgare Mill., family Umbelliferae

The condiment plant, fennel, also known as Florence fennel, finocchio, and saunf, is produced in a limited way in the United States for its seeds as well as its foliage. It is grown extensively in India.

Plant

Fennel may be an annual, biennial, or perennial, depending upon the way it is managed (fig. 110). Cool weather is required for its successful growth. Its foliage is dense and threadlike. The plants are cultivated somewhat like carrots (Knott *1949*).

Inflorescence

There are two kinds of flowers on this umbelliferous plant. The first of the tiny yellow flowers to bloom on an umbel are hermaphrodite with a few isolated staminate ones. These hermaphrodite flowers are completely protandrous. After the five stamens of a blossom dehisce and their pollen drops off, the stigma becomes receptive and continues to be receptive for 2 more days; however, because its own pollen is gone, the pollen must come from other plants. Later-maturing umbels may produce pollen that drops in masses to receptive stigmas below (Kerner *1897*, p. 325;* Purseglove *1968**).

Both nectar and pollen are produced in the florets, which are intensely visited by bees (Youngken *1956*).

Pollination Requirements

Youngken (*1950, 1956*) caged flowering branches and compared seed production with that of open-pollinated branches, and showed that few or no seeds set on the caged branches, but seed set well on the bee-visited ones.

Pollinators

Bees are the primary pollinators of fennel. Narayana et al. (*1960*) found that *Apis florea* constituted 81 percent of the visitors to fennel in India, and they recommended that cultivars more attractive to bees be developed. Youngken (*1950, 1956*) found that honey bees (*A. mellifera*) were the primary pollinators in Washington State.

Pollination Recommendations and Practices

The keeping of colonies of honey bees around or in fennel fields was recommended by Narayana et al. (*1960*). Youngken (*1956*) recommended that more bees be kept in the drug plots or plantings for ideal pollination.

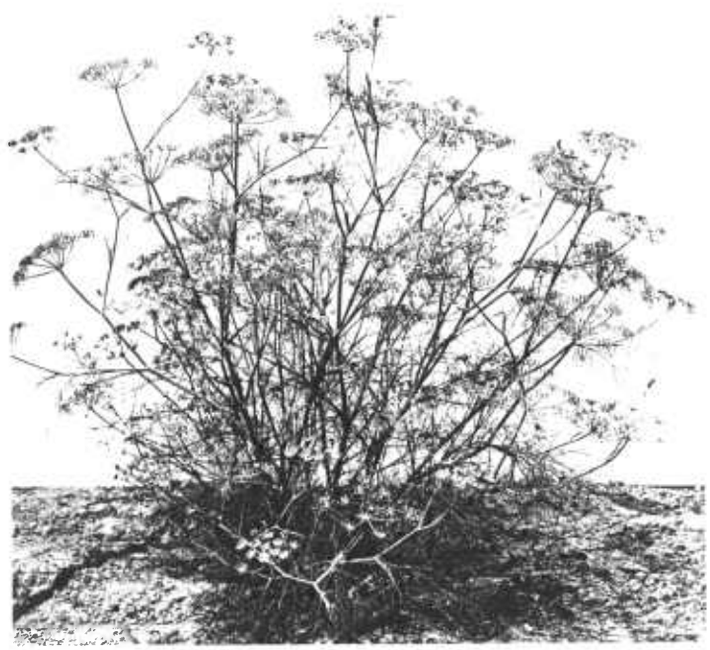

FIGURE 110.—Fennel plant, showing the flower umbels typical of the Umbelliferae family.

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FIG

Ficus carica L., family Moraceae

The common or commercial fig is grown primarily in California, although dooryard and small commercial plantings occur in many other States. About 54,000 tons of the fruit, valued at almost $5 million, were produced on about 18,000 acres in 1969. About one-fourth of this fruit was canned and three-fourths dried, with a small amount consumed fresh.

Plant

The cultivated fig is a small, barely deciduous, soft-wooded, many branched shrub or tree 6 to 20 feet high, with long-stemmed, thick, three- to five-lobed rough leaves 4 to 8 inches long. The fruit, technically referred to as a syconium, is a sweet, round or pear-shaped, infolded fleshy collection of hundreds of tiny inflorescences, each only a few millimeters long. The whole fruit is 1 to 2½ inches long, with a tiny opening or "eye" on the outer end. The primary cultivars grown in California include: 'Calimyrna', 8,523 acres; 'White Adriatic', 3,645 acres; 'Kadota', 2,410 acres; 'Million', 1,753 acres, and 'Conadria', 636 acres.

Inflorescence

Hundreds of tiny florets line the inner wall of the fleshy hollow receptacle. There are four different types of flowers; pistillate, staminate, gall flowers, and mule flowers (Eisen *1897*, *1901*). The influence of these different types of flowers on the development of the fruit depends on the general type of fig plant. The mule flowers produce no pollen, nor do they have receptive pistils, yet the fruit develops into an edible fig. The Smyrna type fig has receptive pistils that must be pollinated, but it has no staminate flowers; therefore, pollen must come from a donor flower—in this case, the inedible caprifig (goat fig), which has pollen-producing staminate flowers near its opening and pistillate gall flowers toward its base.

Each Smyrna fig flower has a single ovary with one ovule, which, if pollinated, develops into a nutlet embedded in the fleshy wall. The flower has four microscopic petals. The style of this pistillate flower is much longer than that of a gall flower. If pollination does not occur, the fleshy part does not develop and the fruit wilts and sheds. If pollination occurs at the time the fruit develops, two or three crops per year are produced. The first crop is referred to as breba figs, the second as profichi figs, and the third as mammoni (Condit *1926*, *1941*).

Pollination Requirements

From the pollination standpoint, the figs grown commercially are basically of three types. The *common* type (for example, 'Mission' cv.) develops its fruit parthenocarpically. The *Smyrna* type (for example, 'Calimyrna' cv.) must be pollinated with pollen from the inedible caprifig. The *San Pedro* type produces its first crop of the season parthenocarpically, but its second crop develops only if its flowers are pollinated (Eisen *1897*, Condit *1932*, *1938*). The 'Kadota' cv. is a common type that will produce fruit parthenocarpically, but if pollinated its seeds will develop, a feature that is desired if the figs are to be dried, but undesired if they are to be preserved (Condit *1927*).

Pollinators

Smyrna (and second crop San Pedro) figs are pollinated exclusively by the hymenopterous fig wasp (*Blastophaga psenes* (L.)), which overwinters in the caprifig fruit (fig. 111). The use of this wasp is the oldest form of man-manipulated insect pollination, a system referred to as caprification. With the exception of date pollination (see "Dates"), this is the oldest form of controlled pollination in plants (Condit and Enderud *1956*). According to Betts (*1940*) the part these insects play in fertilizing the fig was known in 1782, just 11 years before the noted Sprengel published his treatise on insect pollination. This relationship was later challenged and "proved a myth" by the Italian government (Reasoner *1891*). In 1887, when the astute Gustav Eisen announced in Fresno, Calif., the necessity of importing these wasps, he was "hooted down and some of the mob whistled" (Condit and Swingle *1947*), but the need for these insects is now an undisputed fact.

It was common knowledge that Turkish fig growers since time immemorial had tied a few caprifigs on a string at a certain time of the year and hung them in their fig groves to assure a crop (Condit *1920*). When Smyrna figs were brought to California, however, they failed to produce; and when the wasps were brought over and released, they failed to winter over. After 20 years of research, sometimes including intrigue, astute observation, patience, and diplomacy, caprifig plants infested with these wasps were successfully established

in California and satisfactory pollination and fruit set was achieved (Eisen *1891*, Howard *1900*). Then, however, a second problem arose. Growers had difficulty in obtaining Caprifig fruit infested with wasps at the desired time, and in disgust many began the destruction of their orchards. To assist them, the USDA began a program of releasing such figs to growers by the box for pollination purposes (Rixford *1918*).

The systematic distribution of the infested caprifigs tended to stabilize the fig-growing industry, but after a time the growers found that the wasps were the cause of a rot condition in the figs, called endosepsis. To prevent the damage by this contamination, the rearing of the wasps in the laboratory was developed, and wasps could be induced with proper heat control to emerge at desired times into sterile containers where they could live for a couple of weeks (Smith and Hansen *1927*, Metcalf and Flint *1962*). Now, when the endosepsis problem arises, the adult wasps are laboratory reared and delivered to growers at specified times in sterile containers (Bishop *1952*). Most growers, however, continue to maintain their own source of caprifigs and two or three times during the pollination period suspend, in a perforated bag or wire basket in the orchard, a few of the caprifigs with wasps ready to emerge.

The wasps overwinter in the immature stage in the gall flowers of the caprifig. The wingless and practically blind male wasp is the first to emerge as an adult. He crawls about within the caprifig, finds a gall flower containing a female still in her cocoon, gnaws a hole through the top of the cocoon then another hole through the side, inserts his abdomen, and fertilizes the female (Sisson *1970*). The males lives only about a day, does not leave the fruit in which it emerged and consumes no food. The female emerges from her cocoon shortly after copulation and immediately leaves the fruit.

As she passes the pollen-laden male flowers near the fig opening, her moist body becomes coated with pollen. She also has the ability to carry 2,000 to 3,000

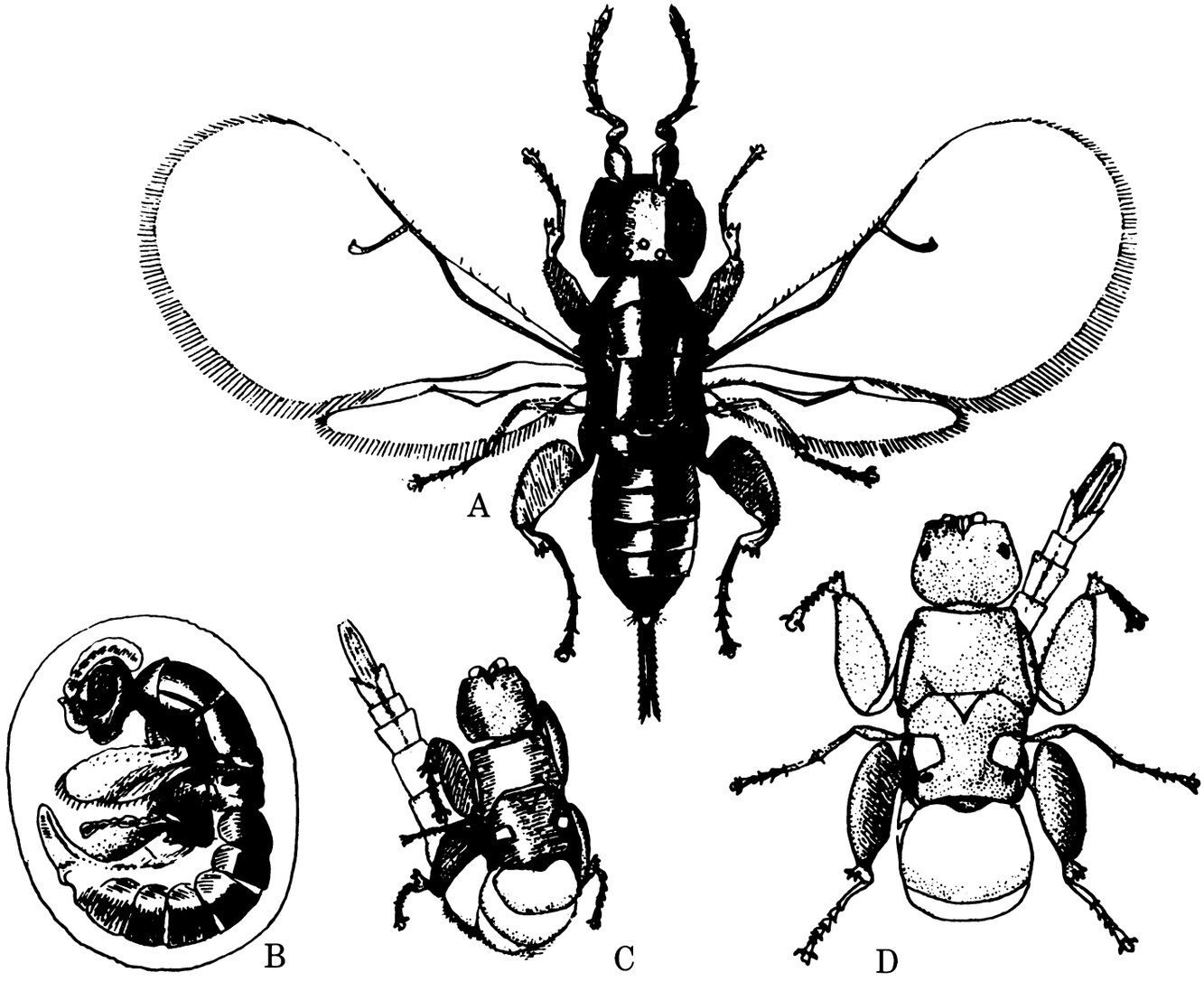

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FIGURE 111.— Fig wasp greatly enlarged. *A*, Adult female; *B*, female still in gall; *C* and *D*, males.

pollen grains in her corbiculae (Ramirez *1970*). She then begins a search for other figs in which she can oviposit. If she finds a caprifig, she enters the small opening, inserts her ovipositor into the short style of a gall flower, and deposits an egg near the ovary.

If she enters a Smyrna fig, she searches about for short-styled gall flowers, but finds only the long-styled ones in which she is unable to oviposit. In her search, she accidentally leaves pollen on the stigmas and fertilization results by the "mess and soil" principle (Faegri and van der Pijl *1966**) rather than the more precise method of pollination caused by bees. In the caprifig, she finds gall flowers and deposits 200 to 300 eggs, then she dies. If she emerges in a Smyrna fig grove, she searches about unsuccessfully for gall flowers, cross-pollinating the flowers in her attempts until she dies of exhaustion.

The symbiotic relationship of the fig and the wasp, each dependent on the other (Ramirez *1969*) similar to the yucca moth and the yucca plant (Riley *1878*) is a strange and difficult to explain phenomenon in the plant-insect relationship.

Pollination Recommendations and Practices

The number of wasps released in Smyrna fig groves depends upon the size of the tree. Simmons and Fisher (*1947*) recommended one caprifig (yielding 200 to 300 wasps) per 18 ft^2 of fig-bearing tree surface, (about five figs for a tree 10 feet in diameter) for highest yield of 'Calimyrna' figs. Because the wasps tend to remain mostly in the tree where they emerge, the infested fruit is placed in about every other tree. An estimated three to five wasps are needed for each fig harvested. The female usually loses her wings when struggling to enter the fig opening, and they remain stuck among the opening scales. A good indication that pollination is adequate in the orchard is the presence of these tiny wings, protruding like a ring of feathers from this hole in the fig.

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FLAX

Linum usitatissimum L., family Linaceae

Flax is grown in the United States for its seed from which linseed oil is pressed and used primarily in paints. The byproduct, linseed meal, is fed to livestock. More than 2.6 million acres of flax were harvested in the United States in 1969, with an average yield per acre of 750 pounds. There were 1.5 million acres in North Dakota, 652,000 in South Dakota, 388,000 in Minnesota, 100,000 in Texas, 17,000 in Montana, and 3,000 in California. Production per acre within the States varied from 2,240 pounds in California to 700 pounds in North Dakota. The value of the crop was $92.9 million.

In addition to flaxseed, the plant is grown in other countries for its fibrous stalk from which linen is made. Economical U.S. production of fiber flax for linen is not feasible.

Plant

Flax is a cool-weather crop but grows in warmer climates if it is planted in the fall and harvested at the beginning of the next summer. The plant is a slender annual with small linear leaves and a crown of flowers that later develop into seed pods (fig. 112). The seed flaxes are 15 to 30 inches tall, more branching, and produce more seed than the taller (30 to 48 inches) fiber flaxes.

An average plant produces two to six five-celled pods or capsules, although capable of producing many more. The pod normally produces two seeds in each cell and averages 8.6 seeds per pod (Kozin *1954*).

The seeds are planted at the rate of 40 pounds per acre, which provides a high-density plant population necessary for maximum seed production.

Inflorescence

Flax flowers are borne on the branch terminals in many-flowered panicles. The petals may vary from white through hues of blue, pink, or lavender (Bailey *1949**). The five petals of the flower unfold at or soon after sunrise, depending upon the temperature, and shed before noon on clear warm days. Flowering continues for several weeks, depending upon soil moisture, but the peak occurs at the end of the first week. New flowers open each day (Knowles et al. *1959*).

The five stamens are attached to a fleshy ring at the base of the flower (fig. 113). This ring secretes nectar from five small flat pits on its outer side opposite each stamen (Müller *1883**). The petals are also attached to this ring, alternating with the stamens. They narrow suddenly at the base leaving a round opening between the bases. The anthers of most cultivars are level with the stigmas on the five erect styles, but in some the styles are shorter and in others longer than the stamens (Yermanos and Kostopoulos *1970*).

There are four types of flowers in our cultivated flax: the common funnel form, disk shaped with large flat petals, star shaped with narrow in-rolled petals, and tubular flowers.

The flowers are hermaphrodite and slightly protandrous (Eyre and Smith *1916*), except for the pollenless male-sterile selections.

Flax provides a small amount of both pollen and nectar for honey bees, the degree of visitation and the material collected apparently depending upon the area and competing floral sources. For example, Scullen and Vansell (*1942*) considered flax a weak source of both pollen and nectar. Alex (*1957*) concluded that the bees collected only pollen, and Smirnov (*1956*) said they collected chiefly nectar. Pellett (*1947**) stated that numerous bees are found on flax only where there are a large number of colonies in the vicinity.

FIGURE 112. Seed flax in bloom.

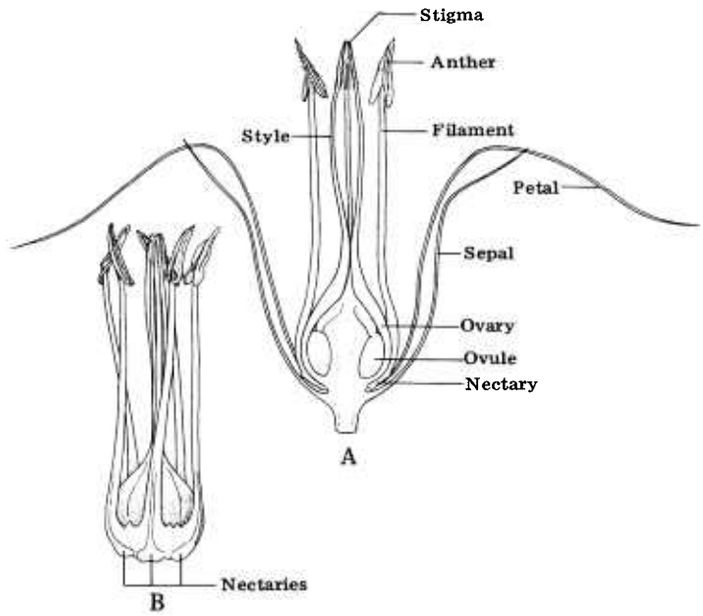

FIGURE 113.—Flax flower, ×3. *A*, Longitudinal section; *B*, flower with perianth removed to show nectaries.

Smirnov (*1956*) stated that honey bees visited the blossoms from 7 a.m. to 1 p.m., with most intense visitation between 8 and 11 a.m. He concluded that, because the petals shed so easily soon after they open, particularly when a bee alights upon one, the bee "learns" to alight below the calyx and extend its proboscis between the petal bases from below to obtain the nectar. Such visitation contributes nothing to pollination, the contribution coming only before the bee adapts the new collecting stance.

Pollination Requirements

Flax is considered to be normally self-pollinated although some crossing (1 to 6 percent) occurs (Dillman *1938*, Dillman and Stoa *1935*, Dillman and Goar *1937*, Masuo *1958*, Robinson *1937*), mostly among the large flowered types. Rubis (*1970*) worked with a male-sterile line having disk-form flowers, and stated that he obtained practically no cross-pollination of the male-sterile lines with lines having tubular flowers; however, good seed set was obtained, indicating heavy cross-pollination, with other lines that had large disk-form flowers.

Self-pollination is influenced by the position of the anthers in relation to the stigmas. If the anthers are above or below the level of the stigmas, there is increased opportunity for cross-pollination (Yermanos and Kostopoulos *1970*). In most commercial cultivars, however, they are on the same level. For a brief period after this type of flower opens, there is space between the anthers and the stigma. This permits cross-pollination to occur if foreign pollen is brought to the stigma. Whether or not cross-pollination occurs, the stamens soon bend inward so their pollen touches the stigma and self-pollination results. Flax is another example of plants that offer opportunity for cross-pollination then provide for selfing for survival of the species (Müller *1883**).

Several tests have shown that bee pollination improves seed yields in fiber flax. Bezdenezhnykh (*1956*) in Russia reported that honey bees in cages increased seed production of fiber flax 22.5 percent over plants in cages without bees. Gubin (*1945*) also studied the effect of bee pollination of fiber flax in Russia and reported that bees increased seed production 22.5 to 38.5 percent. Luttso (*1957*), also in Russia, reported that bee pollination increased seed production by 29 percent, the number of seeds per capsule by 18 percent, and the weight per seed by 11 percent in comparison to fields without bee pollination. Likewise, Smirnov (*1956*) showed a 19 percent increase in the number of seeds per capsule, a 22 percent increase in the total weight of seeds, and a 2.2 percent increase in the weight per seed. He also reported that bee-visited plants set up the crop and ceased blooming earlier than plants from which bees were excluded. The reason for the increased size of the seed in addition to seed number was not explained. Usually, when more seeds are produced by a plant, the size of the individual seed decreases.

The influence of bee pollination on oilseed flax is somewhat different. Hassanein (*1955*) reported that honey bee pollination increased both "quantity and quality" of seeds. However, Pritsch (*1965*) and Alex (*1957*) failed to show any benefit in terms of increased seed production, and insect pollination is generally considered unnecessary on U.S.-grown flax.

Shehata and Comstock (*1971*) discussed the potentials for increased production with hybrid vigor in flax. They obtained an average of 6 percent increase in production with hybrids over the highest yielding cultivar, and they stated that interest in hybrid flax is increasing. For the production of hybrid seed, the pollen must be transferred from the fertile to the male-sterile lines.

Pollinators

Eyre and Smith (*1916*) pointed out that flax pollen is produced only in small quantities and is not the windblown type, so they concluded that cross-pollination was entirely by insects.

Dillman (*1938*) mentioned bumble bees as visitors along with honey bees, and Henry and Chih (*1928*) mentioned honey bees, a "small bee," and thrips, believing that the last-mentioned insects were important agents in cross-pollination in India. Hassanein (*1955*) attributed 90 percent of the crossing in flax to honey bees; Smirnov (*1954*), 26 to 93 percent; and Alles (*1961*), Bezdenezhnykh (*1956*), Luttso (*1957*), and Smirnov (*1954*) concluded that honey bees were the most important agents. When the honey bee collects pollen, it cannot fail to transfer pollen to the stigmas. This is also true when nectar is collected in the normal way.

Pollination Recommendations and Practices

Alles (*1961*) concluded that the number of honey bee visits per flower of fiber flax has a determining effect on flax seed set and weight, but he gave no indication as to how many bees were needed. Kozin (*1954*) reported a sizeable increase in seeds per boll and seed weight when 40 colonies were placed near a fiber flax field, but he did not indicate the size of the field. Also, he stated that there were 226 bees per hectare (90 bees per acre), which seems to be an extremely low population for the number of flowers per acre. Gubin (*1945*) indicated that each flower of fiber flax should receive an average of two honey bee visits. This is the most concrete recommendation for the use of bees on flax. Whether it applies equally to fiber and seed flaxes is unknown.

There have been no recommendations for the placement and use of honey bees as pollinators of seed flax in this country. The evidence indicates, however, that if hybrid seed is produced insect pollinators will be needed, of which honey bees seem to be the best. The number of bee colonies that would be necessary in or around such a field to provide adequate pollination is unknown. Because the plant is not overly attractive to bees, the relative number of colonies needed would be large if competing plants were in bloom. The breeders might devote some attention to the relative attractiveness of cultivars with the thought in mind that if hybrid seed production materializes and bees are utilized the incorporation of lines having greater attractiveness could improve the efficiency of hybrid seed production.

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GOOSEBERRY

Ribes grossularia L. and *R. hirtellum* Michx., family Saxifragaceae

The European gooseberry (*Ribes grossularia* L.) belongs almost wholly to Great Britain. The American gooseberry (*R. hirtellum* Michx.) is the only species of commercial significance in the United States. It is found from Newfoundland to Maryland and west to the Rockies and comprises many cultivars (Hedrick *1938**). Commercial U.S. production consists of about 200 acres, mostly in Michigan and California.

Plant

The gooseberry is a bush-fruit grown for its large berries, which are mostly consumed green in baked pies. It is usually propagated by cuttings as the seeds are open-pollinated, and resulting plants may be quite variable. It is a cool, moisture-loving plant, adapted to cool or cold climates. Production of 300 to 600 bushels (40 lb/bu) per acre is possible (Bailey *1915**, *v. 3, pp. 1201–1760*). Usually, production is limited to a few dooryard plants or at most a few acres. The plant has spines on the woody branches. Severe pruning is necessary to remove excess branches and growth. Little cultivation is required. About 40 cultivars have been listed (Yeager and Latzke *1933*, Berger *1924*).

Inflorescence

In the spring, one to three gooseberry flowers per raceme appear during the flowering period, which lasts less than a month. The calyx tube is round, with the receptacle cup-shaped and about one-half inch across. There are four to five petals, with the same number of stamens attached to the perianth. The ovary is one-celled with numerous ovules. Both nectar and pollen are produced, and both are attractive to pollinating insects (Robbins *1931*).

Pollination Requirements

Yeager (*1935*) stated that, "So far as we know, gooseberries are all self-fertile, hence cross-pollination is unnecessary and only one variety need be grown to get a crop of fruit." He apparently was not distinguishing between self-compatibility and the ability to self-pollinate. Colby (*1926*) also concluded, and apparently for the same reason, that gooseberries can bear fruit without the aid of insects. Robbins (*1931*) stated that insects are the chief agents of pollination. Auchter and Knapp (*1937**) stated, "Practically all commercial varieties of currants and gooseberries are self-fruitful and thus no provision need be made for cross-pollination." Smith and Bradt (*1967**) stated that gooseberries are self-fruitful and self-pollinating. However, Zakharov (*1958*) showed that the percentage of ripe berries, their weight and number of seeds per berry, on the average, was greater in those varieties where bees were working during bloom.

Philp (*1933*) stated that gooseberries and currants are self-fruitful, but they require insect application of the pollen from the anthers to the stigma. Offord et al. (*1944*) stated that seed production depended on insect pollinators, and the flowers of at least four species were self-sterile. (Of 736 self-pollinated flowers not a single mature fruit was obtained, but 621 cross-pollinated flowers within the species set 286 fruits.) They concluded that all seed-bearing fruit of the four species studied, *Ribes roezlii* Regel, *R. nevadense* Kellogg, *R. viscosissimum* Pursh, and *R. glutinosum* Benth. resulted from cross-pollination by insects. "The selfed flowers were pollinated by anthers from within the same protective bag."

Although the above test was performed on different species, there are no data to infer that self-sterility of the cultivated species would be different just because the plant will produce fruit. Apparently, Yeager (*1935*) and Auchter and Knapp (*1937**) believed that because no fruit-set problem arose on isolated cultivars, they were self-fertilizing, when in reality they might have been dependent on insects to carry pollen from plant to plant or anther to stigma within the cultivar. Apparently, insects are of value to gooseberries for maximum set.

Pollinators

Little attention has been given to the pollinating insects on gooseberries, but considering the area in which the plants grow, honey bees should be the best pollinating agents on this plant.

Pollination Recommendations and Practices

There are no recommendations on the use of insect pollinators on gooseberries, and it is probable that where small plantings occur there may be ample pollination. However, the data indicate that if maximum production is desired, maximum pollinator activity should be provided. If there are insufficient local pollinators, they should be supplemented with honey bees.

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GRAPE (INCLUDING RAISINS AND CURRANTS)

Vitis spp., family Vitaceae

The bulk of the grapes produced for the U.S. market are from the many cultivars of the Old World grape, or the "grape of history" (*Vitis vinifera* L.), grown on rootstock of American species resistant to the grape phylloxera insect (Snyder *1937*). Production of table, wine, and raisin grapes in California exceeds by several times that of all of the other States combined. In 1969, California produced 3,600,000 tons of grapes on 457,266 acres. The leading cv. was 'Thompson Seedless' —a raisin, wine, or table grape—with 232,673 acres.

Other important cvs. include other table grapes: 'Emperor' and 'Flame Tokay', and the wine grapes: 'Carignane', 'Grenoche', and 'Zinfandel'. The total production of grapes in all States was 3,902,510 tons, with a value of $273 million. The utilization of grapes was as follows: For wine and grapejuice production, 2,258,757 tons; dried (raisins and currants), 1,015,200 tons; fresh, 557,179 tons; canned, 66,300 tons; and home use 5,084 tons.

Other species of grapes include the only native grape grown commercially, the muscadine grape (*V. rotundifolia* Michx.), the most important cv. being the 'Scuppernong', and the native bunch grape, which have been developed from one or more native species, sometimes hybridized with *V. vinifera*. These more important native species include *V. aestivalis* Michx., the summer or pigeon grape; *V. labrusca* L., the fox grape; *V. lincecumii* Buckl., the post-oak grape; and *V. vulpina* L., the winter grape. Bailey (*1949**) includes *V. labruscana* Bailey, which was derived from *V. labrusca*, and which is the source of the numerous cultivars grown commercially in the northeast. Hedrick (*1924*) stated that more than 2,000 cultivars of grapes are described in American viticultural literature and as many more in European literature.

Plant

The grape is a climbing deciduous woody perennial, with 3- to 6-inch, heart-shaped leaves, inconspicuous panicled flowers, and a cluster of a few to 100 or more spherical or ovoid white, greenish, red, purple, or black fruit (a berry) ¼ inch to over 1 inch in size. In cultivation, the vines are frequently pruned and trained on trellises, 3 to 5 feet high, in such a way that the clusters of fruit can be harvested conveniently, some mechanically. Hundreds of cultivars are grown for different types of wine and grapejuice production, other cultivars are grown for table grape use, or for drying as raisin or currant grapes.

Interplanting of cultivars is necessary for self-sterile cultivars, however, selection for increased degree of self-fertility has eliminated most of the self-sterility. Now most fields are solid plantings, sometimes scions from a single plant.

Inflorescence

The grape flower cluster is a pyramidlike, loosely branched panicle, 1 to 10 inches long, containing up to several hundred inconspicuous greenish florets about one-quarter inch long. The floret usually has five stamens, but the number may range from two to seven (Randhawa and Sharma *1960*), and five green petals (fig. 114). The stamens are about as long as the pistillate column. At the base of the ovary between the stamens are five, rarely six, yellow, fleshy nectaries. Insects are attracted to the flower by the nectar and pollen.

Kerner (*1897*, p. 211*) reported the unusual method of opening of the grape flower. The petals never separate at the top, but are united and serve as a domelike covering for the stamens and ovary. When these organs are mature and ready to function, the petals separate from the flower base, roll up spirally, and remain hanging together for a while like a hood, which is finally thrown off by the tension in the expanding stamens. In midmorning of a warm calm day, these caps fall like a gentle rain beneath the vine. Munson (*1899*) stated that there were three kinds of grape flowers—perfect, staminate, and pistillate.

Knuth (*1908*, pp. 250–253*) stated that *V. vinifera* flowers were complete, the stigma maturing simultaneously with the stamens but remaining receptive after the anthers have withered, making both self- and cross-pollination possible.

Pammel and King (*1930*, pp. 1070–1072*), stated that grape blossoms are visited by bees for nectar and pollen, and when the cap is released, pollen is thrown on the insect. Pellett (*1947**) reported that the nectar yield, in terms of honey production to colonies of honey bees, is not great but that it is of some value. He considered the plant as a better source of pollen than nectar, with honeydew sometimes gathered from the leaves. Sharples et al. (*1965*) studied the pollination of the 'Cardinal' cv. of *V. vinifera* and concluded that bees were attracted to the flowers solely for pollen, with no functional nectaries present. Davydova (*1969*) also reported that honey bees visit grapes primarily for pollen.

Pollination Requirements

The pollination requirements of grapes, somewhat like that of citrus (see "Citrus") are complex and for similar reasons; namely, different species, hybrids, and cultivars are involved. The pollination picture is further clouded by the fact that these have been intercrossed and selected for self-fertility, and that the observations have been reported over a long period of time, from different areas and at different stages in the development of a cultivar. Olmo (*1936*) spoke of one cultivar of *V. vinifera* that was parthenocarpic, being capable of producing fruit without pollination although its pollen was viable.

In general, *V. vinifera* has been considered self-fertile, with the American species ranging from self-fertile to self-sterile (Beach *1892a, b, 1894, 1898;* Booth *1911;* Hedrick *1924*). The muscadine (*V. rotundifolia*) is the most extensively grown example of a self-sterile species (Dearing *1938;* Dickey and Loucks *1938;* Husmann *1916, 1932;* Husmann and Dearing *1913;* Reimer *1910;* Reimer and Detjen *1910*). Although Dearing (*1917a, b*) and Fry (*1968*) reported finding self-fertility in at least three muscadine selections, most cultivars now grown are self-sterile (Magoon and Snyder *1943*). Other self-sterile or partly self-sterile native American grapes include 'Brighton', 'Herbert', and 'Salem' (Kelly *1944*); 'Blue Lake' (Stover *1960*); and 'America', 'Barry', 'Edna', 'Gaertner', 'Last Rose', 'Lindlye', 'Merrimac', and 'Munson' (Magoon and Snyder *1943*).

Beach (*1892a, b*) thought that flowers with recurved stamens could not self but upright ones might self. Dorsey (*1914*) found 11 self-sterile or partly sterile cultivars out of 95 with upright stamens examined, whereas only two of 37 cultivars with reflexed stamens were partly fertile. The others were sterile. This showed that although upright and recurved stamens were not

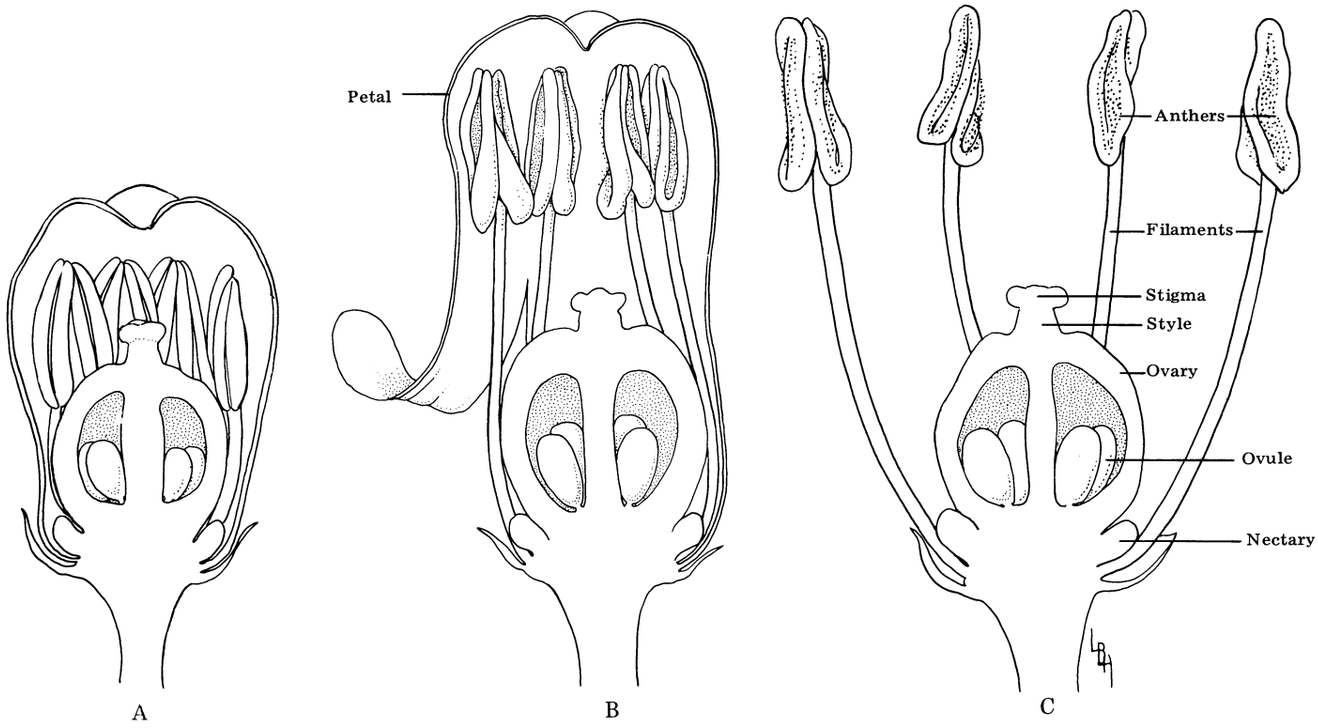

FIGURE 114.—Longitudinal section of the 'Robin' grape, × 20. *A*, Petals, or hood, intact, stamens not lengthened; *B*, petals beginning to loosen, stamens lengthened; *C*, petals fallen, stamens free.

positive proof that flowers were fertile or sterile, they indicated a likelihood—particularly of sterility—of those cultivars with reflexed stamens, with upright stamens being no surety of self-pollination.

In the case of the 'Ohanez' ('Almeria'), cv. of *V. vinifera*, there is no doubt about its self-sterility. Although pollen sprays have been used (Dunne *1942*, Marriott *1950*), the interplanting of other cultivars is considered better (Boehm *1960*). Olmo (*1943*) was convinced that in at least some seasons honey bees were beneficial to this cultivar.

Probably the most thorough test of the pollination requirements of a *V. vinifera* cultivar was conducted by Sharples et al. (*1965*) on the 'Cardinal' cv. (Snyder and Harmon *1951*). In this test, three mature plants were enclosed during the entire period of flowering in each of five 12-mesh-per-inch plastic screen cages containing a colony of honey bees. Five similar cages were used, which excluded all insects except those small enough to enter through the screen. The effect of pollinating insects on these plants was compared with that of five similar open plots.

The test revealed a correlation between seeds and berry weight as follows:

No. seeds per berry	*Mean weight per berry, grams*
0	1.6
1	4.1
2	6.0
3	7.3
4	8.2
5	9.9

The berries in the bee cages and open plots had an average of 1.79 and 1.84 seeds each, compared to 1.65 seeds per berry in the no-bee cage. The clusters averaged 12.1 and 12.3 seedless berries in the bee cages and open plots compared to 16.1 seedless berries in the no-bee cage. This difference, though significant statistically, was not significant economically, in that the primary problem of eliminating shotberries (small, usually seedless berries) was not solved. A satisfactory crop was harvested from all vines. The effect of pollen from other grape cultivars or species was not determined but was proposed for future research.

Gladwin (*1937*) concluded that wind was responsible and that bees played only a minor role. Sharples et al. (*1961*) showed that clipping 1 cm from the inflorescence apex just before blooming was, alone, highly beneficial to quality of fruit set. Golodriga (*1953*) felt that different cultivars of *V. vinifera* reacted differently to pollinating agents.

There are other indications that even *V. vinifera* cultivars are benefited by insect pollination. The 'Ohanez' ('Almeria') cv. is noted for its self-sterility (Boehm *1960*, Dunne *1942*, Hale and Jones *1956*, Magoon and Snyder *1943*, Marriott *1950*), but other cultivars also benefit from cross-pollination (Davydova *1969*), Sosunov *1953*, Steshenko *1958*). Gladwin (*1937*) stated that cross-pollination is not only essential in self-sterile cultivars but that it is also beneficial in self-fertile cultivars. These benefits were substantiated by Iyer and Randhawa (*1965*), Laiok (*1953*), Lavrov (*1956*), and numerous others. Golodriga (*1953*) stressed the importance of selecting the proper pollenizer cultivars for those cultivars that shed or produce inferior berries. There seems to be no published information on

the species and cultivars of grapes that have functional nectaries. The degree to which wind, compared to insects, is responsible for pollination and fruit set, has been established for only a handful of cultivars.

In general, modern grape specialists seem to have assumed that if some fruit set in a cluster in the absence of pollinating insects the plant was self-fertilizing, or wind pollinated, and any difference between "no special pollination problem" and "maximum production of quality fruit" was ignored.

The value of pollinating insects is given no consideration by growers of 'Thompson Seedless' grapes, yet it is well known among growers that cross-pollinated berries are long but self-pollinated ones are round and likely to shed. The degree to which insect pollinators might alter this relationship seems to have been given no consideration.

Pollinators

There is also lack of agreement on the relative value of the pollinating agents on the cultivars of grapes known to benefit from cross-pollination. Einset (*1930*) insisted that insects cannot be depended upon. Gladwin (*1937*) gave major credit to wind and little credit to bees. Knuth (*1908*, p. 250*) and Munson (*1899*) considered both wind and insects of value, although the stigma is not adapted for wind pollination and the amount of pollen produced is small. Husmann and Dearing (*1913*) gave credit to a "small bee-like fly and a beetle," but later Husmann (*1916*) gave the credit to honey bees. Dearing (*1938*) considered the *Halictus* bee excellent but honey bees of sufficient value to warrant placing colonies in larger vineyards of *V. rotundifolia* and *V. munsoniana* J. H. Simson ex Planch. Reimer and Detjen (*1910*) and Olmo (*1943*) gave major credit to honey bees and flies, Steshenko (*1958*) to honey bees, Barskii (*1956*) reported that honey bees increased the weight of grape clusters by 23 to 54 percent, and Davydova (*1969*) associated pollinating insect visitation with increased yield and improved quality of grapes.

Laiok (*1953*) compared bee visitation and grape production of six cultivars in cages with and without bees. In five of the six cultivars, production was greater by 5 to 15 percent in cages with bees. Also, production in an open field decreased as distance from an apiary increased, with 220 kg from 10 bushes at the apiary, 180 kg at 200m, and 150 kg from 10 bushes at 600 m. On the other hand, Randhawa and Negi (*1965*) obtained no difference in set of open and self-pollinated plants of four cultivars.

Dearing (*1938*) considered *Halictus* bees excellent pollinators. Olmo (*1943*) gave considerable credit to the honey bee and a syrphid fly (*Scaeva pyrastri* (L.)). An across-the-board rating of insect visitors to grape flowers doubtless places the honey bee first.

Honey bees visit the flowers for pollen in the forenoon, primarily 9:30 to 11:30 a.m. (Sharples et al. *1965*).

Some growers have objected to the presence of bees near their grapes under the mistaken belief that bees damage grapes, even though this claim has been disproved repeatedly for years (Clay *1886*). If bees are rented for grape pollination they could easily be removed before the grapes are ripe because they do at times feed on the juice of grapes after the skin is broken.

Pollination Recommendations and Practices

The recommendations for pollination of grapes for maximum production of highest quality fruit are not too consistent. In general, breeders have assumed that grapes were either completely self-fertilizing or were cross-pollinated by wind, so that in either case insects were considered of no value. Their assumption may be based in part on the construction of the flower, which would indicate that it is physically capable of transferring its pollen from the anthers to the stigma, or breeders may consider that a plant is self-fertile because bagged blossoms or isolated plants set fruit, without determining the maximum capability to set fruit.

In the case of most American species, and to an unknown degree the European (*V. vinifera*) species, there is evidence that insect visitation ranges from little or no value (Einset *1930*, Sharples et al. *1965*) to that of great benefit (Barskii *1956*, Davydova *1969*, Olmo *1943*, Steshenko *1958*). For example, there seems to be no doubt about the need for insect cross-pollination of the American species *V. rotundifolia*. Dearing (*1938*) recommended the placement of colonies of honey bees in larger muscadine vineyards for maximum production. Husmann (*1916*) also recommended the placement of colonies "here and there about the center" of muscadine vineyards of 100 acres or more. Reimer and Detjen (*1910*) recommended a hive of bees where "a large number of vines are maintained." Armstrong et al. (*1934*) and Armstrong (*1935*) recommended the interplanting of pollen-fertile cultivars within at least 50 feet of muscadine plants.

Steshenko (*1958*) stated that although grapes were normally wind-pollinated, bee visitation increased production. Sosunov (*1953*) and Shpakova (*1961*) agreed and recommended the interplanting of cultivars for maximum set. Davydova (*1969*) also agreed that grapes are wind-pollinated, but that bee visitation, mainly for pollen, increased yield and quality, so he recommended that one colony of honey bees be "appropriately located" per hectare. Barskii (*1956*) also recommended the use of honey bees but believed that one colony per 2 to 5 ha might be sufficient.

There are no recommendations for the use of bees on U.S. grapes. In most instances, cultivars are not interplanted, and large vineyards are likely to be composed of scions of a single plant with no thought given to cross-pollination. The possible value of insect pollinators is given no consideration in grower recommendations. The evidence indicates that there may be a value, to some cultivars by such insect activity (Olmo *1943*). In current agrotechnology, where the grower's net profit is a relatively low percentage of the gross income, even a minor increase becomes economically significant to him. With this thought in mind, a reappraisal of the significance of insect pollination of grapes seems to be justified.

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GUAVA

Psidium guajava L., family Myrtaceae

The guava is grown commercially in India, Brazil, British Guiana, and to a limited extent in Florida, where 2,000 to 3,000 acres are cultivated and many more thousands of acres are wild. The fruit is rich in vitamin C (two to three times the amount in fresh orange juice) and also rich in vitamins A and B with some vitamin G (Webber *1942*). The fruit is consumed fresh or used in the making of jams, jellies, paste or hardened jam, and juice. The greatest commercial use is for jelly (Purseglove *1968**).

Plant

The guava is a shallow-rooted, many branched shrub or small tree 10 to 30 feet in height. The fruit is pale green to bright yellow (fig. 115), 1½ to 4½ inches long, with numerous seeds embedded in the pulp (fig. 116). It is well-known in most subtropical areas of the world (Campbell *1963*). The fruit, 3.7 to 8.8 oz each, may have white, pink, to dark flesh, with 8.8 to 12.5 percent soluble solids and only 0.7 to 7.5 percent of the weight in seeds (Nakasone et al. *1967*).

The plants are usually spaced about 20 feet apart (100 per acre). Purseglove (*1968**) stated that in India a seedling tree 8 to 10 years old will yield 400 to 500 fruit, weighing 140 to 180 pounds, in a year. Grafted or layered trees of the same age yield 1,000 to 2,000 fruits weighing 400 to 700 pounds. Its culture has been described by Ruehle (*1948, 1959*).

Inflorescence

The white flowers, about an inch in diameter, are borne singly or in two- to three-flowered cymes. The stamens are numerous. The ovary has four to five locules with a greenish-yellow style. The capitate stigma extends above the anthers, so that self-pollination without the aid of an outside agency is unlikely (Purseglove *1968**). Hamilton and Seagrave-Smith (*1954*) stated that the flowers are bisexual or perfect and produce an abundance of pollen.

PN-3813

FIGURE 115.—Guava branch, with leaves and fruit.

PN-3814

FIGURE 116.—Variations in size and shape of guava fruit.

Pollination Requirements

Hirano and Nakasone (*1969*) reported that partial self-incompatibility was found in all of the species of *Psidium* studied. Malo and Campbell (*1968*) and Hamilton and Seagrave-Smith (*1954*) found that self-pollination is possible but that cross-pollination by insects resulted in higher yields.

Pollinators

Bees and other insects visit the flowers. Soubihe and Gurgel (*1962*) considered the honey bee to be the main pollinating agent responsible for the 25.7 to 41.3 percent crossing observed between plants. They noted, however, that this degree of crossing varied from plant to plant.

Pollination Recommendations and Practices

There are no recommendations on the use of pollinating insects on guava although the meager information available indicates that they are necessary or at least highly beneficial for maximum production.

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HERBS

Numerous herbs are listed herein under their common names as cultivated crops. Some of these are dependent upon insect pollination, others are benefited. Others, like the drug plants, are grown only in gardens or in the wild. Some of these are also known to be benefited by or dependent upon insect pollination (Lowman and Birdseye *1946*).

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HUCKLEBERRY

Gaylussacia spp., family Ericaceae

There are more than 40 species of U.S. huckleberries. In general appearance, they are so similar to blueberries that the common names are sometimes interchanged (fig. 117). The important difference between the two is in the ripe fruit. The huckleberry has 10 relatively large bony seeds that makes the fruit objectionable for some people to eat, whereas the blueberry may have as many as 65 seeds, but they are small and not objectionable (Darrow and Moore *1962*, Eck and Childers *1966*). Huckleberries are not usually cultivated. The fruit is harvested from wild plants in some areas and sold locally for use in pies.

From an economic standpoint, the value of huckleberries harvested and sold, although unknown, is unquestionably not great. The fruit is of considerable value to wildlife, and the flowers a source of pollen and nectar for bees.

Plant

Three species of huckleberries are of particular interest: the black or common huckleberry (*G. baccata* (Wang.) K. Koch), the box huckleberry (*G. brachycera* (Michx.) Gray), and the dwarf huckleberry (*G. dumosa* (Andr.) T. & G.) (Jannson *1947*).

Where the black or the dwarf huckleberries occur in conjunction with the lowbush blueberry, they are considered a weed and destroyed because of the objectionable large seeds and black fruit (Phipps *1930*).

From a botanical point of view, the box huckleberry is the most famous. Adams (*1949*) described one plant (colony) "estimated to be 13,000 years old, unquestionably the oldest thing alive on earth." (See also Mickalitis *1952*.) The age is apparently more in reference to the colony than to any specific axis cross section.

The black huckleberry occurs from the Atlantic Coast west to Wisconsin and south to Louisiana. It is about 3 feet tall, much branched, with dotted leaves, slender reddish flowers, and black fruit.

PN-3815

FIGURE 117.—Huckleberry bush, with mature fruit.

The box huckleberry forms a low, dark-green carpet 2 feet high, has pinkish flowers, light-blue fruit, and spreads up to 6 inches per year by underground runners.

The dwarf huckleberry is a low plant, usually 1 to 2 feet tall, that bears long, white flower clusters. It yields large quantities of ¼- to ⅓-inch black huckleberries that are used primarily in pies.

Inflorescence

The ¼- to ½-inch flowers of the huckleberry are white to reddish and in axillary racemes. The tubular calyx is five-lobed, with 10 stamens surrounding a single stigma. Nectar is secreted at the base of the corolla. The flowers are attractive to bees for both their nectar and pollen.

Pollination Requirements

The box huckleberry is self-sterile. When cross-pollinated within the clone, only nonviable seed is produced. Viable seed develop only if pollen is transferred from the anthers of one clone to the stigma of another (Adams *1949*). Little is known about the pollination requirements of the black or dwarf huckleberries, but because of the similarity of the blueberry and huckleberry flowers in many other respects, future studies will probably establish that the pollination requirements are also similar.

Pollinators

Honey bees are attracted to huckleberry flowers and are probably the primary pollinating agents under most conditions. Currently, there is no known pollination problem because the plants usually grow in the wild state, and the potential versus actual production as a result of insect pollination is unknown.

Pollination Recommendations and Practices

None.

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JUJUBE, TSAO, OR CHINESE DATE

Ziziphus jujuba Mill., family Rhamnaceae

The common jujube, tsao, or Chinese date, is grown occasionally in the Southern States and California for its edible fruits or as an ornamental. No great importance is attached to this fruit in the United States.

Plant

The jujube is a small deciduous tree that may grow to 30 feet tall. It may have spines at the base of the strongly three-veined alternate leaves. The rather dry, edible, ovoid, orange to brown, ½- to 1½-inch long fruit is similar to a plum or date. It has white flesh and a hard, two-celled stone. The fruit is eaten fresh, in cakes, candied, or used as a dessert. It makes a refreshing drink and is rich in vitamin C (Purseglove *1968**).

Inflorescence

The flowers appear about mid-May at Chico, Calif., and reach their peak within 2 to 3 weeks but may continue sporadically until August. They are small greenish to yellow, in short axillary cymes, with five sepals, five petals, five stamens, and a two-celled ovary with a two-part style (fig. 118).

Ackerman (*1961*), who made a rather thorough study of this plant, stated that the anthers dehisce as soon as the flower opens but that the stigma becomes receptive and nectar secretion starts sometime later (Thomas *1924*), with little fruit set after the first 24 hours.

Pollination Requirements

Ackerman (*1961*) noted that some clones develop fruit from self-pollinated flowers but few set appreciable crops by this means. Such fruit is usually smaller than normal and tends to drop prematurely. He concluded that cross-fertilization between compatible clones was essential for the development of viable seed and the setting of a full crop of fruit.

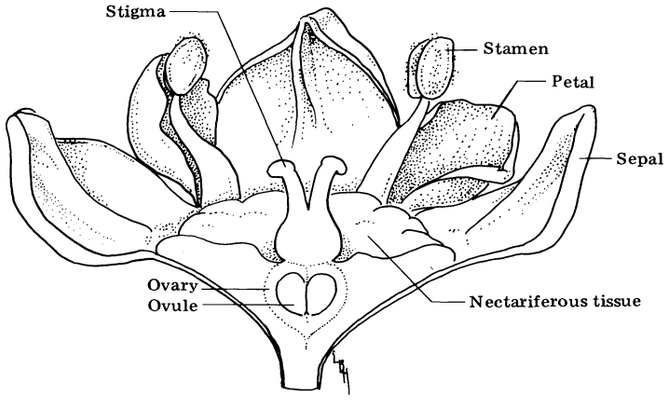

FIGURE 118.—Longitudinal section of jujube flower, × 20.

Pollinators

Ackerman (*1961*) stated that flies and beetles were of no value as pollinators of jujubes. He used honey bees.

Pollination Recommendations and Practices

None.

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KENAF

Hibiscus cannabinus L., family Malvaceae

Kenaf has been grown for centuries throughout the world as a fiber crop. A few thousand acres are grown in Florida for bean poles (Killinger *1969*). Recently, it has been tested as a silage crop and for paper pulp (Killinger *1965*, *1967*). In general, kenaf is grown between 45° N and 30° S latitudes (Purseglove *1968**).

Plant

Kenaf is an erect herbaceous annual, 4 to 22 feet tall (Pate et al. *1954*, Killinger *1965*), with straight and slender green, red, or purple prickly stems. It is photoperiodic, flowering on shortening days of 12.5 hours or less. When grown for seed, 700 to 800 lb/acre have been harvested. The fruit is a capsule of several carpels, each producing several seeds.

When grown for bean poles or forage, the plant, itself, is harvested (Killinger *1967*). About 200,000 poles per acre are harvested when the plant is about 10 feet tall and before it blooms. Only when seed production is desired is the plant allowed to remain through flowering and until the pods are ripe and harvested. Killinger

(*1969*) stated that some cultivars are ready for harvest in early July to early September from seeds planted March 27 to April 5 (120 to 160 days), whereas other cultivars are ready within 60 days, and still other cultivars produce seed and are dead within 100 days after planting.

Inflorescence

The flowers, similar to those of cotton, okra, or the common hollyhock (*Althea rosea* (L.) Cav.), are large (7.5 to 10 cm) with five yellow or red petals with crimson-centers. They usually open just before daybreak, begin to close about midday, and are closed by midafternoon never to open again. Within the corolla, the staminal column, with its short stamens, surrounds the style. The anthers release pollen about the time the flower opens, and the style emerges shortly thereafter. Then, the five-part stigma expands; the lobes become turgid but do not touch the anthers. The corolla closes spirally so that the anthers are pressed into contact with the stigma, and, if cross-pollination has not occurred, self-pollination may result. However, Ochse et al. (*1961**) stated that pollen of the same flower is seldom found on the stigma. Nectar is secreted at the base of the corolla. Nesmeyanova (*1968*) stated that only the nectaries on the outside of the calyx were well visited by bees, but Jones and Tamargo (*1954*) and Tamargo and Jones (*1954*) stated that honey bees visited within the blossom sufficiently to be considered efficient pollinators.

Pollination Requirements

The pollination requirement of kenaf is not too well worked out. Pate and Joyner (*1958*) stated that kenaf has been classified on several occasions as a self-pollinated crop, but that more recently it has been classified as an often cross-pollinated crop. In a hand-pollination experiment, Dubey and Singh (*1968*) observed that some setting began by 11 p.m. and extended to the next 2 p.m., but only between 5 and 9 a.m. did more than 50 percent set. This would indicate that the spiraling action of the closing corolla would likely contribute to perpetuation of the species if previous pollination had failed but would not result in maximum fruit set. Crane (*1947*) (citing Ustinova *1938*) stated that cv. 'Viridis' is entirely self-pollinated while cv. 'Vulgaris' is cross-pollinated 2.6 to 2.9 percent of the time.

As early as 1911, Howard and Howard (*1911*) concluded that the opportunities for cross-pollination are very great; however, studies on pollination of kenaf have dealt mainly with the effects of cross-pollination between strains, with little attention given to the effect of pollination on total production of seed.

Pollinators

Jones and Tamargo (*1954*) concluded that wind is not a factor in kenaf pollen dispersal. A wasp (*Campsomeris trifasciata* (F.) was observed in the field (in Cuba) throughout the flowering period; however, it visited only the extrafloral nectaries on the seed capsule during most of the flowering season. A wild bee (*Exomalopsis similis* Cresson) and a carpenter bee (*Xylocopa cubaecola* Lucas) were seen occasionally in kenaf flowers, but their numbers were too small to be of significance. Jones and Tamargo (*1954*) concluded that the honey bee was by far the most important insect involved in the pollination of kenaf flowers. It visited an average of 1.36 flowers per minute, 20 per foraging trip, and individual flowers were visited by an average of 16.7 ± 1.8 bees per day. The peak of honey bee visitation was between 11:30 a.m. and 2 p.m. No indication was given as to the honey bee colony concentration in the area. Jones et al. (*1955*) recorded a decreasing amount of crossing with increased distance from the plot of marker plants, when five colonies of honey bees were 1 mile away.

No determinations have been made on the effect of pollination on production of kenaf seed. Like its near relative, the cotton plant, kenaf may produce a crop of self-pollinated seed, but possibly at least some cultivars may produce significantly more seed if the flowers are cross-pollinated. This phase in the economics of seed-production should be investigated.

Pollination Recommendations and Practices

Tamargo and Jones (*1954*) concluded that the percentage of natural crossing might be greatly increased if compatible cultivars of similar maturity dates were grown where large populations of honey bees were present. Jones and Tamargo (*1954*) dealing with the same subject, stated that "If the bee population were increased by placing hives of bees around the kenaf field at flowering time, obviously the number of visits per flower could be increased. Likewise the amount of natural crossing could probably be greatly increased."

Other than these rather vague recommendations for placement of colonies of bees in kenaf fields, there are no recommendations for the use of pollinating agents on kenaf.

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KIDNEYVETCH

Anthyllis vulneraria L., family Leguminosae

Kidneyvetch, also known as sand clover or woundwart, is not grown to any appreciable extent in this country.

Plant

Kidneyvetch is a deep-rooted perennial herb about a foot tall. It is a forage plant of some value on poor, light, sandy soil of the more northern latitudes (Graham *1941**).

Inflorescence

The yellow to deep red flower heads are attractive to bees for both their nectar and pollen. The stigma and stamen are enclosed in the sheath of the keel petal. The pressure of a bee visiting the flower squeezes out a string of pollen from the opening in the keel petal. When the pressure is removed, the tips of the anthers return to their former position, and, when pressure is renewed, fresh pollen masses are extruded. At a later stage, the stigma elongates and also projects through the cleft.

Pollination Requirements

Even though surrounded by its own pollen grains, the stigma is unreceptive to them. After the pollen is carried away or no longer viable, the stigma becomes receptive to pollen brought from other flowers. Thus, it is an entirely cross-pollinated plant (Knuth *1908*, pp. 297–298;* Todd *1957*;* Müller *1833*, pp. 172–173*).

Pollinators

Bees are the primary pollinators of kidneyvetch.

Pollination Recommendations and Practices

None.

KIWI

(See "Chinese Gooseberry")

KOLANUT

Cola spp., family Sterculiaceae

Several species of *Cola* are cultivated for the kolanut. Purseglove (*1969**) listed four cultivated species, but van Eijnatten (*1969*) stated that only two were of commercial significance: (*C. nitida* (Vent.) Schott & Endl., which is the main kola of commerce, and *C. acuminata* (Beauv.) Schott & Endl.). The kolanut is native to Africa, with Nigeria the primary producing country. An estimated 140,000 tons were produced in 1960 mostly in Nigeria. This would indicate that something like one-half million acres were involved. A few hundred tons are exported to the United States, where they are used in the preparation of beverages and in pharmaceuticals. In Africa, the kolanut is chewed for its alkaloid properties (caffein, kolanin, and theobromin), which dispel sleep, thirst, and hunger. There seems to be a slight preference for white kolanuts over red ones.

For the above and subsequent discussion, see van Eijnatten (*1969*) and Russell (*1955a, b*).

Plant

The kola tree is a dome-shaped evergreen tree, usually 35 to 50 feet in height. Trees are usually planted from seed, about 20 to 27 feet apart, although vegetative production can be accomplished. Growth of this tropical tree is in flushes. Flowering begins at 6 to 10 years. The fruit matures about 4½ months after flowering. Full fruit production is reached by the 20th year, and the tree may continue bearing until it is 70 to 100 years old. The main harvest period of nuts extends from October

to December, but some nuts may be available throughout the year. The pod is harvested before the nuts are ripe. The follicle is split and the three to six nuts are removed, fermented in heaps for 5 days, washed clean, and stored. They will keep for several months. Average yield is 210 to 250 salable nuts per tree or 12,000 nuts (about 500 pounds) per acre.

Inflorescence

The fetid kola flowers are in several- to many-flowered determinate panicles. The five-sepal, petalless flower is white, with maroon to reddish blotches and streaks emanating from the inner base of the corollalike perianth. Some trees produce only male flowers, but some hermaphrodite flowers are usually on every tree. Usually, the earliest flowers to develop are male; followed by both male and hermaphrodite flowers intermixed. The hermaphrodite flower is 30 to 40 mm across; the male flower, half to two-thirds the size. The male flower is subspherical, the hermaphrodite one is more oval. The hermaphrodite flower produces pollen that will germinate on a proper agar solution but will not fertilize a stigma, so the flower is basically nonfunctional, and should be considered as a pistillate one.

The hermaphrodite flower opens between 4 and 8 a.m. and is apparently receptive only one day, as the majority wither and drop on the second to the fourth day. Naturally, all male flowers shed. When the flower opens, the anthers dehisce a sticky pollen, which largely remains on the anthers. This would indicate that the kola flower is insect pollinated. No reference was found indicating that kola flowers secrete nectar, but since flies are attracted to the flowers quite probably nectar is secreted.

Pollination Requirements

The evidence indicates that pollen must be transferred from the staminate or male flowers to the hermaphrodite or basically female flowers. The pollen must be transferred as soon as possible after the flower opens. Many trees, and probably the majority of them, are self-incompatible, in which case the pollen must come from flowers of other appropriate kola trees.

Considering the large number of flowers on a tree that must set fruit to produce an excellent crop, and considering that the pollen must come from other compatible plants and within a limited time period, it becomes evident that pollen must be transported rather freely between trees.

Pollinators

The pollen of kola trees is not wind transported. Van Eijnatten (*1969*) said that pollination is probably affected by insects, but indicated that relatively few insects visit the numerous flowers. Purseglove (*1968**) stated that the flowers have a fetid odor that attracts flies, which may be the pollinating agent. Cecidomyids, mirids, and ants have also been mentioned (Anonymous *1957*). Nothing is said about bee visitation to these flowers. It is of interest that this is a relatively self-sterile crop, and van Eijnatten (*1969*) stated that, "The low productivity of many kola trees has been a thorn in the flesh of the farmer wherever this crop is cultivated in West Africa." The saturation pollination with one to several honey bee colonies per acre, forcing the bees to forage on what may be a relatively unattractive source of pollen or nectar, might remove that objectionable "thorn in the flesh." It might lift total production to a new plateau or cause a more concentrated set of fruit at a definite period.

Van Eijnatten (*1969*) stated that controlled pollination, apparently referring to hand pollination, could increase the yield ten- to twentyfold. This should appear to be sufficient incentive for the kolanut industry to explore the utilization of honey bees or other bees in the pollination of this crop.

Pollination Recommendations and Practices

None.

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KUDZU

Pueraria thunbergiana S. & Z. Benth. [=*P. lobata* (Willd.) Ohwi], family Leguminosae

Kudzu is a perennial, coarse, rapid-growing, long-lived twining plant. It is grown in the southeastern States for forage, pasture, soil improvement, and erosion control. Two decades ago, 300,000 acres were planted to kudzu in this area (Wheeler *1950*). It is most frequently used along roadsides for erosion control (fig. 119). Interest in kudzu has decreased in recent years, probably because the species is not tolerant to grazing, and because its tendency to spread and crowd out other plants makes it undesirable in many places.

Plant

Kudzu has roundish trifoliate leaves, 2 to 4 inches across, and runners that may reach 60 feet in length. These runners frequently engulf large standing dead

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FIGURE 119.— Kudzu, growing upon a steep slope, controls erosion and affords grazing for cattle.

trees. Kudzu can be established by seeds, cuttings, or young transplants. The crowns of old plants will transplant, but their size and bulk limit their use. For this reason, seeds are preferred. Its propagation has been somewhat handicapped because of its poor seed setting ability (Dabadghao *1949*).

Inflorescence

Kudzu flowers are purple to reddish, and are produced in relative abundance in some areas and on some vines (fig. 120), but many that open will wilt and shed. Turner (*1959*) stated that flowering is unknown in Texas. Mes (*1953*) stated that in Africa flowering occurs during the second season, and the flowers produce a sweet aroma. E. A. Hollowell (personal commun., 1971) stated that the plant must climb before it flowers. Wheeler (*1950*) stated that large purple flowers are produced in relative abundance, and precede the clusters of densely hairy pods, which are about 2 inches long and with usually few or no seed. Tabor (*1942*) noted that more seed set on old vines. Dabadghao (*1949*) also studied seed setting and recorded the appearance of flowers at 3 years of plant age. Mes (*1953*) stated that ripening required 2½ to 3 months after the flower opened and that pollen was on the stigmas of some of the flowers that shed. Mes (*1953*) also noted that fruit setting took place at intervals on all inflorescences simultaneously, followed by a general period of flower shedding. He stated that when the wings and keel are depressed by the weight of a bee, the style, stigma, and anthers emerge through the gap at the tip of the keel; when the weight is removed they recede into the keel. The stigmatic surface is slightly above the top of the anthers. The stamens are all the same length. Pollen is shed when the flower opens.

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FIGURE 120.—Kudzu vine with flower clusters.

Pollination Requirements

Wheeler and Hill (*1957**) noted that three to five seeds per pod frequently mature, but there may be as many as 12. Mes (*1953*) caged a number of inflorescences and all flowers shed; he concluded that cross-pollination is necessary. Wheeler and Hill (*1957**) concluded that a way will eventually be found to produce seed commercially, then the demand will increase. It would seem that if a method can be found to properly handle the pollination of this crop, then increased seed production will result.

Pollinators

Bees are the only insects mentioned as pollinators of kudzu.

Pollination Recommendations and Practices

Although planting seed is preferable to setting young plants or cuttings, the scarcity of seeds precludes this. An appropriate bee population might enable seed production to be practical, but no such usage has been developed. No recommendation currently exists on the use of insect pollinators on this crop.

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LAVENDER

Lavandula spp., family Labiatae

Lavender is grown primarily for its aromatic oil. Cultivation is in southeastern England, and in the Mediterranean area, especially in southern France. Barbier (*1963*) stated that the genus *Lavandula* is represented in France by three species: *L. latifolia* Medic., *L. stoechas* L., and *L. vera* DC., and by a series of individuals differing considerably from one another and referred to as "lavandins." Lavender should be cut for harvest at the last stage of blossoming (Barbier *1958a*).

Plant

Lavender plants are shrubs about 3 feet tall, with ½- to 2-inch linear leaves on numerous stems and branches. The branches terminate in 2- to 10-flowered whorls on tapering spikes.

Inflorescence

The opening of the florets on a spike lasts for over a month. Opening occurs primarily in the morning. The stamens and style of a flower are enclosed in the bilabiate corolla. Nectar is produced in the corolla at the base of the ovary. At flower opening, the anthers unfold exposing pollen on their upper surfaces. The stigma, however, remains in the immature stage, not even reaching to the middle of the corolla tube, so that insects removing pollen cannot pollinate it. Later, the stamens fade, and the style elongates to 1½ times its original length. The stigmatic lobes then diverge and are receptive to pollen, but the pollen from the same flower has already been removed by insects. If the corolla is visited by bees, it fades in 2 to 2½ days; but if not visited, it will persist 10 to 12 days (Knuth *1909*, p. 246*, Barbier *1963*).

Pollination Requirements

Pollen is shed and removed from the anthers before the stigma is receptive, but the stigma may elongate sufficiently to make contact with other pollen-laden anthers and selfing may result (Knuth *1909*, p. 246*). However, Barbier (*1963*) stated that bee visits cause an increase of 16 to 20 percent in yield of essential oils of lavandins, and a temporary increase followed by a heavy drop in yield of the lavenders, the latter being linked to the ripening of the seed. Barbier (*1958a*) deduced that a hormone in the pollen causes the withering and seed initiation, which, "since the lavender is sterile," leads indirectly to the formation of more oil.

Pollinators

Honey bees freely visit flowers of lavender and are the most effective pollinators. Barbier (*1958b*) considered the benefits to bees and lavender reciprocal; lavender is an excellent source of high quality honey, and through its foraging activity the bee induces a noticeable increase in the yield of oil.

Pollination Recommendations and Practices

Barbier (*1958c*) stated that although both beekeeper and lavender grower benefit from bee activity on the blossom, it is to the lavender grower's benefit to attract bees into the plantings.

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LEEK

Allium porrum L., family Amaryllidaceae

Leek, the national flower of Wales (Patton *1968*) (see "Onion"), is another minor crop. Only a few acres are devoted to seed production.

Plant

The leaves of the biennial leek are flat, solid (pithy),

and thick. The bulb is only slightly swollen, giving the stem and bulb a tubular appearance. 'Large American Flag' is the most popular cultivar (Knott *1949*, Patton *1968*). The growing of leek seed is well suited to the mild climate of Vancouver Island, British Columbia (Adamson *1960*). It is mild in flavor and is used both raw and cooked, similar to onions.

Inflorescence

The seedstalk is 3 to 4 feet tall, terminated by a single umbel to 4½ inches across, and contains several thousand bell-shaped florets (Hawthorn and Pollard *1954**). The flowers are protandrous, the inner three anthers dehiscing first, then the outer ones, after which the style elongates and the stigma becomes receptive (Knuth *1909, p. 445*).

Pollination Requirements

Apparently similar to onions.

Pollinators

Honey bees, bumble bees, "bees," flies, and "insects chiefly" have been mentioned as pollinators (Hawthorn and Pollard *1954**, Jones and Rosa *1928**, Minderhoud *1951*, Sanduleac *1961*). Sanduleac (*1961*) stated that bees increased the seed crop 8 to 10 times.

Pollination Recommendations and Practices

None.

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LESPEDEZA

Lespedeza spp., family Leguminosae

Lespedeza is a crop of major importance in southeastern United States. Roughly 164,000 acres were grown for seed production in 1970, producing 36.8 million pounds of seed, valued at $5.2 million. Slightly more than 2 million tons of hay, valued at approximately $50 million, were produced in 1968, the last year the USDA Agricultural Statistics reported on the acreage of this crop.

Lespedeza is grown for hay and pasture, soil improvement, erosion control, seed, and its benefit to wildlife (game birds and deer).

Two types of lespedeza are grown—annual and perennial. The annuals, which are the most important (McKee *1948*), include 'Common' and 'Kobe' (*L. striata* (Thunb.) H. and A.) and 'Korean' (*L. stipulacea* Maxim.) (Elrod *1954*). The most common perennial is 'Sericea' (*L. cuneata* (Dum.) G. Don) also known as shrub lespedeza (fig. 121). Three other perennial or shrub lespedezas, grown to a limited extent, are *L. bicolor* Turcz., *L. intermedia* (Wats.) Britt., and *L. japonica* Bailey.

Plant

The lespedezas are recognized by the small trifoliate leaves, ¼ to ½ inch long, the individual flowers, and the one-seeded jointless pods. The annual lespedezas are often confused with hop clover although there are important differences. Hop clover seeds germinate in the fall, and the plants stay green throughout the winter and then die in early summer. Lespedeza seeds germinate in the spring, and the plants grow slowly until about the time hop clover dies. Also, the flowers differ in color (Essary *1921*, Kinney and Kenney *1925*).

The plants are slightly spreading to erect, depending upon the thickness of the stem, and from a few inches to several feet tall, depending upon the species. The

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FIGURE 121.— Dense growth of 'Sericea' lespedeza, which provides forage and cover for wildlife.

annuals grow to a height of 5 to 36 inches, depending upon soil moisture and fertility. The bush lespedezas reach 5 to 7 feet. At maturity, the leaves on Korean lespedeza turn forward so the branch tip resembles a cone (McKee *1940*). In general, the growth habits of the annual lespedezas are like alfalfa (Pieters *1939a*). 'Korean' lespedeza flowers are borne at the end of the branch, 'Common' flowers are borne all along the stem.

Lespedezas are drought-resistant, warm-weather plants. The hay contains less moisture when cut than alfalfa or clover, and can often be removed from the field after 1 day (Wheeler *1950*). McKee and Pieters (*1937*) stated that only one species, *L. striata*, has been long known to agriculture.

Many cultivars of lespedeza exist. Probably the most extensively grown cvs. are: 'Kobe', 'Tenn. 76', 'Harbin', 'Rowan', 'Summit', and 'Iowa Six' (Henson and Cope *1969*). Seed production is limited to the southern part of the lespedeza region.

If seed is to be produced, one very early cutting of hay may be removed first, then 100 to 400 pounds of seed are harvested although as much as 1,500 pounds have been harvested (McKee *1940*). If grown only for hay, about 1.5 tons per acre are harvested.

Inflorescence

The flowers of the lespedezas are of two types: petaliferous (or chasmogamous) and apetalous (or cleistogamous). In the latter, the petals never unfold, so the flower has the appearance of remaining in the bud stage and in which only self-fertilization takes place (Pieters *1934*). This characteristic, first noted by Torrey and Gray (*1840, pp. 366–369*), has been studied by various workers. In each type of flower, the ovary has only one ovule. The petaliferous flower is similar to the pea flower—small (¼ to ½ inch) with blue to purple petals. The flowers are conspicuous in the shrubby species (fig. 122) but are inconspicuous in most of the herbaceous perennials or annuals (McKee *1948*). The apetalous flowers are all inconspicuous.

Hanson (*1953a*) stated that anthesis or opening of the petaliferous flower occurred from 7 to 10 a.m. The flower is open most of the day, closes before night, and generally does not reopen. In these flowers, the filaments of the nine stamens are fused throughout most of their length. The style extends beyond the anthers, permitting cross-pollination. In the apetalous flowers, the style is J-shaped (Clewell *1964*), so that the stigma touches one or more anthers and selfing can occur. Hanson (*1953b*) stated that the ovary is receptive to fertilization 1 or 2 days before anthesis.

Nectar is apparently secreted at the base of the corolla in the petaliferous flowers because bees visit them freely for both nectar and pollen (Mooers and Ogden *1935*, Van Haltern *1936*, Graetz *1951*, Stitt *1946*).

The reason for the development of the two kinds of flowers on lespedeza is unknown. Hanson (*1943*) concluded that temperature is a strong factor because most of the flowers were apetalous on plants grown at 70° F, but were petaliferous on plants grown at 80°. He was of the opinion that other factors also had an effect. There seems to be no information indicating that bees ever visit the apetalous flowers.

Pollination Requirements

Bohart (*1960**) reviewed the pollination of the forage legumes and stated that the effect of insect pollinators on seed yields of annual lespedeza has apparently never been investigated. McKee and Hyland (*1941*) also indicated that there was no information on natural crossing in lespedeza. There is, however, some information on the influence of insect pollination on some of the species.

Stitt (*1946*) recorded 61.4 to 80.9 percent (average, 70.4 percent) cross-pollination in 'Sericea' which he

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FIGURE 122.—Flowering branch of bush lespedeza (*Lespedeza bicolor*).

attributed to the abundant activity of bees. Graetz (*1951*) showed that *L. bicolor*, *L. japonica*, and *L. intermedia* must be insect pollinated to produce a good seed crop. He stated that 'Sericea' has some flowers that depend on insects and others that self. Donnelly (*1955*) showed that offspring of 'Sericea' petaliferous flowers produced 25 percent more dry herbage and 40 percent more seeds than the self-pollinated apetalous flowers.

Cope (*1966a*, *b*) showed that some 'Sericea' flowers are cross-pollinated by bees and proposed a breeding program of several consecutive generations of intercrossing for more productive plants. Although he did not go into detail about bee populations on the plants, he noted that 1963 was a poor seed production year for lespedeza, and, correspondingly, the percent crossing was the lowest in years. He recognized the need for bees and conjectured that the "natural bee population" was no longer sufficient to maintain the high level of crossing reported for 'Sericea' two decades ago. He did not consider supplementing the local population by bringing honey bee colonies into the area.

Pieters (*1939b*) stated that *L. striata* and *L. stipulacea* are believed to be self-pollinated. There the matter seems to have rested without further study.

The answer may lie in the fact that honey bees are not strongly attracted to these species (Pellett *1947**), and beekeepers make no effort to place their colonies near lespedeza fields. How the bees might act on the flowers under saturation distribution of colonies, such as is used in the pollination of alfalfa and some other crops, is unknown. The data indicate that floral visitation could be obtained on annual lespedezas if this were sufficiently desired. A study of the beneficial effect of bees on seed production of this crop would be most interesting and is needed.

Pollinators

Graetz (*1951*) gave credit to the honey bees for setting the seed obtained in his test on *L. bicolor*, *japonica*, and *intermedia*, but noted that when the honey bees were moved away bumble bees freely visited the flowers. Mooers and Ogden (*1935*) stated that bees (presumably honey bees) visited the flowers of 'Sericea' for nectar. Cope (*1966a*, *b*) referred to the "bees" and the "natural bee population," possibly referring to wild bees on 'Sericea'. Stitt (*1946*) spoke of "natural crossing" and of usually abundant bees on 'Sericea'. Van Haltern (*1936*) stated that "bees" visited 'Sericea', *L. bicolor*, and *L. virginica* (L.) Britt., and, because he was writing in a beekeeping journal, he doubtless was referring to honey bees.

Beekeepers have generally observed that the lespedezas are scant producers of surplus honey. 'Korean' is rated as the best of the major species, *L. bicolor* and *L. cyrtobotray* Miq. are always attractive, although not grown on a large scale anywhere, and 'Kobe' and 'Sericea' are visited at times. Abernathy (*1937*) stated that lespedeza honey comes largely from 'Korean' with possibly a small amount from 'Common'. Derrenbacker (*1936*) concluded that bees get little honey from 'Korean'. Pellett (*1939*, *1952*), Taylor (*1935*), Underhill (*1946*), and Watson (*1938*) considered lespedeza only a minor honey plant. Big differences were frequently observed in the populations of the bees on the crop. These differences were associated largely with climate, but location also seemed to be involved.

The evidence indicates that if heavy populations of bees were desired on the commercial lespedezas for pollination purposes they could probably be obtained if honey bee colonies were concentrated in or around the fields. However, the beekeeper would not be compensated for such action in honey storage by the colonies.

Pollination Recommendations and Practices

The only recommendation for the use of honey bees on lespedeza was by Graetz (*1951*) who recommended a minimum of one colony per acre in connection with *L. bicolor*, *japonica*, and *intermedia*. Because the perennials appeared to be more attractive species to bees than 'Sericea', it would appear that if honey bees were used on 'Sericea' a higher concentration would be desired. The specific need or value, if any, of bees on 'Common' and 'Korean' lespedezas should be explored.

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LETTUCE

Lactuca sativa L., family Compositae

Lettuce is a major U.S. vegetable crop grown on 234,440 acres in 1970 and valued at about $223 million. California produced more than half of the crop (146,000 acres) with Arizona second (50,900 acres). About 2,300 acres were devoted to lettuce seed production, mostly in California. About 2 million pounds of seed were imported.

Plant

Lettuce is an annual, grown from seed for its succulent leaves, which form a head that is harvested a few months after the seed is planted. About a month after the head forms, if lettuce is not harvested, the stem within the head elongates and branches to produce the inflorescence, which is 2 to 4 feet high. The seed is produced by the flowers of the inflorescence. From ¼ to 1½ pounds of seed are planted per acre. An acre yields 300 to 800 pounds of seed (Foster and Van Horn *1957*, Griffiths et al. *1946**, Hawthorn and Pollard *1954**), depending on the cultivar and method of harvest. The seeds are planted in rows 18 to 22 inches apart and thinned to 12 to 14 inches in the row. The heads are sometimes mutilated to permit the flowering stem to extrude and elongate.

Inflorescence

This many-branched plant, with numerous leaves near its base, is relatively leafless toward the terminal. The terminal of the inflorescence is primarily a panicle or cluster of yellow flowering heads. Each head is about one-half inch long and is surrounded by a series of overlapping bracts called the involucre. A head contains 10 to 25 florets (fig. 123) that develop simultaneously. The floret ovary is one celled and produces only one seed (actually a fruit called achene), thus a head may produce 10 to 25 seeds (Hawthorn and Pollard *1954**). All of the florets in a head open on the same day, early in the morning, and close shortly afterwards, never to reopen. In some instances, they are only open one-half hour (Purseglove *1968**, Jones and Rosa *1928**, Thompson *1933*), but remain open longer on cool cloudy days, sometimes until 2 p.m.

Flowering on a plant may continue for 2 months or longer. A seed ripens 11 to 13 days after the flower opens (Jones and Rosa *1928**). Seeds left too long on the plant may shatter and be lost. Therefore, if all of the seeds are to be saved, the heads must be shaken over a bag at intervals. Usually, the plant is cut at the peak of seed setting, and the bulk of the ripe seeds are salvaged.

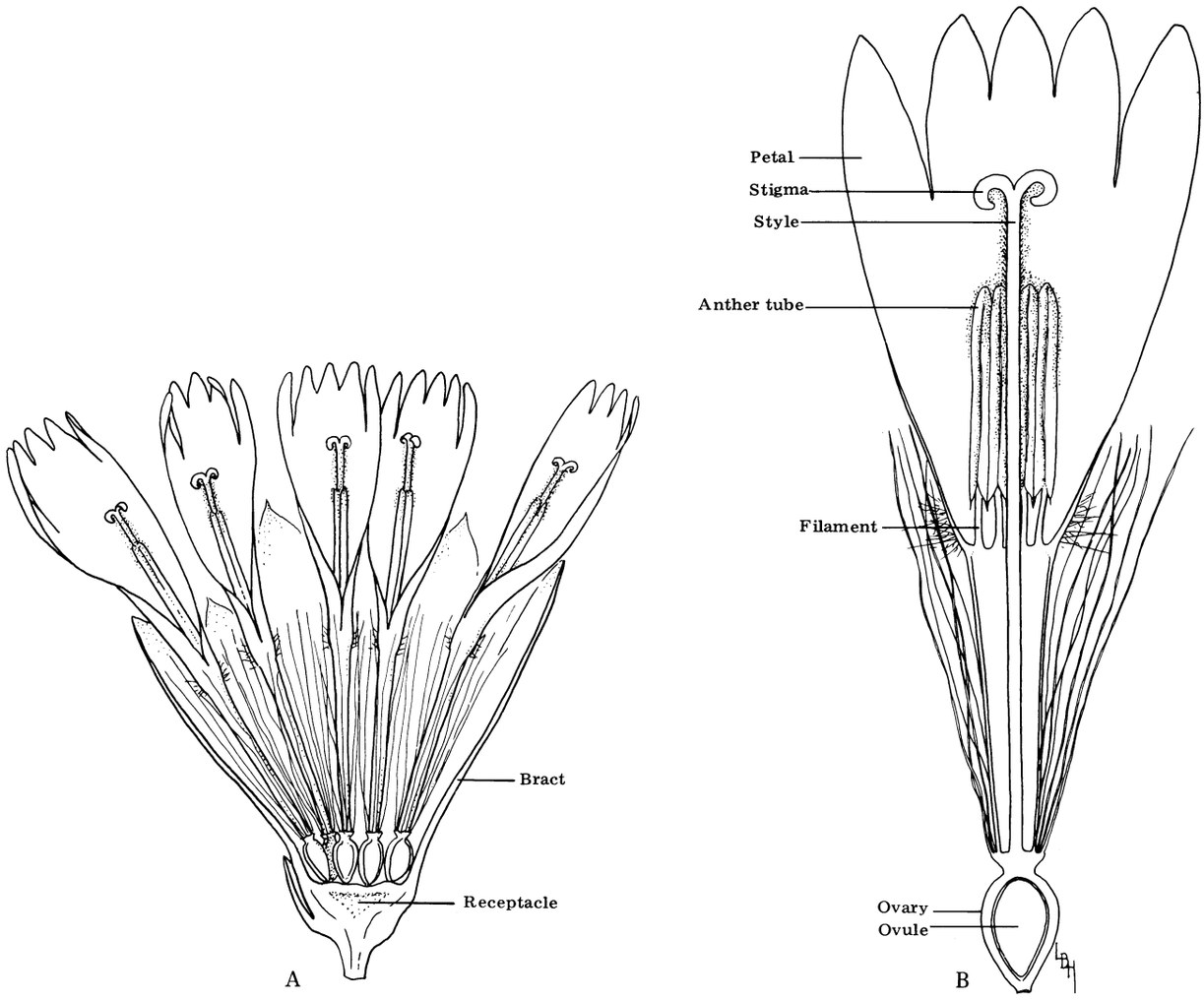

FIGURE 123.—Lettuce flower. *A*. Longitudinal section, × 10; *B*, longitudinal section of one floret, × 30.

The lettuce flower is usually considered to be self-pollinated (Watts *1958*, Thompson et al. *1958*, Oliver *1910*, Jones *1927*, Jones and Rosa *1928**, Hawthorn and Pollard *1954**). The method of self-pollination was described by Knuth (*1908*, p. 690*), who stated that the style emerges through the anther tube and branches when it is about 2 mm above the tube. These two branches curl back upon themselves, usually make contact with pollen grains on the sides of the style, and self-pollination results. The pollen is pushed out of the anther tube by the brushes on the style and is easily available to bees. There is no evidence in the literature that lettuce secretes much, if any, nectar, although Jones and Rosa (*1928**) indicated in a sketch that a nectary exists at the base of the style. Also, Jones (*1927*) and Thompson (*1933*) stated that the bees *Agapostemon texanus*, *Californicus crawford*, and *Halictus* spp. collect "mostly" pollen, indicating that some nectar may be collected also.

Besides honey bees and the above-mentioned wild bees, various other insects have also been reported on the lettuce flowers. Knuth (*1908*, p. 690*) reported "various flies." Watts (*1958*) reported various species of hover-fly and a few butterflies, although he was unsuccessful in getting hover-flies to pollinate heads enclosed in muslin bags. Jones and Rosa (*1928**) mentioned flies and several species of short-tongued bees. Hawthorn and Pollard (*1954**) stated that the flowers are frequently visited by wild bees and other insects. Honey bees have been observed by the author collecting pollen from lettuce flowers in southwestern Arizona.

Pollination Requirements

The structure of the lettuce flower encourages self-pollination and the plants are self-compatible; therefore, seeds can be produced on plants bagged to exclude insects. The pollen is not windblown. However, cross-pollination has been observed (Thompson *1933*, Thompson et al. *1958*, Watts *1958*). To determine if insects affected the transfer of pollen, Jones (*1927*) compared stigmas of flowers exposed to open pollination with those bagged to exclude pollinating insects. He observed 70 bagged flowers, of which 58 had no pollen grains on their stigmatic surfaces, and the other 12 flowers bore only one to seven grains. However, of 70 flowers exposed to pollinating insects, all stigmas had from 4 to 51 grains of pollen present. This showed that

pollinating insects contribute to the effective transfer of pollen to the stigma, within the flower and likely between flowers. As a result, Jones and Rosa (*1928**) concluded that cross-pollination between plants may be much more frequent than was formerly supposed. When Flemion and Henrickson (*1949*) bagged dill plants with insect pollinators present, they obtained 1,000 seeds per umbel compared with only 59 per umbel on plants caged without insects present. If the authors had performed a similar test on lettuce, the test by Jones (*1927*) indicates that they might have obtained similar results.

Furthermore, the discovery of male sterility in lettuce (Ryder *1963*, *1967*) opens the way for production of hybrid lettuce seed, if means can be found to effectively transfer the pollen from male-fertile to the male-sterile plants. So far, the only conceivable way is to have insects transfer the pollen. Without the presence of pollen on the male-sterile plants, the insects must be enticed there by the presence of nectar. Because the flower is only open briefly, the concentration of insects would need to be high for effective cross-pollination.

Pollinators

Although flies, wild bees, and butterflies have been mentioned as visitors to lettuce flowers, none of them are present in commercial lettuce fields in a sufficient quantity when desired to cross-pollinate male-sterile lines necessary for hybrid seed production.

Honey bees can be supplied at any time by commercial beekeepers and honey bees are concerned with collecting nectar. Therefore, they would appear to be the only potential insect at present that would be suitable for pollinating the male-sterile plants.

Pollination Recommendations and Practices

None.

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LIMA BEANS

Phaseolus lunatus L., family Leguminosae

In 1970, 70,630 acres of lima beans were grown for processing. The crop was valued at $14.5 million. USDA Agricultural Statistics no longer reports the fresh market acreage.

Plant

The majority of the acreage is devoted to the bush type of lima beans, an annual with a somewhat woody stem and determinate type of growth, about 2 feet high. The vining, climbing, or pole type may grow to 10 feet and has indeterminate flowering habits, so that fruit is continually produced as long as climatic conditions favor plant growth. With determinate types, most of the inflorescences develop about the same time, which results in a more or less uniform set of fruit. In fact, satisfactory yields are dependent upon obtaining a "capacity set" of pods (fig. 124) during the first 2 weeks of the blossoming period (Hawthorn and Pollard *1954**). Lima beans require a long growing season, but without excessively high temperatures, such as is found along the coast of southern California and in Delaware.

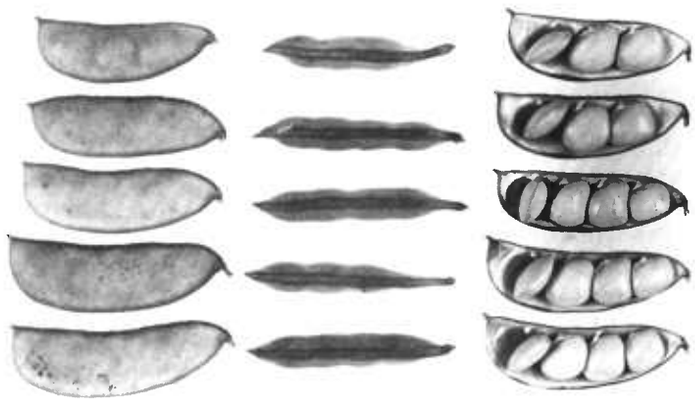

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FIGURE 124.—Lima bean pods.

Inflorescence

The white or cream-colored, legume-type flower of the lima bean is borne at the end of a pedicel on a 2- to 4-inch-long raceme. Usually, only a small percentage of the flowers on a raceme set. Various reasons for this failure have been given, including high temperature and low humidity (Cordner *1933*), improper soil moisture (Lambeth *1950*), and inadequate pollination (Amos *1943*). In the flower itself, the keel is elongated into a spirally twisting beak. The style, which follows the spirals of the keel, is also twisted. It is bearded below the stigma (fig. 125). Knuth (*1908*, pp. 339–340*) stated that the stigma, and a portion of the spirally twisted style with pollen adhering to the brush of hairs, projects from the tip of the keel petal when this is depressed and returns again when the pressure is removed. The anthers surround the style and shed their pollen upon it, but the stigma is never dusted before it is exserted. If the stigma is pollinated by the insect visitor before it is touched by its own pollen, cross-pollination can result.

Anthesis occurs between 7 and 8 a.m. The flower never closes, but the corolla is shed after a few days. Nectar is secreted at the base of the corolla and is the source of a fine quality honey. Bees also visit the plant for its pollen.

Nectar secretion seems to be greatest when plants first come into bloom, and it remains intense for about a week—then tapers off.

Pollination Requirements

Magruder and Wester (*1942*) caged plants and concluded, without taking data, that set of pods on most families under the cloth was as good as, if not better than, on uncovered plants. However, Amos (*1943*) caged plots to exclude bees, and compared production with plots that were shaded, but otherwise left open to bee visitation. He reported about a 30 percent increase in yield due to the presence of bees. He stated that 30 colonies were within 1 mile of the test plots, but the acreage of beans in bloom was not given. Because the observations were made in an area of commercial lima bean production, there could have been hundreds of acres of beans and the honey bee colony per acre ratio

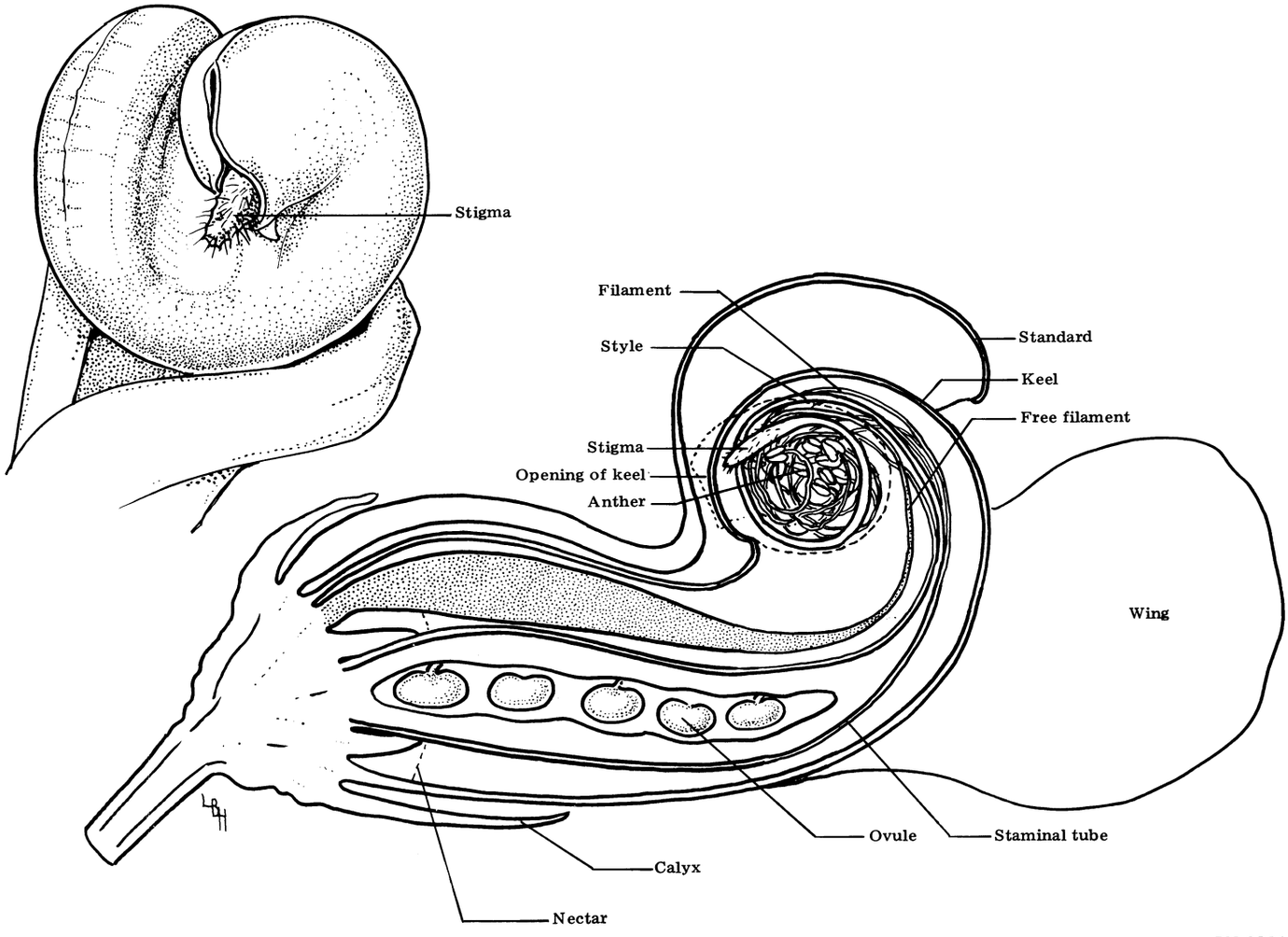

FIGURE 125.—Longitudinal section of 'Murphy' lima bean, ×7. Inset shows tip of keel and stigma protruding, enlarged.

could have been quite low. The increase was in numbers of pods, beans per pod, and total weight of beans. He gave no indication as to the pollinator density in the field.

Wester and Jorgensen (*1951*) found hybrid vigor in all lima bean crosses tested, with production exceeding the best parent in all cases. They stated that a high percentage of crossing was needed. Others have noted that this occurs naturally in some areas now (Magruder and Wester *1940*, Barrons *1939*, Welch and Grimball *1951*, Magruder *1948*).

Allard (*1954*) caged plants with and without bees to obtain a measurement of bee activity in terms of hybrid beans produced. He obtained 2.38 percent hybrids from caged plants visited by bees, and 1.06 percent in cages from which bees were excluded. In open plots dusted with DDT, he obtained 0.21 percent hybrids; but in other plots not dusted, he obtained 1.48 percent hybrids. These experiences and observations indicate that the lima bean, like other beans, is capable of self-pollination but cross-pollination can and does occur. The amount of crossing and its value seem to depend upon the number and species of insect pollinators present or the degree of insect visitation to the crop.

Boswell (*1961*) stated that the lima bean does not benefit from the intervention of insects; however, other works are not in complete agreement.

Pollinators

Allard (*1954*) gave thrips credit for the cross-pollination he obtained. In the light of other research on lima beans, as well as on thrips as pollinators, his data are quite open to question. Incidentally, Mackie and Smith (*1935*) also gave thrips credit for cross-pollinating beans. Jones and Rosa (*1928**) noted that honey bees, bumble bees, and other insects visit the flowers and cause cross-pollination.

Vansell and Reinhardt (*1948*) compared production from caged and open plots and also from areas of high and low general bee activity throughout the flowering period. They noted that 34.4 percent of the flowers set in the area where bee activity was high and continuous, but only 5 to 22 percent set where insecticides were applied. Because of the insecticide applications, most of the colonies were moved away during part of the flowering period, resulting in low pollinator activity. In fact, they recorded one bee per yard of row before the evacuation of the colonies began, but only one bee per 33 yards of row afterwards. Yet even with this low bee activity, they reported a greater yield in both number and weight of beans from open than from the caged plants. Wester and Jorgensen (*1950*) stated that bumble bees and honey bees were responsible for most of the lima bean crossing in the field. Anderson (*1959*) reported that lima bean plants caged with bees set more beans during early blooming period, and the beans were larger than in cages where bees were excluded. He reported that bees visited lima beans in abundance.

Pollination Recommendations and Practices

Despite the rather promising results on the value of ample insect pollination on the increased production of lima beans by Amos (*1943*) and Vansell and Reinhardt (*1948*) and the intriguing study by Drayner (*1956*) on the value of cross-pollination to increased production of subsequent crops, there has been no follow-up. Beekeepers move their bees to lima bean fields to obtain honey crops, and some growers encourage placement of apiaries in the vicinity of their crops, because they feel that the bees "help." The number of pollinators supplied to crops in this manner is probably not sufficient for maximum activity on the blossoms. The use of bees as pollinators of lima beans is not recommended by the States in which these crops are grown, nor are there data to indicate the appropriate pollinator population desired for maximum production. Studies leading to such a recommendation are needed. In the interim, the meager data available would indicate that growers would materially benefit if they arranged for placement of numerous colonies in and adjacent to their lima bean fields at flowering time and took steps to protect these pollinators from harmful pesticides.

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LITCHI OR LYCHEE

Litchi chinensis Sonn., family Sapindaceae

The litchi, or lychee, is grown for its agreeable sweet-acid tasting, white fleshy, juicy, translucent aril, or pulpy covering of its seed, which may be eaten fresh, canned in sirup, or dried to produce "litchi nuts."

The litchi was introduced into Florida in the 1880's but remained only a novelty until 1940 when an association of litchi growers was formed and some 250 to 300 acres were cultivated (Palmer *1956*). Less than half that acreage exists now, due to urbanization and the occasional freezing weather that kills the plants. A few trees are grown in California.

Plant

The plant is a dense, polygamous, oval evergreen tree, which grows to 30 feet high. It is widely scattered throughout the tropics but does well only at higher altitudes. It is propagated vegetatively, 20 to 50 trees per acre. It will grow about anywhere citrus will grow, but young plants are extremely sensitive to cold and require cold protection. The plants will produce as much as 10,000 pounds of fruit per acre. The fruit must ripen on the tree, then is harvested over a 6-week period. The shelf life of the fresh fruit is only 10 to 14 days (Palmer *1956*).

The round fruit, about the size of a large strawberry, is pendant in a loose cluster or panicle of several dozen fruits (Cobin *1952*) (fig. 126). The leathery skin is covered with sharp-tipped tubercles and is usually red when ripe. The seeds are dark brown (Groff *1921*).

The self-compatible 'Brewster' cv. comprises the bulk of the trees in Florida, but it is noted for being a light and irregular bearer. 'Mauritius' is a new and promising cultivar (Young *1966*, Knight et al. *1968*, Campbell and Malo *1968*) but is not resistant to anthracnose.

The lychee tree lives for centuries. Banta (*1952*) reported that two trees in China are said to be 1,200 years old, the largest being 10.5 feet in diameter. Lychee thrives in the Florida citrus belt, but California's climate is generally too dry. Banta (*1952*) stated that a 4-year-old tree will produce 2 to 3 pounds of fruit, and a 12-year-old tree yielded 308 pounds.

Inflorescence

The small (2 to 3 mm), greenish-yellow flowers are in terminal clusters, sometimes a foot long. They are present from mid-February through March. They have no petals, about eight stamens, a two-lobed stigma, an ovary on a short stalk, and one ovule in each of its two or three sections (Bailey *1949**). Grove (*1951*) stated that there are staminate and pistillate flowers. Butcher (*1957a*), however, distinguished three types of flowers: Male or staminate flowers with no functional ovary, which appear first; female or functionally pistillate flowers with anthers that do not dehisce; and imperfect hermaphrodite flowers. Pollen produced on the last type is most viable (Mustard et al. *1953*). In some years, certain cultivars produce only male flowers, and as a result no fruit sets. The reason for this is unknown but should be explored.

A nectary occurs on every flower as a large fleshy crenulate gland within a cup-shaped calyx and to which the stamens and pistils are inserted. Nectar is secreted only in the morning. The nectar is highly attractive to honey bees and flies. Lychee pollen seemed unattractive to wild bees in Florida (Butcher *1957a*, Nakato *1956*). When lychee trees are plentiful, honey bees gather immense stores of high-quality honey (Groff *1943*).

Khan (*1929*) cited two examples to show the floral variation on an individual panicle. On one plant, the panicle began flowering and for 10 days bore only male flowers. The next 11 days, the flowers were mixed (male or female). The remaining 6 days, only male flowers opened. Another panicle had male flowers for 13 days, mixed flowers for 2 days, all female for 2 days, mixed again for 3 days, and all male for the last 7 days. From 20 to 50 percent of all the flowers were functionally female.

FIGURE 126.—Litchi tree with mature fruit.

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The flowers open throughout the day but mostly before 6 a.m. Anther dehiscence also occurs more or less throughout the day and night, but it reaches its maximum around 10 a.m. Ultimate fruit set ranges from 2.8 to 8.2 fruits per panicle.

Pollination Requirements

Mustard et al. (*1953*) concluded that shedding of fruit may be due to fertilization failure and embryo abortion. Chaturvedi (*1965*) reported 43 percent fertilized flowers on open pollinated branches, zero percent on branches bagged with muslin, and 15.5 percent on branches bagged under mosquito cloth. Das and Choudhury (*1958*) also reported no set of fruit on bagged panicles.

Pandey and Yadava (*1970*) reported that only 0.03 to 0.10 percent of flowers caged to exclude insects set fruit, whereas 0.7 to 11.2 percent (100 times as many) flowers exposed to insect pollination set fruit. Butcher (*1957a, b*) also reported that no fruit set on a tree caged to exclude insect pollination, proving that lychee plants require insect pollination. These tests supported Campbell and Malo (*1968*) by showing that the lychee is self-fruitful and that interplanting of compatible cultivars is unnecessary, but the pollen must be transported from anthers to stigmas for fruit set.

Pollinators

Butcher (*1957a, 1958*) reported that in Florida the insect visitors to lychee flowers in order of numbers were: Calliphorid and screw-worm (*Callitroga* [=*Cochliomyia*] *macellaria* (Fab.)) flies and honey bees. No wild bees were seen on the plant although they were present on other flora. Pandey and Yadava (*1970*) reported that in India *Apis* spp. and *Melipona* spp. comprised 98 to 99 percent of the total visitors. Chaturvedi (*1965*) mentioned honey bees, flies, ants, and wasps as floral visitors. Groff (*1943*) considered bees the most outstanding beneficial insects on lychee. Butcher (*1957a*) concluded that the value of the honey bee was obvious in the setting of lychee fruit. Das and Choudhury (*1958*) stated that the chief pollinators were bees, other Hymenoptera, and flies.

Pollination Recommendations and Practices

Although no specific number of colonies per unit of lychee has been recommended, Butcher (*1957a, 1958*) stated that supplying honey bees to lychee plantings is an important and practical recommendation for assuring adequate pollination and fruit-setting. He further felt that the bees should be present continuously throughout bloom. The degree to which growers go to in the use of bees has not been recorded.

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LOQUAT

Eriobotrya japonica (Thunb.) Lindl., family Rosaceae

The loquat is also called Japanese plum, Japanese medlar, and rush orange. It is not grown commercially to any extent for its fruit in the United States (Campbell *1965*), but it is a common southern dooryard and ornamental plant. It will do well wherever lemons grow.

Plant

The loquat is a rather long-lived symmetrical evergreen to 25 feet tall, with oblong, stiff dark-green leaves 8 to 12 inches in length (Bailey *1949**). Condit (*1915*) recommended that the plants be spaced 12 feet apart in the row, and rows 24 feet apart for commercial production.

The fruit, which ripens in the spring, can be damaged by slightly below freezing temperatures (Mowry et al. *1967**). The 1- to 3-inch pear-shaped fruits, four to 10 per cluster, have three to five seeds, and yellow flesh. They are used fresh or in preserves or jams and in making a delicious jelly (Kennard and Winters *1960**). There are many cultivars in Florida, some trees of which may yield as much as 300 pounds fruit (Campbell *1965*).

Inflorescence

The name "Eriobotrya" (Greek: woolly inflorescence) refers to the profusion of small woolly flowers born in a terminal dry-bracted panicle. Flowering occurs from October to February, sometimes in up to three flushes of blooms in a season. The second one usually sets the most fruit (Chandler *1958**). Blossoms in the northern part of Florida and similar regions seldom bear fruit because of cold injury. Bees visit the blossoms freely for nectar and pollen. A copious quantity of nectar may collect in the open cavity around the ovary, below the base of the anthers. In warmer areas of China, the loquat is reported to be the principal source of surplus honey in November (Pellett *1947**).

There are 10 to 50 small fragrant white flowers in a panicle, only about 12 percent of which develop into fruit. Each flower has five petals, five stigmas, about 20 stamens, and five carpels (fig. 127). Each carpel has two ovules; therefore, 10 seeds may develop, although rarely more than three to five do so (Smock *1937*, Campbell and Malo *1968*). Thinning of fruit may be necessary if the set is too heavy, but usually the set is too light for economic production.

Pollination Requirements

The pollination requirements seem to vary with cultivars of loquat, but all are benefited by, and some require, cross-pollination. Crescimanno (*1958*) reported that even individual cultivars vary widely from year to year in the amount of fruit set through self-pollination. He found that bagged blossoms set only 0.0, 16.5, and 1.3 percent; whereas, open blossoms set 4.2, 12.0, and 21.7 percent; and crossed flowers (the last 2 years) set 60 and 55 percent of the blossoms. High temperatures

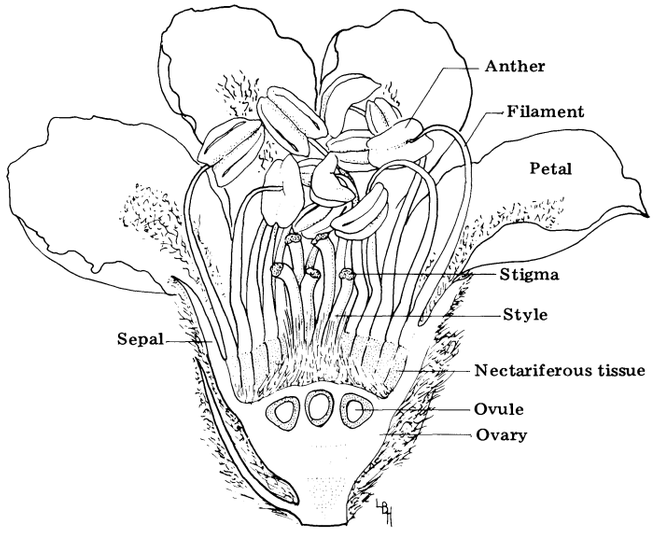

FIGURE 127.—Longitudinal section of loquat flower. ×4.

seem to be detrimental to fruit set. This could be the result of a decreased period of stigma receptivity or pollen viability associated with inadequate pollinator activity. Mortensen and Bullard (*1968**) reported that cross-pollination was beneficial to all varieties and necessary in some. Kennard and Winters (*1960**) also reported that the flowers are self-incompatible, so several trees should be planted close together to assure cross-pollination.

The details of the flowers' period of receptivity is not known, however Singh (*1963*) found that pollen will remain viable 35 to 45 days at room temperature, 22 months at 0° C., and 26 months in a deep freeze.

Pollinators

Nothing is mentioned in the literature about the pollinating agents for loquat. However, honey bees visit the flowers freely and are usually the primary visitors. Presumably, they are satisfactory pollinating agents.

Pollination Recommendations and Practices

None. Where maximum fruit set is desired, plants should probably be in close proximity and bees should be present in abundance during flowering.

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LUPINES

Lupinus angustifolius L., family Leguminosae

Blue lupines are grown for grazing, soil improvement, and cover, primarily in southern Georgia and northern Florida. Two decades ago, more than a million acres of lupines were grown. Since then, the acreage has dropped sharply and so have the number of species because of virus infection of the plants. Presently, some 300,000 to 400,000 acres of blue lupines are grown mostly for forage or in citrus groves (Edwardson *1963*; J. R. Edwardson, personal commun., 1971).

Plant

Blue lupines usually have upright branches, 1 to 4 feet tall, with nitrogen-fixing *Rhizobium* nodules on the roots, as occurs with most other legumes. The stems are relatively coarse. The seeds are relatively large, and the flowers are in large terminal or lateral racemes. The leaves may consist of 5 to 11 leaflets arising at a common point. The dense foliage will provide as much as 40,000 pounds of green manure per acre (McKee *1948*).

Inflorescence

The flower cluster is a 6- to 12-inch upright raceme, and each floret is ½ to 1 inch in size. The petals may be shades of blue, purple, or pink. They are supposed to be nectarless but fragrant (Knuth *1908*, pp. 271–272;* Edwardson et al. *1963*), although Pellett (*1947**) stated that some lupines are honey plants. The blue lupine is not a honey plant, but the pollen is attractive to bees.

The anthers dehisce before the flower opens, and after they release the pollen they shrivel, leaving the pollen in the hollow cone of the flower. When insects visit the flower, their weight causes the stamens to extrude pollen through the opening in the keel, ahead of the stigma, where pollen-carrying insects can effect crossing. Automatic self-pollination does not occur (Knuth *1908*, pp. 271–272*). To protect the bee visitors, Edwardson et al. (*1963*) recommended the use of insecticides only when the bees were not visiting the plants.

Pollination Requirements

McKee et al. (*1946*) and McKee and Ritchey (*1947*) stated that most flowers of blue, white, and yellow lupines are self-fertilized, but some crossing within (but not between) species occurs. Julen and Akerberg (*1948*) stated that even in some plant species considered to be self-fertilizing, seed setting is improved by insect visits. This applies particularly to yellow lupine.

Kozin (*1967*) found that visits by honey bees substantially increased the number of pods set in three of five cultivars, the length of pod in 7 of 13 cultivars, the number of seed in all cultivars tested but three, and the weight of seed for all cultivars but two. The visits also increased the germination qualities of the seed. Wallace et al. (*1954*) quoted Troll (*1948*) as saying that cross-pollination is always more frequent in yellow lupine than blue and that the extent varies with the distance to the nearest apiary. They showed practically no hybrids resulted from bee activity on blue lupines but 19.9 percent from plants of yellow lupine, both of which were only a quarter of a mile from an apiary. They also noted that honey bees work the sweet yellow lupines. Forbes et al. (*1971*) concluded that blue lupine is highly self-compatible, and fully capable of self-pollination in closed flowers independent of insect pollination. However, their data show that both 'Rancher' and '65G-251' selections produced more seed when there was no barrier to pollinating insects than when either poultry wire of 2.5 cm mesh or fine screen enclosed the plants. This would indicate that insects have a beneficial effect.

Pollinators

Kozin (*1967*) showed that honey bees represented 83 percent, bumble bees 9.6 percent, and other insects 7.4 percent of the visitors to "fodder" lupine. He further noted that 56.5 percent of the bees collected pollen and inserted their proboscis into the flower. Leuck et al. (*1968*) also considered the honey bee to be the most important pollinator on blue lupine. Forbes et al. (*1971*) considered neither bumble bees nor thrips of consequence and attributed the range of crossing they observed (from 0 to 12.0 percent) to known honey bee population densities.

The honey bee, then appears to be the primary floral visitor. Kozin (*1967*) recommended that honey bees be widely used for increasing the seed crop of lupines, but the species of lupines involved was not given. Todd (*1957**) listed white, yellow, and blue lupines under the heading "Seed Production Increased by Bees." Horovitz and Thorp (*1970*) considered the bumble bee to be better than the honey bee in the pollination of *L. nanus* Dougl.

Pollination Recommendations and Practices

None.

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MACADAMIA

Macadamia integrifolia Maiden & Betche and *M. tetraphylla* L. A. S. Johnson, family Proteaceae

About 4,000 acres of macadamia trees were in production in Hawaii in 1970 with another 4,700 acres of new but not yet producing trees (Wallrabenstein *1971*). About 140 acres were in California, mostly in San Diego County (Swedberg and Nelson *1970*), and a few acres on trial in Arizona. Coit and Miller (*1951*) stated that new cultivars were producing 1.5 tons of nuts (825 pounds of meat) per acre. Hamilton and Storey (*1956*) reported 500 tons of nuts harvested from 2,721 acres (1,395 of which were nonbearing acres) in Hawaii—about 700 pounds per productive acre. Production of as much as 7,000 lb/acre have been obtained (W.C. Mitchell, personal commun., 1971). The grove must be about 15 years old before the income from it pays the investment and expenses (Keeler and Fukunaga *1968*).

The specific name of macadamia was formerly considered to be *M. ternifolia* Maiden & Betche (Hamilton and Fukunaga *1959*), but now there are considered to be two species involved (Krauss and Hamilton *1970*), although only *M. integrifolia* nuts are processed commercially.

Plant

The macadamia is an evergreen tree, native to Australia, where it may grow to a height of 50 to 60 feet. Elsewhere, however, it rarely exceeds 30 feet. The leathery leaves of *M. integrifolia* are narrow and long, up to 20 inches, serrate, with many spines along the edges. Those of *M. tetraphylla* are shorter, with few or no spines. The fruit is a fleshy exocarp or husk, enclosing a spherical ½- to 1-inch hard brown shell or nut, a true seed, which contains the oval kernel or sometimes two hemispherical kernels (Hartung and Storey *1939*). On maturity, the exocarp splits and the nut falls to the ground (Mowry et al. *1967**). The shell is tough and difficult to crack. The kernel is delicious with high energy value (9.3 percent protein, 78.2 percent fat, and 8 percent carbohydrate) (Kennard and Winters *1960**). The plants are grown about 20 feet by 35 feet apart (62 trees per acre) (Hamilton and Fukunaga *1959*). They come into bearing in 5 to 7 years. The macadamia is also an excellent dooryard ornamental.

Inflorescence

The ¼- to ½-inch tubular flowers are borne in groups of three to four, with 100 to 500 of them on a whiplike terminal or axillary pendulous raceme about as long as the leaf (fig. 128). Urata (*1954*) stated that one short stamen is attached to each of four petals, but Storey (*1957*) stated that the flowers were without petals, the stamens being attached to the petallike sepals. Kennard and Winters (*1960**) also referred to them as petalless flowers. The flowers on *M. integrifolia* are ivory white, on *M. tetraphylla* they are pink. The ovary with two ovules, bears a long straight style with a small terminal stigma. The style forms a sharp loop in its midsection just before the flower opens. The pollen is shed within the flower 1 to 2 days before it opens, then 1 to 2 hours before opening, which is about 7 to 8 a.m., the sepals

curl back exposing the anthers closed over the tip of the style. Then, the anthers separate, and 5 to 10 minutes later the style breaks free and straightens, extending beyond the now empty anthers, but its stigma does not become receptive until some time later. The stigma comprises only the very apex of the style, approximately 1 mm across. It is capable of receiving only 10 to 12 grains of pollen (Schroeder *1959*). The pollen of a specific flower, however, is generally removed by insects before the stigma is receptive (Knuth *1909*, p. 356*), so pollen must come from another flower. The main flowering months in Hawaii are January and February.

Honey bees collect pollen freely from macadamia (Urata *1954* and Gary et al. *1972*). Nectar is secreted at the base of the blossom. Schroeder (*1959*) commented that secretion of nectar is not in any quantity to attract insects. One report (Anonymous *1958*) stated that macadamia flowers produce a gas that is highly toxic to bees, with the suggestion that this gas might have a somewhat repelling effect on bees. Apparently, the bees are not repelled.

Pollination Requirements

Urata (*1954*) and Schroeder (*1959*) stated that most trees are at least partly self-sterile but are cross-compatible; therefore, pollen must be moved from tree to tree for good fruit set. Knuth (*1909*, p. 356*) concluded that self-pollination was unlikely in the Proteaceae. Hamilton and Storey (*1956*) stated that usually only 1 to 20 flowers on a raceme set fruit, but no reason was given for this small percentage of set. Later, Storey (*1957*) stated that only 1 to 2 percent set fruit. The minuteness of the stigma indicates that wind is not a factor in pollen transfer.

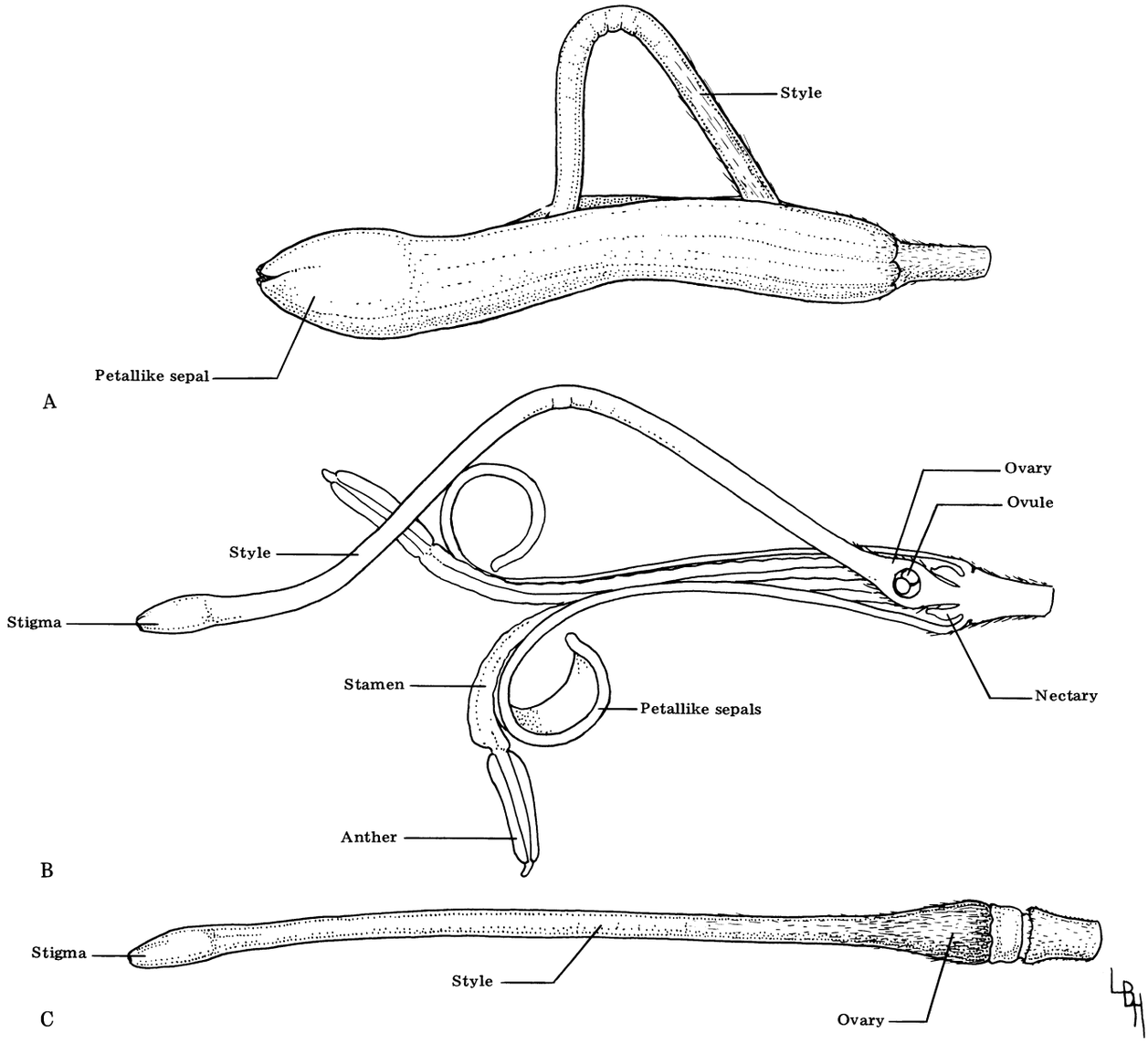

FIGURE 128.—Flower of macadamia (*Macadamia integrifolia*), ×20. *A*, Complete flower with reflexed style just before petal-like sepals separate to release stamens; *B*, longitudinal section of the open flower; *C*, style straightened after pollination has occurred.

Pollinators

Urata (*1954*) stated that honey bees are the most common pollinating insects on macadamia flowers, primarily collecting pollen. He gave no indication of the relative number of bees per flower or tree, or the relative bee population in the area. Shigeura (*1967*) and Shigeura et al. (*1970*), working with 100, 75, and 20 trees of three cultivars of *M. integrifolia* concluded that moving commercial apiaries beside the plantings caused 59 percent increase in production over previous years without bees, although one cultivar showed no increase. Nothing was said about the activity of the bees on the flowers, and no suggestions were made as to how the bees might be used to increase production.

Pollination Recommendations and Practices

There are no recommendations on the use of bees or other pollinating insects on macadamia flowers. The evidence strongly indicates that for highest production the use of honey bees as pollinators should be encouraged—sufficient bees to provide ample cross-visitation between trees throughout the flowering period. There is no evidence as to the number of bees needed nor of the relative competition between flowers of macadamia and of other plants in the vicinity. Two to three colonies per acre are recommended for the pollination of the highly attractive almond trees and probably as many are needed on macadamia. A study of this phase of macadamia production is badly needed.

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MAMEY SAPOTE

Calocarpum sapota (Jacq.) Merr., family Sapotaceae

The mamey sapote, mamey, or sapote is native to Central America but is grown primarily as a dooryard planting in mildest temperature areas of California and Florida. (Also see "White Sapote," p. 380.) Campbell (*1967*) stated that it is easy to grow in southern Florida, where there is a ready market for its fruit. The related species (*C. viride* Pittier), the green sapote, has fruit 2½ to 3½ inches long, with brownish-green skin, sweet reddish-brown flesh, and a pleasant almondlike flavor (Whitman *1966*).

Plant

The mamey sapote is a large evergreen tree that may grow to 80 feet tall. The leaves are as much as 4 inches wide by 12 inches long. The russet-brown, ovoid fruit is 3 to 6 inches long. The somewhat granular, firm flesh is red to reddish brown and sweet. It may be eaten out of hand or used in preserves or sherbet (Kennard and Winters *1960**). There is usually one large seed. The plant is propagated by seeds. Mowry et al. (*1967**)

stated that old trees can withstand temperatures as low as 28° F for several hours, but younger trees are quite susceptible to cold.

Inflorescence

The ½-inch, whitish, nearly sessile, bisexual flowers are produced in great numbers, six to 12 together in the axils of fallen leaves on old wood. The flower has five lobes to the corolla, five stamens alternating with five stamodia, a five-celled ovary, and a slender style with the stigma extending beyond the corolla (Bailey *1949**).

Pollination Requirements

The construction of the flower indicates that insect pollination would aid in the setting of the fruit.

Pollination Recommendations and Practices

None.

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MANGO

Mangifera indica L., family Anacardiaceae

Several hundred acres of mango are grown commercially in Hawaii in addition to numerous dooryard plantings (Yee *1958*). Singh (*1960*) reported that mangos cover about 7,000 acres in Florida but D. O. Wolfenbarger (personal commun., 1970) estimated that there were only about 2,000 acres.

Mango is grown for the egg-shaped, 2- to 6-inch long, greenish or yellowish to reddish fruit, which has a skin slightly thicker than that of a peach. The juicy, sweet to acid flesh around the hard mono- or polyembryonic stone is a popular fruit for millions of people in the tropical and subtropical areas around the world.

Plant

The mango is an erect, multibranched evergreen tree characterized by its dome-shaped canopy. It may reach 100 feet although most trees are less than half that height, and it may live 100 years or more. The tree grows in frost-free areas of the world from sea level to 4,000 feet. Heavy rains during flowering will drastically reduce fruit production. Mangoes have a decided tendency to biennial bearing, and many cultivars produce only one good crop in 3 to 4 years (Purseglove *1968**). On the other hand, some double or even triple cropping (the setting of fruit at two or three different times during the year) also occurs (Naik and Rao *1943*).

Inflorescence

The mango inflorescence is a branched terminal panicle, 4 to 24 inches long, with from a few hundred to several thousand individual flowers, requiring up to a month for all to open. The number of panicles may range from 200 to 3,000 per tree with 500 to 10,000 flowers per panicle—100,000 to 30 million per tree. The proportion of perfect to staminate flowers may vary from 1:4 to 2:1 (Ochse et al. *1961**). Sometimes, the entire tree comes into bloom at one time, covering itself with sweet-scented flowers.

There are perfect and staminate flowers on the same panicle. The perfect flower, 5 to 8 mm long, has a globular ovary (rarely two or three) and a lateral style, which is absent in the staminate flower. Both generally have one, but sometimes two or even three, functional stamens and several sterile staminodes. There are usually five greenish-yellow sepals and three to nine, but usually five, cream-colored petals that take on a pinkish tinge before falling (Naik and Rao *1943*). In the perfect or hermaphrodite flower, a nectar-secreting fleshy disk surrounds the ovary. The stamen is on the outer margin of this disk. The pistil and stamen are the same length; therefore, pollinating insects that feed on either nectar or pollen are likely to transfer pollen from the anther to the stigma (Juliano and Cuevas *1932*, Sturrock *1966*).

The flower opens early in the morning, and the stigma is immediately receptive. Maximum pollen shedding is from about 8 a.m. to noon. This delayed pollen shedding can result in inadequate stigma fertilization (Spencer and Kinnard *1956*). When the flowers open, they secrete nectar in considerable quantity, which attracts a large number of insects (Mukherjee *1953*); however, relatively little pollen is produced on the anther (Popenoe *1917*).

Pollination Requirements

There has been some lack of agreement on the pollination of mangos. Young (*1942*) made pollination studies on the 'Haden' mango in Florida, which he said made up 90 percent of the commercial plantings in that State (the 'Tommy Atkins' is the current popular cultivar), and found no significant difference between percentages of set in selfed and cross-pollinated flowers. Sturrock (*1944*) also considered the flowers self-fertile. This self-fertility was supported by the earlier work of Popenoe (*1917*), who stated that the mango is self-fertile but cross-pollination increases fruit set. However, Singh et al. (*1962*) reported that crossed flowers set fruit whereas selfed ones did not, indicating a degree of self-sterility. The actual degree of self-fertility and sterility in individual cultivars has not been determined,

but there is apparently some variation. Self-sterility is not, however, a major problem in fruit set.

Within the cultivar there is a definite need for transfer of pollen from anther to stigma by an outside agent. Popenoe (*1917*) stated that some of the embryos are capable of development without fertilization; however, Naik and Rao (*1943*) obtained no parthenocarpic fruit set of more than 100,000 flowers studied. Fraser (*1927*) stated that fruit bud formation and pollination were the two big problems in growing mangos. He pointed out that in some cases only 2 to 3 percent of the flowers on a panicle are perfect—in others 60 to 70 percent. Wolfe (*1962*) concluded that getting flowers to set fruit was more of a problem than getting the trees to produce flowers.

The effect of cool weather adversely affects pollen tube growth, but this was not considered to be a factor of major importance by Young (*1955*). Chapman (*1964**) and Ruehle and Ledin (*1955*) considered that the lack of efficient pollination might be responsible in part for the low yields of some Florida cultivars.

The studies indicate that the need for cross-pollination between mango cultivars is not critical, at least for most cultivars, but there is need for pollinating insects to transfer the pollen from anthers to stigma within the cultivar to obtain satisfactory crops of fruit.

Pollinators

Several agents have been given credit as pollinators of mango. Wagle (*1929*) showed that there was some selfing and some wind pollination, but insects (bees, ants, and flies) played an important part.

Popenoe (*1920*) disagreed with other writers that the mango is wind pollinated. He pointed out that the flowers have none of the characteristics of a wind-pollinated flower, and he considered the mango to be an insect-pollinated plant. Galang and Lazo (*1937*) and Singh (*1969*) agreed with him.

Recent studies in India[29] showed that plants caged to exclude all insects set no fruit and gall-midges were ineffective as pollinators, but a plant caged with a colony of honey bees where harmful insects were excluded set a heavy crop.

Singh (*1961*) reported that over 65 percent of the perfect flowers were never pollinated—a strong indication that wind is not an effective pollinating agent. Complaints about lack of adequate fruit set in larger plantings particularly of monoclonal cultivars are frequent (Singh *1969*). Fraser (*1927*) concluded that the important problem was finding out which insects were important as pollinators.

The statement was made by Singh (L.B.) (*1960*) that honey bees do not visit mango flowers, but Singh (S.) (*1954*) listed this plant as a source of pollen and nectar for bees. Popenoe (*1917*) reported that honey bees were the most important hymenopterous insect visitor to mango flowers, but the number present was variable, possibly because of the location of apiaries or other relatively more attractive flora. This probably explained the low population of honey bees reported by Simao and Maranhao (*1959*).

Pollination Recommendations and Practices

There is no indication that the recommendation by Young (*1942*) to place colonies of honey bees in mango groves has become an accepted practice; however, the chances are likely that such bee usage is needed today much more so than when his studies were made. The evidence is quite strong that concentration of colonies of honey bees within the mango grove would result in increased floral visitation and possibly more stabilized set of fruit, particularly in some years. The mango flowers do not appear to be overly attractive to honey bees, and they tend to open in large numbers at a time of year when many other flowers are also available, so visitation in commercial groves is likely to be far below that necessary for maximum floral visitation. If such is the case, a heavy concentration of colonies in the grove, possibly three to six per acre, may be necessary to obtain maximum fruit set.

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MUNG BEAN, GREEN OR GOLDEN GRAM

Phaseolus aureus Roxb., family Leguminosae

At one time the mung bean was a crop of considerable importance. Martin and Leonard (*1949**) stated that in 1945 110,000 acres were grown in Oklahoma.

In 1967, when records on this crop were discontinued, 34,000 acres were harvested, yielding 400 pounds seed per acre, for which a price of only 0.06 cents per pound was obtained. Mung bean is an important crop in India where it rates as the most wholesome among the pulses. The beans are boiled and eaten whole, parched and ground into flour, eaten green as a vegetable, or used for bean sprouts (Yohe and Poehlman *1971*). The crop is also grown for hay, green manure, and as a cover crop (Purseglove *1968**).

Plant

The mung bean is an erect or suberect, deep-rooted, many-branched, rather hairy, annual herb 1½ to 5 feet tall. The gray, black, or brownish pods, 2 to 4 inches long, may contain 10 to 15 small, round, usually green but sometimes yellow or blackish seed.

Inflorescence

The inflorescence is an axillary raceme, with 10 to 25 pale-yellow flowers, 1½ to 2 cm long, and clustered at the top. Pollen is shed the afternoon before the flower opens the following morning. The flower fades the same afternoon. Only about half of the flowers (64 percent) open to permit possible cross-pollination.

Pollination Requirements

Purseglove stated, "The flowers are fully self-fertile when bagged and almost entirely self-pollinated." However, van Rheenen (*1964*) stated that when he alternated varieties in the row, he obtained 2.8 to 3 percent crossing.

Pollinators

There seems to be no information on the pollinators involved.

Pollination Recommendations and Practices

None.

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MUSKMELON

Cucumis melo L., family Cucurbitaceae

The muskmelons grown commercially in this country were classified by Whitaker (*1970*) into "varieties." Variety *reticulatus* Naud. includes the cantaloupes and 'Persian' melons, and variety *inodorus* Naud. includes

the Casabas and the Honey Dews. There are numerous cultivars of each.

Muskmelons are grown in most States, but more than one half the acreage is in California. The bulk of the muskmelon crop is cantaloupes, combined with a small acreage of Casabas and 'Persians', which amounted to 111,800 acres in 1970. Honey Dews were produced on 13,200 acres. The combined farm value of all muskmelons was $93.3 million.

Plant

Muskmelons are trailing annuals, the vines, if unchecked, spreading to about 10 feet. The leaves are 4 to 8 inches across, and their 6- to 10-inch upright stem enables them to form a protective arborlike canopy over the flowers and fruit. The one to six melons per plant develop from the yellow hermaphrodite flower in the axis of the leaf. At maturity, about 6 weeks after the bloom appeared, the round to oblong melon is 4 to 8 inches in diameter. The frost-susceptible plants are usually grown in 6-foot rows, 4 to 24 inches apart in the row, with the best yield from plants 6 to 12 inches apart in the row (Pew *1952*, Davis and Meinert *1965*).

All forms of *C. melo* readily hybridize, as for example the 'Pershaw', which is thought to be a cross between the 'Persian' melon and the 'Crenshaw', Casaba, or the 'Honey Ball', which is a cross between the Honey Dew and the 'Texas Cannon Ball'. Rosa (*1926*) reported some self-incompatibility in the 'Persian' and the Honey Dew.

The bulk of the discussion which follows will concern cantaloupes.

Inflorescence

Most American cultivars of muskmelons are andromonoecious, bearing staminate and hermaphrodite flowers on the same plant (fig. 129). The numerous staminate flowers are borne in axillary clusters of three to five in all axillary positions not occupied by the few slightly larger solitary hermaphrodite flowers. The flowers are ¾ inch to 1½ inches across, with five petals united to slightly beyond the staminal column, then separated and broadly spreading (Whitaker and Davis *1962**). Griffin (*1901*) reported 512 staminate and 42 hermaphrodite cantaloupe flowers per vine. McGregor (*1951*) showed, however, that this ratio varies depending upon bee activity and fruit set. When bees were excluded, no fruit set and the ratio was one hermaphrodite to four staminate flowers, but in caged and open plots visited by bees the ratio was one hermaphrodite to 10 staminate flowers. Apparently, failure of the plant to set fruit stimulates production of a higher proportion of hermaphrodite flowers.

The staminate flower, supported on a thin stem,

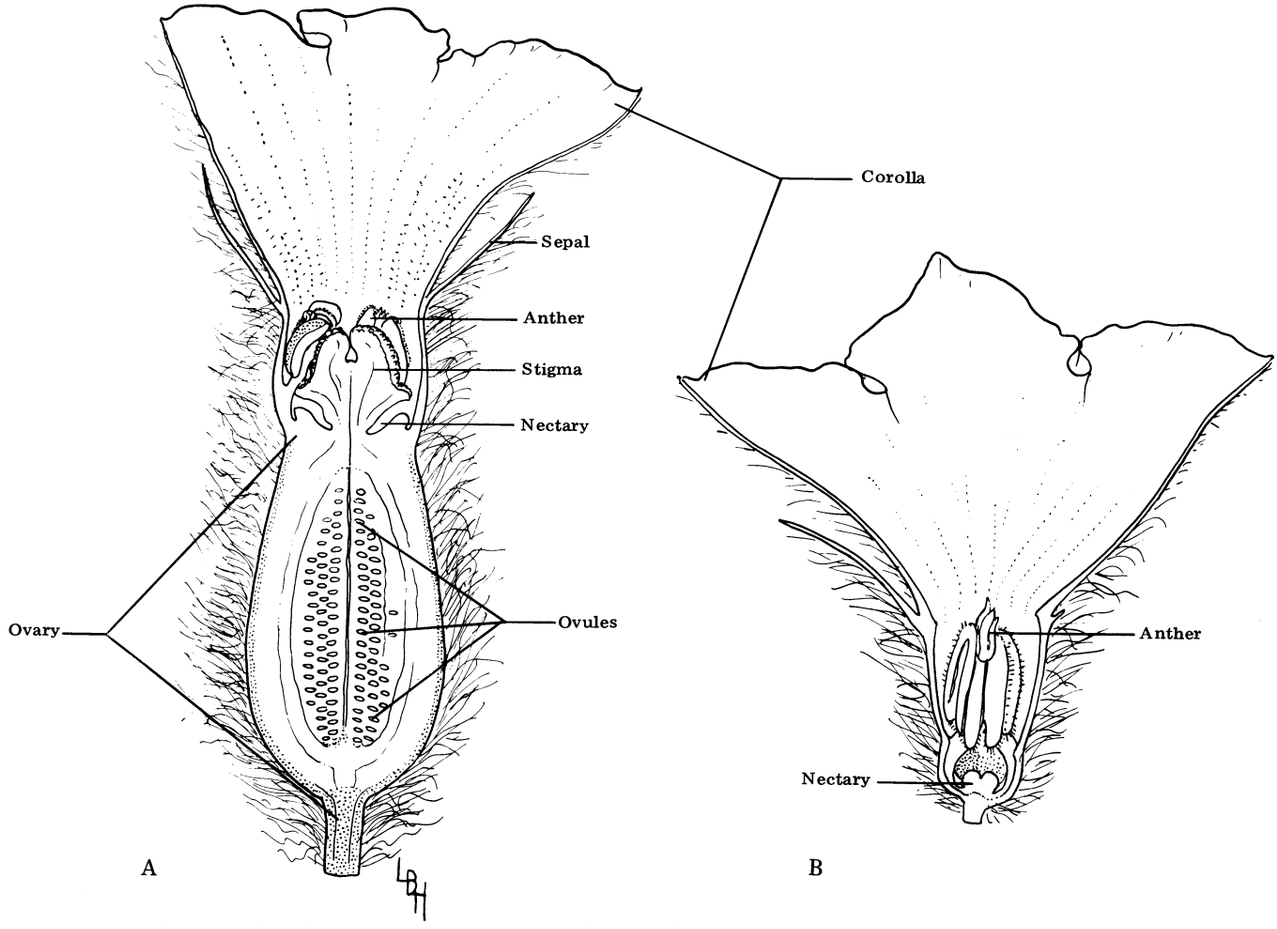

FIGURE 129.—Longitudinal section of muskmelon flower, × 4. *A*, Hermaphrodite; *B*, staminate.

consists of the corolla, a single whorl of five stamens, only a few millimeters long, two pairs of which are united, with the anthers almost filling the small corolla tube. At the base of the corolla, a rudimentary style is surrounded by the nectaries (Judson *1935*). The hermaphrodite flower has anthers and a broad, usually three-lobed stigma on a 1- to 2-mm style, the base of which is surrounded by the nectaries. The corolla of the hermaphrodite flower is on the end of the elongated ovary (Jones and Rosa *1928**, Judson *1949*).

The muskmelon flower opens some time after sunup, the time depending upon the sunlight, temperature, and humidity. When the temperature is low, the humidity is high, or the day cloudy, opening is delayed. The flower closes permanently in the afternoon of the same day. Bee activity begins on the flower shortly after it opens, reaches a peak at about 11 a.m., and ceases about 5 p.m. (McGregor and Todd *1952**). At Davis, Calif., the flower opening and attraction for bees is an hour or so later in the day (Mann *1953*).

The flower is attractive to bees for both pollen and nectar. Collection of pollen by bees usually ends before noon, but nectar collection continues into the late afternoon. Only about 1 percent as much nectar per acre is secreted by muskmelons as is secreted by alfalfa. Foster et al. (*1965*) showed that muskmelon plants infected with mosaic viruses produce less nectar than healthy plants.

Pollination Requirements

The isolation of muskmelon plants from pollinating insects and the caging of bees on the plants have proven that hermaphrodite flowers are incapable of performing self-pollination. The pollen must be transferred from the anthers to the stigma by insects (Alex *1957a, b;* Bohn and Davis *1964;* Mann *1953, 1954;* Mann and Robinson *1950;* McGregor and Todd *1952*, 1952;* and McGregor et al. *1965*).

Muskmelons with fewer than 400 seeds are usually so small they are classed as culls. At least one viable pollen grain must be deposited on the stigma and fertilize an ovule if a seed is formed. The effective period in which this pollen can be deposited on the stigma is no more than a few hours in the morning, and if the temperature is high, the period may be only a few minutes. Single massive deposits of pollen by hand on the stigma are seldom as effective in the setting of fruit as repeated bee visits (Mann and Robinson *1950*, Wolf and Hartman *1942*). Muskmelon flowers are self-fertile (although not self-fertilizing), but when pollen comes from a different plant, the fruit that results may be slightly heavier (Rosa *1926*). Also, a high correlation exists between the number of seeds in a muskmelon and its size—the more seeds the larger the fruit. Increased bee visitation is associated with greater number of seed.

Pollinators

Tontz (*1944*) mentioned ants as possible pollinators of muskmelons and squash. Annand (*1926*) indicated that thrips might be pollinators of muskmelons, but Tsyganov (*1953*) considered one bee equal to 11,000 thrips. The value of thrips and ladybird beetles was discounted by McGregor and Todd (*1952*, 1952*) when they obtained no set of marketable cantaloupes in cages where honey bees were excluded and these insects were common, but a satisfactory set in cages supplied with bees. Bohn and Mann (*1960*) showed, with the mutant nectarless, the dependence of high muskmelon yields on honey bee pollination. The value of bees as pollinators of muskmelons, stated by Beattie and Doolittle (*1926*), Ivanoff (*1947*), Rosa (*1927*), and Rosa and Garthwaite (*1926*) is now firmly established. Because of their relative abundance in commercial fields and their attraction to muskmelon flowers, honey bees are the most important of the muskmelon pollinators. Beattie and Doolittle (*1926*) stressed the need for bees on muskmelons grown in greenhouses.

Honey bees visit muskmelon flowers as soon as the flowers open (fig. 130). They collect both nectar and pollen, move freely from flower to flower and plant to plant, and continue visiting the flowers until late afternoon. McGregor et al. (*1965*) showed that a honey bee visit to each flower about every 15 minutes is desirable for maximum fruit set. They calculated that one bee for each 10 hermaphrodite flowers is necessary to provide this rate of visitation. Whitaker and Bohn (*1952*) showed that variations in visits by honey bees occur between plants sometimes only a few feet apart if there is a variation in the microclimate around the plants. This means that many flowers must receive more visits than necessary if all are to receive the optimum number.

Growers prefer muskmelon fruit that is produced near the base of the plant. Such fruit is referred to as

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FIGURE 130.—Honey bee visiting muskmelon flower.

"crown set," or the set of fruit from the hermaphrodite flowers on the first to third spur. When there is heavy bee activity, a heavy crown set results (Rosa *1924*, Whitner *1960*). Such fruits are sweeter (McGregor and Todd *1952**, *1952*), and are usually more oval than later fruits, which tend to be oblong.

Iselin et al. (*1974*) grew cantaloupes in an air-inflated plastic greenhouse. Their plants, shielded from bees, set no fruit, but plants visited by bees fruited normally. Bee foraging activity was similar to activity outside the greenhouse. They also reported that raising the CO_2 content of the air in the enclosure increased the soluble solids (sugar content) of the ripe melons from 8 to about 12 percent.

Usually, the set of one or two fruits prohibits the set of further fruit until the first ones mature. Thus, when McGregor and Todd (*1952*) excluded bees for 3 weeks after initial flowering and then permitted unlimited visits to the flowers, 80 percent of the marketable fruit was set within the first 3 days, but the total production was not significantly different from production in cages where bees were constantly present. The fruits that set later were less sweet than crown-set fruit.

In studies on hybrid vigor in muskmelons, Foster (*1963*, *1967*, *1968a*, *b*, *c*), Foster and Levin (*1967*), and Bohn and Davis (*1957*) found that F_1 hybrids produced twice as much fruit as commercial cultivars, and other characters were improved. Bohn and Whitaker (*1949*) reported male sterility in the muskmelon, a character useful in hybrid seed production. Munger (*1942*) also showed that utilization of hybrid vigor was practical. In the utilization of hybrid vigor, pollination by bees is essential.

Taylor (*1955*) studied the production in 37 muskmelon fields in the Salt River Valley of Arizona in relation to proximity to honey bee colonies. In 20 fields with an average of one-half colony per acre within a mile, production was 1.06 melons per plant and 242 crates per acre. In 17 fields with no hives of bees in the "visible vicinity," production was only 0.67 melon per plant and 161 crates per acre. Honey bees were visiting muskmelon flowers in all fields.

Pollination Recommendations and Practices

Bees, primarily honey bees, are the major pollinating agents of muskmelons. The number of bees necessary for maximum pollination is the critical question. Taylor (*1955*) showed the economic significance of an inadequate supply. McGregor et al. (*1965*) demonstrated that one honey bee for each 10 hermaphrodite flowers should insure maximum pollination. This figure has not been extrapolated into colonies per acre—a rate that varies with conditions in, as well as beyond, the field. McGregor and Todd (*1952**, *1952*) suggested one colony per acre for maximum muskmelon production. Peto (*1951*) used one to five colonies per acre on small fields. Pew et al. (*1956*) recommended one colony per acre placed in the shade on the edge of the field, but Eckert (*1959**), without supporting data, recommended only one colony per 2 acres. Rupp (*1969*) reported a decrease of pollinated flowers with distance from the apiary (only 18 percent set on plants 600 m away but 40 percent set on plants within 100 m of the apiary), but he gave no indication as to the ratio of colonies per acre or bees per flower. Sims (*1960*) recommended one good strong colony per acre, the colony filling two deep hive bodies and having 750 to 1,000 in^2 of brood. The Arizona Agricultural Experiment Station (*1970*) recommended one bee per 100 flowers in the field.

Because of the great increase in the number of flowers on the vine as the plant growth increases, the number of colonies required to provide this number might vary from a small fraction of a colony per acre to several colonies. Providing one honey bee for each 10 hermaphrodite flowers is the safest way to insure an adequate pollinator population at all times.

Practically all of the research on the pollination of *C. melo* has been on cantaloupes. The flower structure of the other types of muskmelons are identical or similar to that of cantaloupes. Until evidence is presented to the contrary, the assumption would appear to be safe that the pollination requirements are also the same for all cultivars of muskmelons.

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MUSTARD

Brassica spp., family Cruciferae

Three species of mustard are grown commercially for their seed from which an excellent oil and the condiment, table mustard, is produced. They are (1) *B. hirta* Moench (*B. alba* (L.) Rabenh.), white or yellow mustard; (2) *B. juncea* Coss, Indian (oriental and brown types), Chinese, leaf, and trowse mustards and rai; and (3) *B. nigra* (L.) Koch, black mustard. (Also see "Cole Crops," p. 164, and "Rape," p. 315.)

Mustard is a minor crop in the United States, but in 1941, 124,000 acres were grown in Montana, with small amounts in North Dakota, Oregon, and Washington (Shaw *1956*). The crop in Canada is expanding with about 200,000 acres in 1970 versus 4 million acres of rape (Downey et al. *1970*), and its importance is likely to increase in the United States. Black mustard is not grown in Canada, and the major acreage is devoted to yellow mustard.

Yields of 1,000 to 1,500 pounds of mustard seed per acre are obtained in Canada (Downey et al. *1970*), which is more than the U.S. production of 468 to 714 pounds reported by Shaw (*1956*), the 451 to 524 pounds reported by Robinson (*1964*), or the 500 to 1,000 pounds of brown or 250 to 1,000 pounds of yellow mustard reported by Martin and Leonard (*1949**).

Mustard and rape production is similar in many ways, however, each crop is a serious contaminant of the other. For that reason, the two crops should not be grown on the same farm and preferably not in the same area.

Plant

Young mustard plants are quite similar to many other *Brassica* plants; however, differences soon begin to appear. The rosette of broad basal succulent leaves, about 1 foot high, produces the upright flowering stem that reaches 1½ to 10 feet and terminates with the inflorescence. The upper leaves are much smaller than the lower ones and may be deeply lobed or entire and more or less oval. The growing season is similar to that of wheat or slightly shorter. Like rape, mustard is a cool season crop, but is more drought tolerant than rape. The seeds do not shatter, so the seed crop can be harvested (combined) without undue loss. Mustard is usually seeded at the rate of 4 to 10 lb/acre, depending upon the type and cultivar (Downey et al. *1970*).

When mustard and rape were compared, Downey et al. (*1970*) stated "In comparison to 'Echo' rapeseed, yellow mustard is a few days later in maturing, has yellow seed that is about twice the size, and shows more vigor in the seedling stage. Yellow mustard begins flowering at the same time but continues to flower longer. It is similar to 'Echo' in height, is more resistant to shattering, but slightly lower in yield." In general, the mustards are slightly taller and also have thinner leaves and smaller flowers than rape. *B. nigra* may grow to 10 feet or more in height, with four-sided pods less than 1 inch long. *B. hirta* and *B. juncea* grow only to 2 to 4 feet, with *B. hirta* having pods ¾ inch to 1½ inches long with strong constrictions between the seeds, whereas pods of *B. juncea* are longest, 1½ to 2½ inches.

Inflorescence

The mustard inflorescence is an aggregate of yellow florets at the apex of the raceme, that give a field a deep golden appearance when fully open. The structure of the flower, as given under "Cole Crops," applies equally to the mustard flower. Free (*1970**) indicated that the two outer nectaries were somewhat functional but Nieuwhof (*1969*) stated that they were inactive. Mustard is an excellent source of nectar and pollen for honey bees (Pellett 1947*).

According to Howard et al. (*1915*), the floret opens between 9 a.m. and noon, and remains open for 3 days. Usually, the stigma projects about 2 mm beyond the petals the afternoon preceding opening of the flower, and is immediately receptive. Soon afterwards, however, the corolla begins to grow and reingulfs the stigma. Then the stamens lengthen so that the anthers are level with the stigma, but when the corolla opens, they turn half around. At this period, nectar secretion by the inner nectaries begins. Just before the flower closes, the anthers turn to their former position, and, if any degree of self-fertility exists, selfing can result.

Pollination Requirements

Müller (*1883**) stated that the position of the anthers in relation to the nectaries and stigma makes cross-fertilization likely but by no means inevitable on the visit of pollinating insects. The flower is so constructed that pollen from another flower is likely to be transported to it before its own pollen comes in contact with the stigma. Some of the self-pollen may contact the stigma without the aid of insects, but this contact can be abetted by the bees' visit to the flower. Sampson (*1957*) showed that compatibility varies with species, cultivar, and even the age of the plant.

Free and Spencer-Booth (*1963*) found that bees more than doubled seed production of *B. alba*. In *B. juncea*, production was increased only 14 percent, an amount that was not statistically significant in their test, but could be of great significance to the grower. Pritsch (*1965*) also obtained significantly greater yields of white

mustard in cages with bees than in cages where bees were excluded. Olsson (*1952*) obtained a set of 64.7 percent of the flowers, with 2.46 seeds per pod, and 1.75 g per pod with bees excluded, but with bees present these values were increased to 95.3, 4.08, and 2.69, respectively, more than doubling total production. Koutensky (*1959*) also showed that the seed yield of white mustard was increased 66 percent by honey bee pollination. Howard et al. (*1916*) indicated that *B. juncea* was self-fertile but abetted by wind, Downey et al. (*1970*) stated that oriental and brown mustards (*B. juncea*) are generally self-pollinated, but yellow mustard (*B. hirta*) is a cross-pollinated crop. They further stated that wind and bees are both effective in pollination. Free (*1970**), citing Akhter (*1932*) and Olsson (*1960*), indicated that *B. nigra* is largely self-sterile.

The above references indicate that yellow mustard is immensely benefited by bee pollination, but the value to oriental or brown mustard is minor, although the actual effect of supplemental pollination has not been too well tested.

Pollinators

Olsson (*1955*) found pollen on glass slides exposed 1, 5, 20, and 40 m from fields of rape, turnip rape, and white mustard and he deduced that wind was important in the pollination of these crops. Howard et al. (*1916*) also believed that wind contributed to pollination. However, mustard is basically an insect-pollinated type of crop, with ample pollen and nectar to attract pollinating insects. Honey bees in particular are attracted to it, and they were shown by Free and Spencer-Booth (*1963*) to be of great benefit to *B. hirta* and possibly to *B. juncea*.

The data indicate that repeated visits would be beneficial, thus an ample supply of bees should be present. The number of bees per unit of mustard flowers has not been determined. The flowers are highly attractive to bees for both nectar and pollen so there is no problem in getting visitation if sufficient bees are in the area and the weather permits floral visitation.

Pollination Recommendations and Practices

No colony recommendations have been made for mustard. Downey et al. (*1970*) stated, "It has not been found necessary to supply honey bees to produce good seed yields." How maximum production is obtained is not explained, because they indicated that most of the 200,000 acres devoted to mustard seed production is of *B. hirta*, and the data indicate that production of *B. hirta* provided with bees is double that where no bees are provided. This indicates that the provision of bee colonies to yellow mustard fields in adequate numbers, probably one to two colonies per acre, should be encouraged.

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NIGER

Guizotia abyssinica (L.f.) Cass., family Compositae

Niger is grown for its seeds, which yield a yellow, edible semidrying oil with little odor and a pleasant nutlike taste. The oil is used in cooking, oil lamps, soaps, and paints; the pressed cakes are used for

livestock feed; and the seeds are fried and eaten or used in chutneys or as a condiment. According to Purseglove (*1968**), niger is grown primarily in Ethiopia (100,000 to 200,000 tons of oil produced per year) and India (75,000 tons per year). Chavan (*1961*) stated that India had 716,000 acres of niger.

Plant

The plant is a branched annual herb, ½ to 1½ m tall. The period of growth of the plant to the time of flowering is about 3 months, then another 1½ months are required to ripen the seeds. Pure stands yield 350 to 400 pounds of seed per acre (Purseglove *1968**).

Inflorescence

The yellow 2- to 3-cm flower heads develop in the leaf axil, two to five in a cluster. Each head contains about eight ray florets and 40 to 60 hermaphrodite disk florets (Free *1970**). Within the disk floret, the anthers are united to form the corolla tube. The style extends through this tube, and the hairy forked stigma is above. The floret opens and liberates its pollen early in the morning, the style emerges about midday, and the stigma lobes separate and curl backward toward evening.

Pollination Requirements

Howard et al. (*1919*) found that cross-pollination was common. They reported that the stigma lobes rarely curled back sufficiently to touch their own style, indicating that the plants were self-sterile. This explains why isolated plants set no seed. Although the flowers are hermaphrodite, they are not self-pollinating. Bhambure (*1958*) confined plants in two cages 1.2 by 1.2 mm, and tagged 40 flower heads in each cage. In one of these cages, bees (*Apis cerana*) were introduced. In the cage with bees, 40 seeds per head developed. In the one without bees, only 15 seeds per head were harvested. Chavan (*1961*) obtained similar data.

Pollinators

The meager data indicate that this important crop is largely dependent upon pollinating insects, and growers who desire maximum bee activity in the field would do well to provide an ample bee supply to each field where seeds are desired.

Pollination Recommendations and Practices

None.

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NUTMEG AND MACE

Myristica fragrans Houtt., family Myristicaceae

Nutmeg and mace are produced in the tropical areas of Indonesia and the West Indies. Purseglove (*1968**) indicated that annual production of nutmeg amounted to about 170,000 cwt (1 cwt = 112 lb). About 1 pound of mace is obtained for each 10 pounds of nutmeg. This would indicate that between 15,000 and 20,000 cwt (2,240,000 lb) of the volume produced was mace.

Plant

The nutmeg tree is bushy, 30 to 40 feet tall, resembles an apricot, and the trees are usually spaced about 30 feet apart. It produces a pale orange-yellow fruit about 2½ inches long, that resembles an apricot, but when ripe the ½-inch thick husk separates into two pieces, disclosing the dark-colored nut, covered with a brilliant scarlet network (aril) known as mace (Nicholls and Holland *1929*). When the nuts are harvested, the aril is separated from the nut and sold as mace, and the nut marketed as nutmeg. The seeds must be planted within 3 days after harvest or the viability is lost. The plant will begin fruiting at 5 to 6 years of age, but is at its best by 15 years and will remain at this productive level another 10 to 20 years (Ridley *1912**). A plant may produce 1,800 fruits in a year, yielding 20 pounds of nutmeg and 2 pounds of mace (Nicholls and Holland *1929*).

Inflorescence

The nutmeg tree is dioecious, with male flowers on one tree and female flowers on another. Occasionally, a plant may have a few flowers of the opposite sex, that is, a male tree may have a few female flowers. Occasionally, also, the sex of the plant may change entirely, particularly it may change from all male or staminate flowers to completely female or pistillate flowers (Ridley *1912**).

The bell-shaped pendant, light-yellow flowers are in small cymes on a woody stalk one-half inch in diameter. The 5- to 10-mm male flowers are more globose than the female ones, and have a mass of cylindrical stamens 8 to 12 mm and extending to the flower opening. The slightly larger (10 mm) female flowers, seldom over three in a raceme, are dilated at the base, with a tiny, two-lobed stigma and an ovary that largely fills the corolla. Nectar is produced in both types of flowers at the base of the corolla. The development from flower to ripe fruit requires 6 to 9 months (Flach and Cruickshank *1969*). There may be three flowering cycles during the year.

Pollination Requirements

There seems to be little doubt that cross-pollination is

required between trees as there are insufficient flowers of both sexes on any one tree. The pollen must be transported to the numerous pistillate flowers to set the 1,500 to 2,000 nuts expected per year on a mature tree.

Pollinators

Nutmeg is insect pollinated, but there is lack of agreement as to what insects are responsible. Flack and Cruikshank (*1969*) stated that "natural pollination is carried out by a moth." Ridley (*1912**) stated that he had seen only small bees and small beetles visit the flowers. Nicholls and Holland (*1929*) stated that pollination is effected only by wind and insects. Purseglove (*1968**) said that pollination is probably effected by small insects. It becomes evident that there is insufficient information on the pollination of this crop, but logically its pollination is by insects.

Pollination Recommendations and Practices

None, yet the evidence indicates that for stable production the grower of nutmeg should arrange for a stable pollinator population on these flowers.

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OIL PALM

Elaeis guineensis Jacq., family Palmaceae

The oil palm or African oil palm is one of the leading oil palms of industrial importance as a source of vegetable oil and fat. Under favorable conditions, it yields 2 tons of oil per acre. It grows naturally in tropical Africa from Senegal to Angola, especially in the coastal belt 100 to 150 miles in depth from Sierra Leone to the Cameroons. In 1951, 200,000 tons of the oil was produced in the Belgian Congo (Johnson and Raymond *1955*). Plantations of this palm are being expanded in West Africa and Southeast Asia, especially in Malaysia.

This production would indicate that there are at least 100,000 acres. Recent development of new cultivars is expected to increase the yield of oil by 20 percent. Oil production per acre in Asia is much higher than in Africa (Sparnaaij *1969*).

To obtain the oil, the pulpfruit is boiled. The nuts are then removed from the fibrous material, cracked, the kernels removed, and the oil pressed from them (Johnson and Raymond *1955*).

Plant

The oil palm is erect, monoecious, and may reach 30 feet in height with a trunk or bole 12 inches or more in diameter. It produces clusters of nuts, each of which has two locules and is about 1½ inches long, the aggregate weighing as much as 100 pounds. The nuts are classified into three types according to the shell thickness; namely *dura* (3 to 8 mm thick), *tenera* (up to 3 mm thick), and *pisefera* (with no shell). The plant itself has a dense head of pinnate leaves, 10 to 15 feet long, and in the leaf axil is the separate dense staminate or pistillate inflorescence.

Inflorescence

The staminate inflorescence may consist of 200 spikelets, with each spikelet bearing 700 to 1,200 florets (fig. 131). It may produce 3 ounces of pollen. The pollen is released over a 5-day period, and most of it on the third day after flowering starts; the pistillate inflorescence may have as many spikelets but only five to 30 florets on each. The pistillate floret is larger than the staminate one and bears an ovoid or nearly cylindrical three-celled ovary. The florets take about a week to open, the individual floret being receptive 36 to 48 hours (Sparnaaij *1969*).

Pollination Requirements

Pollen must be transferred from the staminate clusters to the pistillate ones. There is no indication of

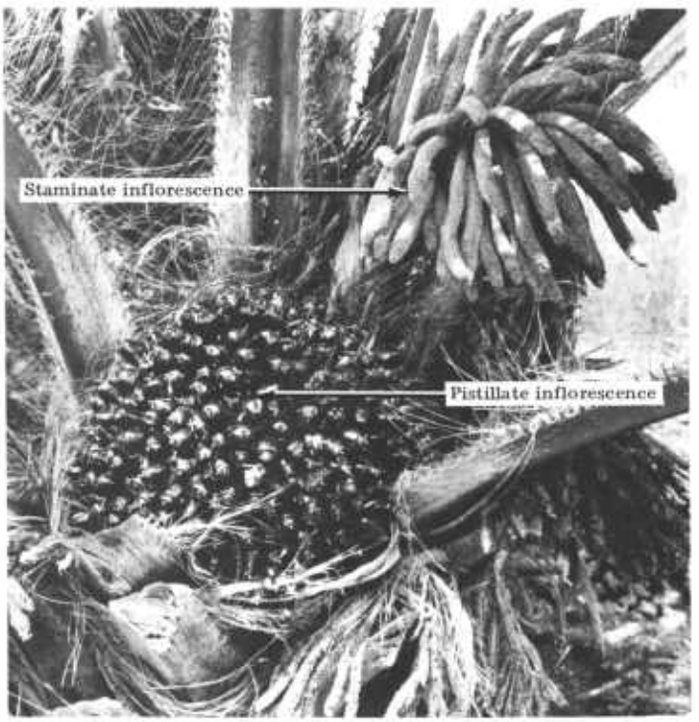

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FIGURE 131.—Fruit and inflorescence of African oil palm.

parthenogenetic development; furthermore, Sparnaaij (*1969*) stated that the *pisefera* nuts are often partially sterile. The oil palm male and female inflorescences open at different times on the plant; thus, rarely is the plant self-fertilized (Wrigley *1969*).

Pollinators

There is lack of agreement on the pollinating agents involved on oil palms. Ochse et al. (*1961**) considered the flowers to be largely, if not exclusively, wind pollinated. Hardon and Turner (*1967*) considered them wind pollinated, pointed out the large amount of pollen produced, and noted that the pollen is distributed at least 55 feet from the original source.

However, Sparnaaij (*1969*) stated that both insects and wind contribute to pollen transfer. He noted that specialists in Africa generally assign the principal pollinating role to insects, whereas in Asia wind pollination is considered most important.

If insects are of significance, they must be attracted to the pistillate flowers by the nectar and to the staminate flowers by pollen and/or nectar.

Pollination Recommendations and Practices

None. Because of the economic importance of this crop, its pollinating agents should be studied.

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OKRA

Hibiscus esculentus L., family Malvaceae

Okra is primarily a southern vegetable garden plant, grown for its immature pods, which are consumed when cooked either alone or in combination with other foods (fig. 132). Hawthorn and Pollard (*1954**) showed 475 acres devoted to seed production in 1951. Miller (*1949*) indicated yields of 1,000 to 1,500 pounds of seed per acre. At a planting rate of 8 pounds of seed per acre (Knott *1949*), this 475 acres should supply sufficient seed to plant 60,000 to 70,000 acres of okra.

Plant

Okra is an upright annual, 3 to 6 feet tall, with a main stem and several branches. It is susceptible to frost but can tolerate hot weather and will grow anywhere cotton will grow. It is usually planted in 3- to 3½-foot rows, the plants about 1 foot apart in the row, after all danger of frost is past. The pointed angular, ribbed or round pods, 3 to 5 inches long, are made up of five to nine carpels, each carpel capable of producing about 30 seeds. The okra leaf is similar to that of cotton, 4 to 12 inches across. There are numerous cultivars.

Inflorescence

The single showy okra flower, as much as 2 inches across, resembles the cotton flower, with its wide corolla usually made up of five yellow to cream-colored petals (fig. 133). The erect sexual parts consist of a five- to nine-part style, each part with a capitate stigma, surrounded by the staminal tube bearing numerous filaments (Purewal and Randhawa *1947*, Purseglove *1968**).

The flower opens shortly after sunrise and remains open until about noon. The petals wilt in the afternoon

FIGURE 132.—Okra plant with pods.

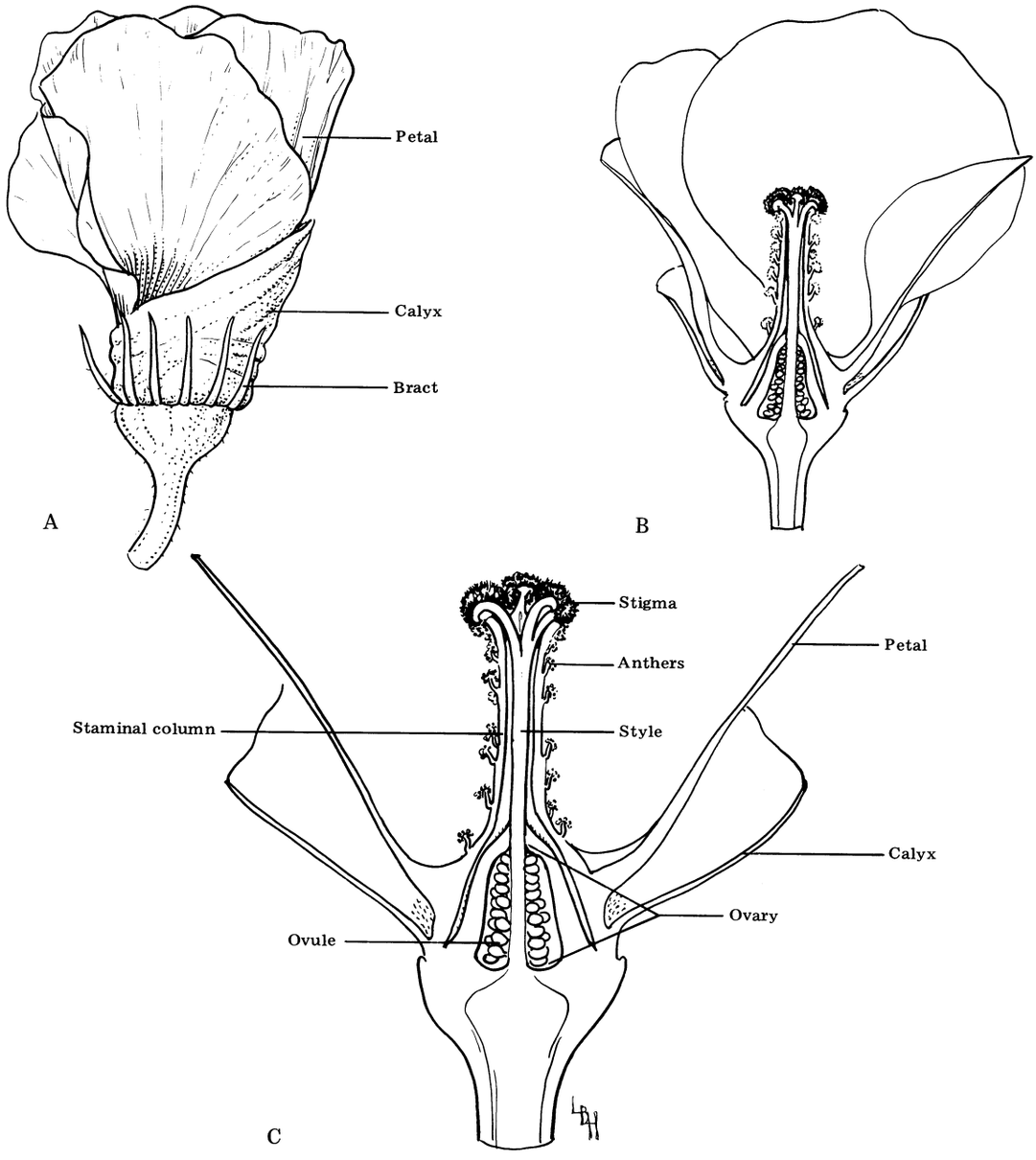

FIGURE 133.—Okra flower. *A*, Side view, × 1; *B*, longitudinal section, × 1; *C*, longitudinal section of staminal column, × 2½.

and usually fall the following day. The anthers dehisce 15 to 20 minutes after the flower opens, and some of the pollen comes in contact with the stigma.

Pollination Requirements

The okra pollen grain is large with many pores, and every pore is a potential tube source; therefore, many tubes can develop from one pollen grain (Purewal and Randhawa *1947*). Okra is self-fertile, and, when the anthers come in contact with the stigmas, self-pollination may result; however, cross-pollination also occurs. Purewal and Randhawa (*1947*) reported that 100 percent of both bagged and open flowers set fruit, but they did not indicate the degree of seed setting in the two treatments. They also reported 4 to 18 percent cross-pollination.

If the anthers deposit an adequate number of pollen grains on the stigmas to fertilize all of the ovules, an outside agency is not needed to transfer the pollen. However, if an inadequate amount of pollen contacts the stigmas leading to each carpel, and some of the ovules are not fertilized, that area around the unfertilized ovule is less well developed.

Pollinators

Okra is not wind pollinated. It is freely visited by honey bees and bumble bees, but the value of insect pollinator visitation is unknown. Studies should be made of seed production and pod development of bagged, selfed, and cross-pollinated okra flowers to clarify the pollination requirements and needs for pollinators.

Pollination Recommendations and Practices

None.

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OLIVE

Olea europaea L., family Oleaceae

The olive is grown commercially in California on about 27,000 acres where 52,000 tons, valued at $12.8 million, were produced in 1970. In addition, in 1970, we imported 16.3 million gallons of olives in brine and 64 million pounds of edible olive oil.

Plant

The olive tree is usually 15 to 20 feet tall, but sometimes reaches 30 to 35 feet when fully developed and properly nurtured, with oval 1- to 3-inch gray-green leaves and gray branches. Its beauty, sturdiness, and symmetrical growth make it a prized ornamental as well as a commercial fruit tree. It will live hundreds of years in mild, arid climates. It blossoms profusely in the spring, producing the well-known oval, one-seeded, green to blue-black fruit about an inch long. It is cultivated somewhat like other warm-weather fruit or nut trees. In the grove, the trees are spaced well apart (35 to 40 feet) so the sunlight can reach the tree on all sides.

Inflorescence

The cluster of one to two dozen, 4 mm, cream-colored to white fragrant flowers that develops in the axil of the leaf is usually shorter than the leaf itself. The individual flower has four valvate corolla lobes, a short four-toothed calyx, and two stamens that produce pollen copiously and little, if any, nectar (fig. 134). The flower opens before pollen is released from the anthers so cross-pollination can occur before selfing with the flower is possible. The flower may be either perfect and potentially fruitful with a plump green pistil, short style, and green ovary; or only staminate with a yellow abortive pistil (Condit *1947*). No purely pistillate flowers occur. Most cultivars are self-fertile, but some are self-sterile, and others are intermediate (Crider *1922*, Morettini *1957*, Mort *1952*, Pierce *1896*). Occasionally, a poor fruit crop results from a flowering of almost entirely staminate flowers (Hartmann and Opitz *1966*).

Honey bees collect pollen rather sparingly from the olive even though it is present in great abundance at flowering time. Sometimes, an olive honey flow is reported by beekeepers, but Silvestri et al. (*1947*) and Pellett (*1949**) believed that the food source was honey dew from aphids on the olive and not nectar from the blossoms.

Pollination Requirements

The pollination requirements of different cultivars of olives vary considerably. Crider (*1922*) listed two self-sterile, one partly self-sterile, and five self-fertile cultivars. Bradley et al. (*1961*) showed in greenhouse studies that even in self-pollinating cultivars, the pollen tubes of other cultivars grew down the style faster than self pollen tubes under the same temperature conditions. They found that if pollen tube growth was too slow, the embryo sac began to degenerate before the tube reached it; therefore, no fertilization would result. They concluded that "the chances of fertilization were greater in cross- than in self-pollinations, as indicated by the higher percentages of pistils in which a pollen tube reached the embryo sac."

Hartmann and Opitz (*1966*) stated that most varieties examined in Italy were self-sterile, a few were self-fertile, and some were partially self-fertile. They also stated that both in Portugal and in California satisfactory crops are obtained when some cultivars are planted in solid blocks although highest and most consistent yields are obtained in orchards where two cultivars are interplanted. This, they said, reaffirmed former studies at Davis and Winters, Calif., that cross-pollination of some varieties will increase fruit set in some years.

Pollinators

Wind is considered the primary agent in the transfer of olive pollen. Honey bees visit the trees for pollen, and the general knowledge of bee activity on other plants would indicate that if they moved freely from plant to plant they would effectively transfer some pollen between varieties. Should insignificant wind movement—in the proper direction—occur during flowering so that it would fail to transfer the pollen adequately then the activity of honey bees could supplement wind activity.

Honey bees do not collect olive pollen as avidly as they do that of other plants. To create heavy olive flower visitation, might require a relatively heavy concentration of honey bee colonies in or near the grove. There is no information on the concentration that might be desired. Studies in this area would be productive.

Pollination Recommendations and Practices

None.

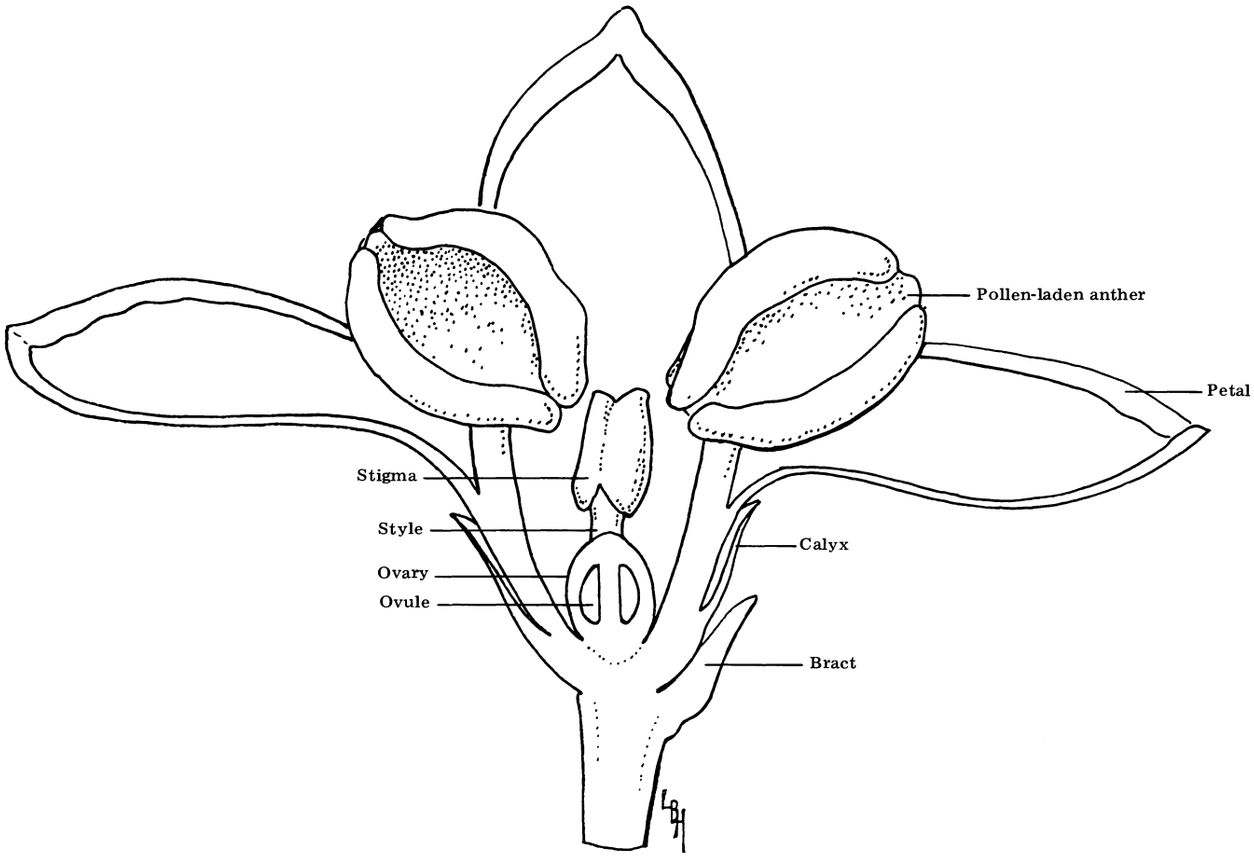

FIGURE 134.—Longitudinal section of olive flower, × 20.

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ONION

Allium cepa L., family Amaryllidaceae

Onions are grown in just about every country in the world. They are used in salads, as a raw or cooked vegetable, and as a condiment. Five related species of *Allium*, sometimes grouped with or referred to as onions, are also used in lesser amounts for food seasoning or embellishment. These include *A. ascalonicum* L., shallot; *A. fistulosum* L. (see "Welsh, Japan, or Spring Onion"); *A. porrum* L. (see "Leek"); *A. sativum* L., garlic; and *A. schoenoprasum* L. (see "Chives"). Garlic and shallot present no pollination problem, as they seldom flower, and when flowers do appear on garlic they are sterile so seeds are unknown. Both are propagated by bulblets or cloves (Bailey *1949**, Mann *1952*, Mann and Little *1957*).

As shown in table 14, the six *Allium* species can generally be distinguished from each other by gross characteristics.

Table 14.—Gross characteristics of Allium *species*

Species of *Allium*	Shape of leaves	Length of stalk	Character of bulb
		Inches	
Onion	Round, hollow	24-48	Large.
Welsh onion	do	12-20	Indistinct.
Chive	Round and hollow, forming tufts and sods	6-24	Do.
Shallot	Round, hollow	([1])	Numerous, small.
Garlic	Flat, narrow; 24 to 36 inches long, 1 inch wide	([1])	Bulbs with several parts (cloves).
Leek	Flat and leafy toward base; 24 to 36 inches long, 2 inches wide	24-36	Slightly broader than the stem.

[1] Flower stalk rare.

About 4,000 acres of onions were grown for seed in 1969, the value of the seed being about $4 million. This seed was used to produce 100,750 acres of green (shallot, scallion) or bulb onions of commerce, valued at $107.8 million.

Seeds of the southern types of onions are produced in southern California and southwestern Arizona. Northern type seeds are produced primarily in Colorado, Idaho, New York, Oregon, and Utah (Hawthorn and Pollard *1954**). Better seed growers obtain 800 to 1,000 pounds of seed per acre (Comin *1946*), although there are great variations in yields with years, growers, fields, and cultivars. Best seed yields are obtained when the seeds are produced on nontransplanted or seed-to-seed plants (500 to 700 lb/acre with more than 1,500 lb/acre reported) as compared to 300 to 500 lb/acre with up to 1,000 lb/acre reported from seed-to-bulb-to-seed production (Duncan *1965*). Sakharov (*1958*) reported the equivalent of 533 lb/acre in Russia.

Plant

When the plant is grown for production of green or bulb onions, it is treated as an annual, which rarely gets more than about 1 foot tall. The seeds are planted in the field or started in protected areas then transplanted, when a few inches tall, into the field. A few weeks later, when the top growth or the bulb has reached the proper size or condition, the entire plant is harvested and the desirable parts marketed. No seeds are produced and no pollination is involved.

When seeds are produced in western Idaho and eastern Oregon the mother bulb is replanted either late in the fall to overwinter in the soil or held in storage for spring planting. Seed-to-seed production is accomplished in the same area and in the Southwest by sowing seed in July and leaving plants to develop a seedstalk the following spring. According to Vincent (*1960*), larger bulbs of 3 inches or more produce more seeds per acre (690 pounds) than smaller ones; 2½ to 3 inches (685 pounds), 2 to 2½ inches (680 pounds), or 1½ to 2 inches (495 pounds).

In the springtime, the bulbs initiate normal growth, then produce from 1 to 20 flower stalks, 3 to 4 feet tall. This is referred to as "bolting," an undesirable trait in green or bulb onion production but essential in seed production. Bolting is strongly influenced by day length and temperature (Jones and Emsweller *1936*), and cultivars are bred to bolt at certain times in different areas. For this reason, northern and southern types are not interchangeable. Many cultivars have been developed for different regions and purposes—northern and southern, purple and white bulbs, strong and mild-flavored (Magruder et al. *1941*).

Inflorescence

The ashy-gray, 50 to 2,000 florets are borne in a simple oval umbel 6 to 8 inches across at the top of the elongated seedstalk. The individual floret, only 3 to 4 mm in length, has six stamens in two whorls of three each, a simple wandlike style leading to a three-celled ovary with two ovules in each cell (fig. 135). The anthers of the three inner stamens open first, and one after another, shed their pollen. Then the anthers of the outer whorl open, also at irregular intervals. Most of the pollen is shed between 9 a.m. and 5 p.m. of the first day the flower is open. All of it is shed within 24 to 36 hours after the flower opens and before the stigma becomes receptive (Jones and Rosa *1928**, Rodrigo et al. *1936*). Nectaries occur at the base of the stamens, and the nectar accumulates between the ovary and the inner stamens (Knuth *1909*, pp. 453–458*; Roberts and Struckmeyer *1951*).

When flowering begins, only a few flowers open each day on an umbel, but the number increases until at full bloom 50 or more florets may be open on a single day. They continue to open over a 2-week period, and 30 days or more may be involved in the flowering on all of the flower stalks. Moll (*1954*) showed that a flower may be pollinated as much as 6 days after it opens and found no significant difference in the percentage of set flowers pollinated 1 or 3 days after opening. Mann and Woodbury (*1969*) stated however, that pollen germination declined rapidly after the first day to zero percent by the sixth day. They concluded that the decline would be much more rapid under field conditions, making the age of the pollen an important factor in pollination. Nye et al. (*1971*) were in agreement in that they found that pollen taken from flowers opening in the morning was two or three times as viable as that taken from the flowers in the afternoon.

The flowers are attractive to many species of bees and other hymenoptera, flies and other diptera, and numerous other orders of insects that feed upon the nectar,

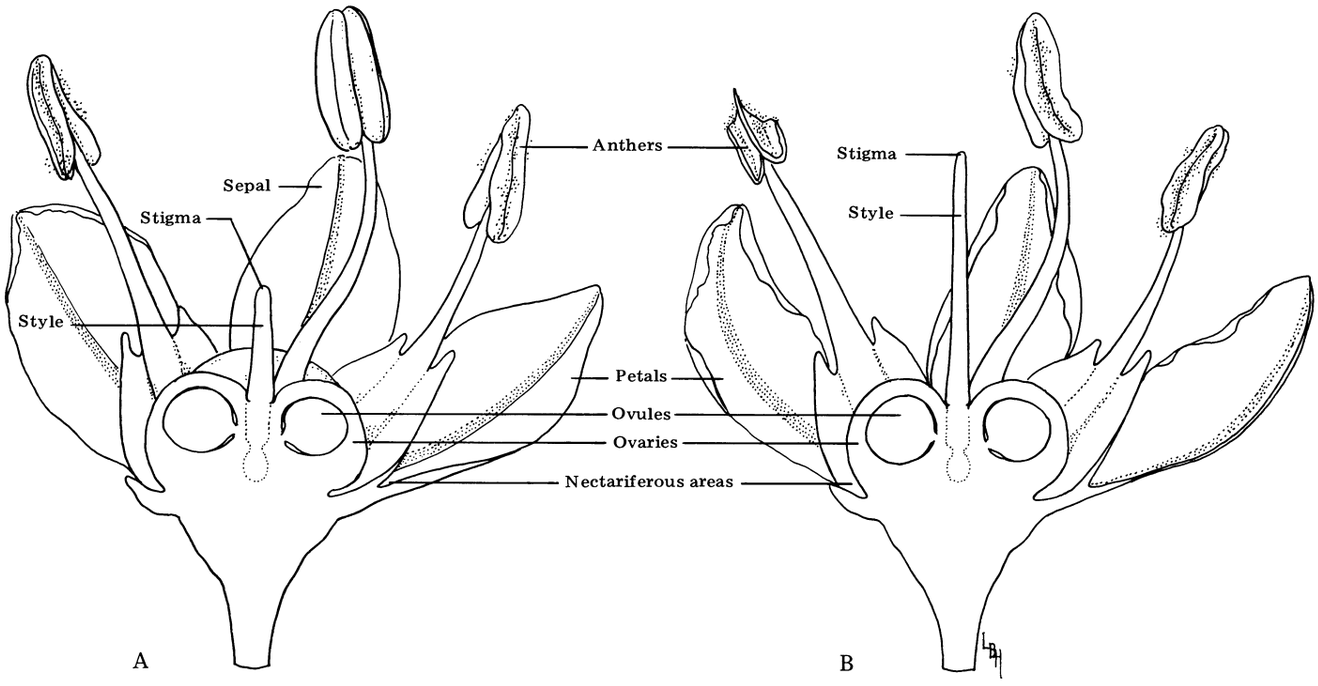

FIGURE 135.—Onion floret, ×10. *A*, Male or staminate stage, with anthers releasing pollen, but style short and stigma not receptive; *B*, female or pistillate stage, with anthers no longer releasing pollen, but style elongated and stigma receptive.

pollen, or both (Lederhouse et al. *1968*, Bohart et al. *1970*, Jones and Emsweller *1934*, Shaw and Bourne *1936*). The nectaries are shallow, and, unless the nectar is rapidly removed by insects, it can be easily seen glistening in the sunlight like a tiny jewel.

Beekeepers occasionally obtain crops of onion honey with a characteristic onion flavor that disappears after a few weeks. Ewert (*1942*) reported that superphosphate and potassium fertilizers caused the nectar of onions to be richer in sugar, but the volume was not increased. The effect on the insect visitors was not reported. Waller (*1970*) and Waller et al. (*1972*) believed that a high level of potassium in the nectar might be an important clue to the reluctance of bees to visit onion flowers. Jula et al. (*1965*) calculated that onions produced 71 percent as much nectar per day as the highly attractive sainfoin.

Pollination Requirements

Pollination in the onion flower occurs when pollen is transferred from the dehiscing anthers of one floret to a receptive stigma of another floret. Effective transfer of pollen between florets on an umbel or on an individual plant can transpire through the action of an outside agent, but self-pollination within the floret is impossible. Cross-pollination between plants is common and even obligatory in the fertilization of male-sterile onions used in hybrid seed production. Van der Meer and van Bennekom (*1968*) reported only 9 percent self-fertilization, and later (*1969*) they concluded that seed set was less at lower temperatures than at higher ones.

The discovery of male sterility in onions (Jones and Emsweller *1936*) made the production of hybrid onions possible under commercial conditions, and most of the onion seed produced now is hybrid seed. The procedure for utilization of male-sterility in the onion, which should be applicable to any crop plant in which male sterility is inherited in a similar way, was shown in detail by Jones and Clarke (*1943*).

In the production of hybrid seed, the grower plants a male-fertile row of a desired line to supply pollen to three to 10 rows of the male-sterile line (Franklin *1958*), from which the hybrid seed will be obtained. Naturally, the greatest volume of hybrid seed possible is desired; therefore, the male-fertile or "bull" rows are kept at a minimum provided pollen is distributed sufficiently to set seed. Erickson and Gabelman (*1956*) showed that pollen dispersal from a point was logarithmic, with pollination at 7 feet from a source being only one-half that occurring at 1 foot. To secure maximum seed set, the grower encourages pollen dispersal to the maximum degree possible (Jones and Mann *1964*).

MacGillivray (*1948*) showed that highest seed production occurred at Davis, Calif., when plants received more than sufficient irrigation. Likewise, Hawthorn (*1951*) obtained consistently higher seed yields with higher soil moisture. Nye (*1970*) reported that pollinator response to "wet" treatments was scarcely apparent, but use of nitrogen and phosphorus fertilizers caused decreased flower attractiveness.

Pollinators

Wind is not a factor of significance in onion pollination (Erickson and Gabelman *1956*). Insects are the primary vectors. When onion breeders want to get seed from a specific plant, they enclose the flowering umbel within a bag or cage and introduce flies to transfer the pollen, or, if cross-pollination is desired, the umbels of

the two lines are enclosed (Jones and Emsweller *1933*). In large cage breeding work or pollination studies, honey bees are the primary agents used (Bohart et al. *1970*, Moffett *1965*, Shirck et al. *1945*, Walsh *1965*).

In commercial production of seed, the provision of an adequate number of flies is impractical so the industry depends upon the honey bee as the primary pollinating agent. Bohart et al. (*1970*) reported 267 species of insect visitors on onion flowers, the most important of which were honey bees, small syrphid flies, halictid bees, and drone flies (fig. 136). Of these, only the honey bee can be manipulated and used in large-scale onion seed production. Kordakova (*1956*) and Sakharov (*1956*) gave major credit to the honey bee as a pollinator of onions in Russia.

Honey bees are effective pollinators of open-pollinated onions because both pollen and nectar are available on all umbels (fig. 137). In hybrid seed production where male-sterile plants are used, only the nectar collectors move freely from pollen-sterile to pollen-fertile plants, making the necessary transfer of pollen from male parent to female parent. Honey bees then become less than ideal pollinators of male-sterile onions. Pollen-collecting bees confine much of their activity to the pollen-producing rows without adequately visiting and cross-pollinating the male-sterile rows (Lederhouse et al. *1972*). A strictly nectar-collecting type of honey bee would be ideal because it would cross-visit and effectively pollinate the male-sterile flowers. In the absence of this perfect type of bee, the grower can only try to compensate by having more honey bees present in the field. Shasha'a's [30] conclusion, that too many bees may be detrimental, needs further study.

PN-3824
FIGURE 137.—Honey bee collecting pollen from onion blossoms.

FIGURE 136.—Onion breeders place flies in a cage with onion flower heads to cross-pollinate specific plants.

The lack of intense attractiveness of onions to bees, may cause the bees to neglect the crop, particularly if another highly attractive crop is in flower. The grower's only alternative is to make his crop as attractive as possible with best cultural practices and to use a heavy population of bees. Even then, the seed yielding potential of the crop may never be attained (Franklin *1970*).

More research is needed on the factors that affect attractiveness of onions to honey bees (Sanduleac *1969*, Singh and Dharamwal *1970*). Franklin (*1970*) noted that mere placement of colonies of honey bees in the onion field does not guarantee that the bees will work the onion. Although Nye et al. (*1971*) reported an average of 100 bees per 100 feet of male fertile rows and a maximum of 40 per 100 feet on the male sterile rows, the number of honey bee visitors needed per onion plant, umbel, or linear feet of row has not been determined.

Stuart and Griffin (*1946*) used different rates and times of application of nitrogen on onions in the

[30] SHASHA'A, N. S. LIMITATION STUDIES OF SEED SET IN THE ONION (ALLIUM CEPA L.) (LILIACEAE). Ph. D. dissertation, Utah State Univ., Logan. 1972. [Unpublished.]

greenhouse, and used honey bees to provide the pollination. Their best production was 3.2 seed stalks per plant and 7.5 grams of seed per plant with a high nitrogen application from August 15 to January 1, low nitrogen during January-February (blooming), then high nitrogen until maturity.

Pollination Recommendations and Practices

As early as 1936, Shaw and Bourne (*1936*) indicated that growers of onion seed might find it useful to provide themselves with a supply of bees. They did not go into detail as to number of colonies, strength, or location. In a brief note without details, Hamilton (*1946*) stated that a grower produced much more onion seed than he had in the past after he rented eight colonies of bees. Sanduleac (*1961*) stated that bees increase production of onion and leek seed in Romania eight to 10 times, and he recommended about two colonies per acre. Without supporting data, Le Baron (*1962*) stated that the use of bees for pollination of onions in the Imperial Valley of California was a "must," and that two colonies per acre had given good results (fig. 138).

There have been no clear-cut guidelines on the use of bees for maximum onion seed production, and many beliefs based on limited observation have arisen. These include the size of the colony cluster, its relative stage of development, and previous usage. The growers have learned through experience that the use of honey bees is essential and are frequently frustrated by the erratic activity of the bees. They have generally adopted the practice of renting five to 15 colonies of bees per acre and having them placed in or adjacent to their seed fields at flowering time. One suggestion has been to have about two colonies per acre delivered when flowering is well started, then an additional two per acre at 3- to 4-day intervals to take advantage of "naive" bee behavior and maintain some level of nectar foraging activity throughout the blooming period.

PN-3825

FIGURE 138.—Honey bee colonies placed by onion field to pollinate the flowers in commercial seed production.

Much information is needed on the factors that influence the activity of bees on onion flowers because, as Franklin (*1970*) pointed out, the mere placement of colonies in the field does not guarantee that the bees will work the onions. Continuous nectar foraging activity is the essential factor in hybrid onion fields especially during the peak period of flowering.

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PAPAW OR PAWPAW

Asimina triloba (L.) Dunal, family Annonaceae

The papaw, not to be confused with the papaya, is native from New York to the Gulf of Mexico and west to Wisconsin and Texas (Gould *1939*). It is rarely cultivated other than as a dooryard planting, but it (Anonymous *1969*) is just awaiting final development. Its fruit is most prized of the native species of Annonaceae. It belongs to the same family as the cherimoya and related custard apples and produces a similar, delicious, many-seeded fruit.

Plant

The papaw is a small, shrubby, deciduous tree, 15 to 20 feet tall, with straight upright branches forming a rounded crown. The oblong, glossy leaves are 6 to 12 inches long. The plants usually occur in thickets of many specimens in a small area. The greenish to yellow, banana-shaped fruit is 3 to 7 inches thick and turns brown when ripe (fig. 139). It ripens in the fall. The seeds are about an inch long, flat, blackish brown, and imbedded in the soft, edible pulp (Walden *1963*). From ½ to 1 bushel of fruit may be harvested from one tree.

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FIGURE 139.—Papaw branch with leaves and fruit.

Inflorescence

The chocolate, dark-purple, or maroon-colored flowers are about 2 inches across. They occur on last year's growth, solitary or in small clusters. They are protogynous, the three to 15 stigmas becoming receptive about 24 hours before the pollen is shed from the surrounding anthers borne on short fleshy filaments. The short styles lead to the numerous ovules to produce the large compressed seed (Ochse et al. *1961**). There are six petals, the three inner ones small and erect, the larger ones forming a corolla similar to a tulip blossom.

Pollination Requirements

The stigma, being receptive before the anthers dehisce their pollen, requires pollen from another flower. Selfing is impossible (Ochse et al. *1961**).

Pollinators

Evidence has shown that pollination is accomplished by insects especially honey bees bringing pollen from older flowers. Knuth (*1908*, p. 54*) stated that "In the first (female) stage of anthesis the three inner petals lie so close to the stamens that insect visitors (flies) cannot suck the nectar secreted at the bases of the former without touching the already mature stigmas. In the second (male) stage the stigmas have dried up and the inner petals have raised themselves so that the anthers—now covered with pollen—are touched by insects on their way to the nectar. Cross-pollination of the younger flowers is therefore effected by transference from the older ones."

Pollination Recommendations and Practices

None.

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PAPAYA

Carica papaya L., family Caricaceae

The papaya is sometimes called papaw or pawpaw, but in the United States these names are generally restricted to *Asimina triloba* (L.) Dunal (see "Papaw").

Papayas are grown to a limited extent in continental United States. They have been tried in Texas and in California, have never exceeded a few hundred acres

even in Florida (Harkness *1967*), but are more common in Hawaii and Puerto Rico. The 1964 United States Census of Agriculture showed that 32 farms in Florida produced almost 1.5 million pounds of fruit, while 266 farms in Hawaii produced almost 22 million pounds.

Papayas grow from about 32° N. to 32° S. latitude, from sea level to 5,000 feet altitude. They are killed by frost but do well in full sun or under irrigation. They do not occur in the wild, probably originated in Mexico or Costa Rica, and now consist of many cultivars (Purseglove *1968**).

The ripe fresh fruit (90 percent water, 4 to 10 percent sugar) (Wolfe and Lynch *1940*) is eaten throughout the tropics for breakfast, dessert, in salads, jams, ice creams, and soft drinks. The dried latex or "milk" of immature fruit yields papain, a proteolytic enzyme similar in action to pepsin, which is used as a meat tenderizer (Becker *1958*). It also creates shrink-resistance in wool.

Plant

The papaya is a dioecious or hermaphrodite herbaceous plant, rather than a tree, that grows to 30 feet tall, but more frequently 10 to 20 feet. It is grown for its melonlike fruit, on a rarely branched trunk, having a terminal crown of palmately lobed leaves to 2 feet across. The fruit weighs 1 to 20 pounds, may be 3 to 20 inches long, oblong to round, with a five-angled cavity that may contain more than 1,000 blackish, round seed 1/8 to 1/4 inch in diameter. Pistillate flowers produce ovoid-oblong to nearly round fruits, but hermaphrodite flowers usually produce pear-shaped, cylindrical or grooved fruits (fig. 140). The skin it thin, smooth, and green, turning yellowish or orange when ripe. The flesh is orange or reddish orange and soft, with a mild pleasant flavor. The fruit matures 6 to 8 months after pollination (Bailey *1949**). Purseglove (*1968**) stated there were many cultivars but that they were difficult to maintain in dioecious plants. He considered the hermaphrodite cv. 'Solo' to be one of the best, producing pear-shaped fruit about 4 inches by 6 inches and weighing about a pound. When 'Solo' is grown, the female plants are removed so that fruits of uniform shape and size are produced on the hermaphrodite plants.

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FIGURE 140.—Papaya fruit on a section of the plant.

The usual spacing of these plants is 8 to 12 feet apart (Purseglove *1968**), but when male and female plants are used one male is used for each 10 to 25 female trees (Greenway and Wallace *1953*, Harkness *1967*). Yields in a season may vary from 30 to 150 fruits per tree, usually 20 to 40, and may amount to as much as 150 tons per acre. For papain production in East Africa, one male for every 25 to 100 female plants is recommended (Purseglove *1968**).

Inflorescence

The fragrant but complex flowers of the more or less dioecious papaya are described and illustrated by Lassoudiere (*1969*). In general, the five-petal *staminate* flowers occur in pendant panicles, 25 to 75 cm long, the corolla is trumpet shaped, 2.5 cm long, narrow, and creamy-white or yellow, with 10 short stamens inserted at the throat of the corolla in two whorls. The 3.5 to 5 cm *pistillate* flowers are solitary or in small cluster, 3 inches or more long, on a short stalk in axils along the trunk (Popenoe *1920*, Pope *1930*). The corolla of five fleshy yellow petals is almost completely free of the large, 2 to 3 cm, pale-green ovary, which is terminated by five sessile deeply cleft, fan-shaped stigmas. Some selections produce a higher percentage of female flowers than others (Sfemanthani *1965*). Pistillate plants can be recognized easily by the long (3 to 4 feet) hanging panicle on which no fruit or only inedible fruit is produced (Harkness *1967*). The nectar is relatively thin (24 to 34 percent), and bees usually prefer to visit the staminate flowers only for pollen (Allan *1963*).

In addition, there are three types of *hermaphrodite* flowers (Higgins and Holt *1914*; Storey *1937*, *1941*, *1958*, *1969*), namely:

Hermaphrodite, *elongata*, has an elongate pistil that develops into an elongate fruit, and 10 stamens borne at the throat of the corolla.

Hermaphrodite, *pentandria*, has a more or less globose ovary that develops into a five-furrowed fruit, and five stamens attached by long filaments near the base of the ovary and lying in furrows between the lobes of the ovary.

Hermaphrodite, *intermedia*, has some or all (2 to 10) of its stamens distorted, and its pistil distorted and developing into a ridged or irregular-shaped fruit.

Furthermore, staminate and hermaphrodite plants may undergo sex reversal and become pistillate (Free *1970**). Such sex reversal does not occur in pistillate plants; however, pistillate plants may be sterile in warm weather then become fertile during cool weather. Honey bees collect pollen from the staminate and hermaphrodite flowers and nectar from the pistillate and hermaphrodite flowers. The corolla tube of the staminate flower is too narrow to permit entrance by the bees and too deep to permit their proboscis to reach the nectar secreted at the base of the corolla (Bayless *1931*). Hummingbirds (Brooks *1936*) and sphinx moths (Stam-

baugh *1960*, Traub et al. *1942*) can apparently reach this nectar. Malan (*1964*) reported that honey bees were the most active insects around papaya flowers.

Pollination Requirements

Pollen must be transferred from the staminate flowers to the pistillate ones if seeded fruit develops. Some commercial varieties are known to be parthenocarpic; therefore, pollinating agents are not necessary. Harkness (*1967*) stated that hermaphrodite flowers will self if bagged but did not indicate how the pollen would be moved from the anthers to the stigmas. Cheema and Dani (*1929*) and Traub et al. (*1942*) showed that flowers bagged to exclude pollen set fruit, but it was seedless with both size and quality reduced. The pollen should come from staminate plants, because pollen from hermaphrodite ones is inferior (Wolfe and Lynch *1940*). The length of time individual flowers are open, and releasing pollen or receptive to pollen, has not been determined. Since 1,000 or more seeds may be produced in a single fruit, well over 1,000 viable pollen grains must be deposited on the stigma while it is receptive. Fruits with fewer than 300 seeds are usually not marketable (Allan *1963*), and the more seeds, the larger the fruit. The Hawaiian types are generally known to be able to set fruit without the need of any staminate plants.

Pollinators

Purseglove (*1968**) stated that the method of natural pollination is not known with certainty. Stambaugh (*1960*) stated that sphinx moths are the sole pollinating agents of the papaya. Prest (*1957*) and Agnew (*1941*) considered wind as the primary agent. Agnew also stated that bees are occasionally seen gathering pollen although they are not particularly attracted by the flowers on the pistillate plants. Storey (*1941*) considered papaya to be pollinated by wind and insects. Brooks (*1936*) gave honey bees some credit, but he and Traub et al. (*1942*) also gave credit to the hummingbird moth for the transfer. Marin Acosta (*1969*) recorded 17 species of insect pollinators, including *Trigona* spp. and *Xylocopa* spp.

Allan (*1963*) showed that the papaya in South Africa is pollinated by insects, especially honey bees. When he covered plants with a 16-mesh-per-inch screen, only two fruits per plant developed, and they had an average of only six seeds. This showed that not wind but larger insects pollinated the flowers. Malan (*1964*) showed that neither wind, nor gravity-dispersed pollen, nor insects that could pass through 16 mesh-per-inch wire gauze were effective. He believed that honey bees were the most effective pollinating agents of papaya and recommended their use by growers.

Pollination Recommendations and Practices

There seems to be no recommendation for the use of pollinating agents on this crop, other than the recommendation by Malan (*1964*) that growers of papaya use bees, and by Allan (*1963*) that growers keep bees in their orchards. The data, however, indicate a need for pollen transfer from stamens to pistils, and, since the honey bee is an easily managed pollinating agent, its value and use should be more thoroughly explored. In the meantime, the placement of beehives around papaya groves would appear to be good assurance that sufficient pollen is likely to be transferred to result in maximum quality fruit.

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PARSLEY

Petroselium crispum (Mill.) Nym., family Umbelliferae

Parsley is grown "nearly everywhere in home and market gardens alike" (Hawthorn and Pollard *1954**); thus, there is a relatively large demand for seed. In 1969, the United States produced 97,000 pounds on 139 acres and imported another 115,000 pounds. The green leaves are used as a garnish and as a seasoning of soups and other foods. Turnip-rooted parsley (var. *radicosum* Bailey) is grown for its thick parsniplike tapering root.

Plant

Parsley is normally a biennial when grown for seed. During the first year, it forms a dense rosette of leaves. In the second year, it develops a 3- to 6-foot stem with small greenish-yellow flowers (Jones and Rosa *1928**). The umbels are less dense than those of carrots. The seed is harvested in the fall by the method used in carrot seed production (see "Carrots") (Hawthorn and Pollard *1954**).

Inflorescence

The bisexual, 2-mm floret of the compound parsley umbel has five greenish-yellow petals, five stamens, two styles, and a two-celled ovary, each cell of which produces one seed. The flowers are less showy than those of carrots. According to Knuth (*1908*, p. 459*), nectar is secreted by an epigynous disk, which is freely exposed in the middle of the floret. He also indicated that the stamens ripen successively; then, after all have ripened and withered in a flower, the style begins to grow and the stigma becomes receptive.

Pollination Requirements

Darwin (*1889**) stated that bagged parsley plants set as many seeds as open plants, but the crossed seed produced by the open-pollinated plant had a very slight advantage. Jones and Rosa (*1928**) stated that the flowers are self-fertile, but their drawings indicate that the flower must receive pollen from another. Hawthorn and Pollard (*1954**) stated that the flowers are potentially self-fertile, but did not explain how self-fertilization might be accomplished.

Pollinators

No other information was found that insects, wind, or gravity influenced the pollination of parsley, except for the statement by Hawthorn and Pollard (*1954**) that insects aid in its pollination. If the stigma does not become receptive until after all pollen has disappeared, the nectar of the flower must lure the insect. Nectar-collecting insects and not pollen collectors would therefore appear to be the primary agents.

Pollination Recommendations and Practices

None.

PARSNIP

Pastinaca sativa L., family Umbelliferae

Parsnips are grown as a root crop like carrots, celeriac, and turnip-rooted parsley. The other umbelliferous crops are grown for their leafy tops (celery, chervil, parsley), seeds (anise, caraway, coriander), or both seeds and foliage (dill, fennel). Technically, the "fleshy root" that we eat is that portion of the plant below the leaves but above the taproot. Only about 50 acres are devoted to parsnip seed production. About 2,000 pounds of seed was imported in 1968.

Plant

According to Jones and Rosa (*1928**), the seeds are planted and the edible portion develops slowly the first year. During the second spring, a 3- to 6-foot branched, grooved, and hollow stem develops, with flowers in broad compound umbels. The seeds are harvested in the fall, and the roots, having given up their stored food in the development of the stalk, decay. Although all the common umbelliferous vegetables are slow growing, the parsnip is perhaps the slowest (Hawthorn and Pollard *1954**).

Inflorescence

The broad compound umbels of parsnips are less

compact than those of carrots. The ovary of the small, yellowish-green flower bears two styles, which are united at their base to form the large nectary or stylar foot. According to Beghtel (*1925*), nectar secretion begins before the anthers begin to dehisce. The stigma becomes receptive about 5 days later, and nectar secretion continues into the period of stigma receptivity. Just when secretion ceases has not been determined.

Pollination Requirements

The flowers on the outer edge of the umbel open first. They are normally pollinated with pollen from flowers toward the center of the umbel. The innermost flowers have receptive stigmas after all of the pollen on the umbel has disappeared. Unless insects bring pollen from other umbels to fertilize these stigmas, no seeds are produced. The pollen can come from umbels on the same plant or from other parsnip plants.

Pollinators

The flowers attract various insects (Hawthorn and Pollard *1954**). Knuth (*1908*, p, 495*) indicated the flowers especially attract beetles and dung flies. Pellett (*1947**) stated that parsnips are valuable honey plants, indicating that honey bees visit the flowers freely. The construction of the flower would indicate that honey bees as well as many other species of bees should be satisfactory pollinators if present in sufficient abundance.

Pollination Recommendations and Practices

There are no recommendations on the use of pollinating insects in the production of parsnip seeds. The construction and relationship of the sexual organs of the flower would indicate that insect visitation is necessary for seed set and that a high population of visitors is most likely necessary for maximum seed production.

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PASSIONFRUIT AND GIANT GRANADILLA

Passiflora spp., family Passifloraceae

The passionfruit is a perennial, vigorous, climbing, woody vine that produces an edible round or ovoid fruit with many small seeds. The fruit is eaten alone or in fruit salads, sherbets, ice cream, jams, and in cool drinks.

Commercial production of passionfruit in the United States is limited to Hawaii. A few plants are grown in dooryards in southern Florida and commercial planting in that area is recommended (Morton *1967*). No production figures are available, although Morton (*1967*) stated that in 1958, 1,200 acres was devoted to production of yellow passionfruit in Hawaii (see below), and the industry was firmly established on a satisfactory economic level. The volume of production of this crop is small compared to most other fruit crops. Worldwide, the greatest volume of production is in Brazil, but the fruit is also produced in Colombia, Venezuela, Australia, New Zealand, Kenya, South Africa, India, and Indonesia.

Passionfruit is known in Hawaii as lilikoi, in Australia as golden passionfruit, in Brazil as maracuja peroba, and in South Africa as yellow granadilla.

There are about 300 species of *Passiflora*, most of which are native to the warmer moist regions of the Americas, and many produce edible fruit, but only two species are cultivated—*P. edulis* Sims and *P. quadrangularis* L.

There are two recognized forms of *P. edulis*. The purple passionfruit, f. *edulis*, is the normal form. Its fruit is egg shaped or round, 1½ to 2½ inches in diameter, and purple when ripe. It has the best flavor but does not grow well in the wet lowlands. The yellow passionfruit, *P. edulis* f. *flavicarpa* Degener, presumably originated as a mutation from the purple passionfruit (Akamine and Girolami *1959*). Its fruit is slightly larger, 2 to 2½ inches in diameter, and deep yellow when ripe. The crop is suited to the lowlands of the tropics, but the fruit is more acid than that of the purple passionfruit. There are various cultivars of the yellow passionfruit.

Passiflora quadrangularis L., the giant granadilla, is also cultivated to a limited extent in Brazil for local consumption. It grows best in a hot moist climate, and produces a round or oblong, pale-yellow to yellowish-green fruit when ripe, which may reach 6 by 12 inches in size.

Plant

Cultivation and pollination requirements of both species are similar and will be combined in subsequent remarks. The plants are usually set in rows 10 feet apart with the plants 6 to 10 feet apart in the row. The vines are trained onto a trellis about 7 feet high. They are cut back to the ground each year but send up new runners to produce the next crop. A plant may be productive 4 to 6 years. The crop is usually grown from seeds in the nursery and transplanted to the field 3 to 4 months later when about 12 inches high. No information is available on seed quality in relation to cross-pollination between cultivars, which could influence productivity. Propagation by cuttings is possible, but is usually not practiced. Plants that are started in the fall produce a light crop the next year. If they are started in the spring, they produce a light crop the same year and a good crop the next year (Meurant *1959*).

Average yields in Kenya are 15,000 pounds of fruit per acre per year (Purseglove *1968**); however, 40,000 lb/acre of fruit with 35 percent juice content has been produced from choice strains of yellow passionfruit in Hawaii (Morton *1967*). Willis (*1954*) stated that in

Australia a yield of 100 bu/acre may be expected the first summer, 12 to 15 months after planting. The relation of pollination to these drastic differences is not given but likely plays an important part.

Inflorescence

The attractive and fragrant complete flower is 2 to 3 inches in diameter. It is solitary on the vine amongst the large 4- to 6-inch by 5- to 10-inch, three-lobed leaves. It has three bracts, a five-lobed calyx tube, five white spreading petals, a colorful filamentous corona, five strong stamens with large anthers, a triple-branched prominent style, each branch with an enlarged stigma, and a single ovary with several hundred ovules that, when fertilized, form the small seed within the fruit (fig. 141).

The passionfruit was named by early missionaries in South America who saw in it the implements of crucifixion, that is, the crown of thorns (corona), the five wounds (five anthers), the nails of the cross (divisions of the pistil), the whips and cords (the tendrils on the vine), and the spear (leaf).

Flowers of the purple passionfruit open at dawn and close about noon. Flowers of the yellow passionfruit open about noon and close at the end of the day. Flowering extends from early spring to late fall. Peak flowering occurs in late spring when one flower can be found per 2 to 5 feet of row (Nishida *1963*). Nectar is secreted at the base of the pistil stalk (Akamine et al. *1954*). The nectar is relatively rich (50 percent soluble solids).

The style is upright when the flower opens but recurves downward shortly afterwards until each branch is about on a level with the anthers. Shortly before the flower closes, the style returns to its upright position. About an hour is required for each change to occur. In some flowers, the style may remain erect, but such flowers are female-sterile, although their pollen is functional. The most effective time for pollination is after the style has recurved. At this time, the stigma is in the position where it is most likely to be brushed by pollinating insects, and the stigmatic fluid is present to insure adhesion by the pollen grains so the pollen tube growth can start. The stigma is receptive from the time of flower opening to closing (Cox *1957*). Pollen is released before the flower opens and before the stigma is receptive. The pollen is not windblown.

Pollination Requirements

The flowers of passionfruit are self-sterile, and some plants are even self-incompatible (Akamine and Girolami *1957*). Care must be taken, therefore, in the

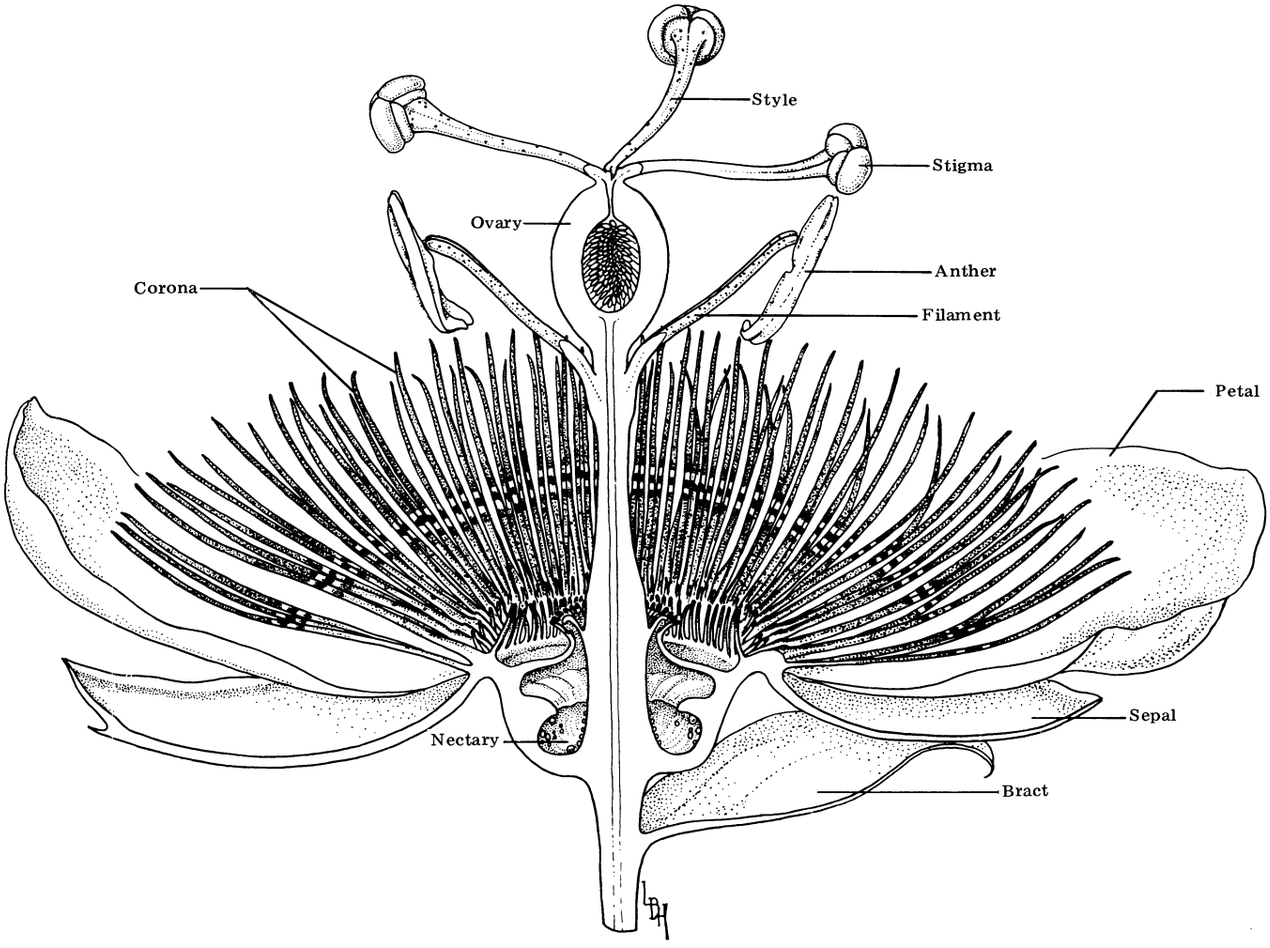

FIGURE 141.—Longitudinal section of passion fruit flower, × 2.

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selection and distribution of compatible clones or cultivars in the field to insure maximum fruit production (Gilmartin *1958*). The amount of pollen deposited on the stigma determines the number of seeds set and size of the fruit. The ovule must be pollinated and the seeds developed if juice is to form in the aril (pulp sac) (Knight and Winters *1962*, *1963*). A fruit can develop as many as 350 seeds. Unless about 100 ovules develop into seeds, the fruit is likely to be "hollow" (light in weight and with little juice). Few fruit develop with fewer than 50 seeds. There is no parthenocarpic set of fruit.

Akamine and Girolami (*1959*) found that fruit set, numbers of seed, fruit weight, and juice yield correlated with numbers of pollen grains deposited upon the stigma. They concluded that the maximum effect of pollination was not attained with their largest number (1,776) of pollen grains deposited on a stigma. This shows the importance of adequate bee visitation and pollen transfer between flowers within the brief span of time of stigma receptivity for maximum set of fruit.

Pollinators

Honey bees and carpenter bees (*Xylocopa sonorina* Smith, but known in Hawaii as *X. varipuncta* Patton) (Nishida *1954*, *1958*, *1963*) are the primary pollinators of passionfruit. Where they are abundant, carpenter bees are doubtless the best pollinating agents because of their larger size. Unfortunately, they are scarce or nonexistent in some areas. Honey bees can be established wherever desired, but they sometimes show preference for more attractive plants than passionfruit. Various species of diptera are sometimes frequent visitors to the flowers, but they are of little value in transferring the pollen between plants. They tend to feed, then rest, without going immediately to the next flower, as the nectar and pollen collecting bees normally do. Other insects in Hawaii never more than occasionally visit the flowers and are of no consideration as pollinators of passionfruit. In Brazil, *Trigona* spp., and *Epicharis* spp., are frequent visitors and are unlikely to sting, a factor of concern to some growers. In India, *Apis cerana* is the primary pollinator (Sriram and Raman *1961*).

Honey bees may visit the flowers for nectar or pollen or both. The nectar-collector crawls to the base of the style to the nectary, whereas the pollen-collector crawls busily over the anthers and is soon recognizable by the pellets of pollen in the corbiculae or pollen baskets on its hind legs. The type of food gathered depends upon competing food sources. Satisfactory crops are usually obtained with adequate pollinating agents.

Sriram and Raman (*1961*) reported that hand pollination of the flowers increased the set of yellow passionfruit by 21 percent over open pollination, whereas it increased set of granadilla by 84 percent.

Nishida (*1963*) noted that, because pollen is released shortly before the stigma is receptive, some growers feared that complete removal of pollen from the anthers by honey bees might be detrimental to fruit set (Bowers *1953*), but experimental results have not confirmed this. If all the pollen is removed from the flowers by honey bees, which is highly unlikely, at least the flower is pollinated first.

Nishida (*1963*) also noted that when flowering reached its peak (120 flowers per 200 feet of row), the honey bee population was 35 per 200 feet, or one bee for each four flowers. The number of carpenter bees varied according to their local population.

Pollination Recommendations and Practices

One of the major problems in passionfruit production is in obtaining a satisfactory set of fruit. This set can only occur when an abundance of pollinators are visiting the flowers and transferring pollen between compatible cultivars. One carpenter bee per 50 feet of row or one honey bee per four blossoms may be sufficient. The optimum number for maximum pollination of passionfruit is unknown. Pope (*1935*) mentioned large moths and hummingbirds, but in general, moths are not daytime feeders and hummingbirds are never sufficiently prevalent to pollinate crops grown commercially.

Honey bee colonies can be transported and increased wherever and whenever desired. Placement of redwood boards, poplar, or sisal logs can serve as carpenter bee nesting sites and may aid in increasing their numbers. Logs with carpenter bee nests in them may be transported to a field to establish this insect in a new area.

The yucca plant produces a flower stalk that eventually dries and becomes a choice nesting site for the carpenter bee; therefore, this plant might be grown near passionfruit fields. The larger the planting of passionfruit, the more efficient becomes the activity of the two primary pollinating agents—the carpenter bee and the honey bee—because competing plants are relatively reduced.

On most insect-pollinated crops, and this would appear to include passionfruit, the most satisfactory and surest way to supply ample pollination is by stocking the area with sufficient honey bee colonies. The number per acre of passionfruit might vary enormously with the (generally small) size of the crop and with competing plants.

A fact worth considering would be the interplanting of the purple passionfruit that has flowers open and attractive to bees from dawn to noon, and yellow passionfruit with flowers open from about noon to dusk. This might tend to lure and hold the activity of the bees within the field throughout the day and increase their pollinating effectiveness.

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PEACH AND NECTARINE

Prunus persica (L.) Batsch, family Rosaceae

The peach and the nectarine (*P. persica* var. *nectarina* (Ait.) Maxim.) differ primarily in that the nectarine has a smooth skin, but the peach is covered with needlelike hairs or fuzz. Nectarines are known as a single factor mutation of the peach. Nectarinelike fruit has been obtained from peach trees and peaches have been found on nectarine trees (Philp and Davis *1936*).

The farm value of the 1970 peach crop was $176.3 million compared to $10 million for nectarines. Peaches are grown on about 200,000 acres, 81,810 acres of which are in California. Nectarines are produced almost exclusively in California on 7,790 acres (Kitterman and Nelson *1971*).

Plant

The deciduous trees, set in the orchard about 20 feet apart, are usually trimmed to 8 to 16 feet in height (fig. 142). There are scores of cultivars only recognizable by the type of fruit they produce. Flowering occurs at about the same time each spring on all cultivars except for a few early and late blooming cultivars. The plant usually requires some winter chilling to promote normal growth and flower development in the spring. Freestone cultivars, those with fruits that break away easily from the stone or seed, are much more popular for the fresh market than the clingstone type in which the flesh of the fruit is firmly attached to the stone. The freestone 'Elberta' cv. has been the most popular of all cultivars, but it is being replaced by firmer, more attractive cultivars. The highly perishable fruit must be harvested at a precise stage of ripening.

PN-3828

FIGURE 142.—Peach orchard in bloom.

Inflorescence

The many attractive pink or reddish blossoms of the peach and nectarine appear in the spring at about the time leaf development begins (fig. 143). The structure of the flower is ordinary in that sepals are present but small; there are usually five rather oval petals, 25 to 40 mm across, and 15 to 30 pollen-laden anthers surrounding the single erect pistil through which the pollen tube reaches a single ovary, which contains two ovules. Following fertilization, only one ovule normally develops at the expense of the other, leading to the development of a one-seeded stone. As a result, the fruit develops asymmetrically (Stewart et al. *1967*). The peach ovary is covered with a dense coat of hairs. The nectarine ovary is usually bare, similar to that of the plum (figs. 144, 145).

Most cultivars produce pollen at the time the stigma is receptive. Nectar is secreted at the base of the corolla. The flowers are highly attractive to honey bees and other pollen- and nectar-collecting insects. The fact that only one ovule must be fertilized for a peach fruit to set as compared to hundreds of ovules in other fruit such as melons or papayas, enormously simplifies the pollination of the peach.

Normally, the flowers are fully closed at 6 a.m., but most of them are open by 10 a.m., and all are open by noon. They do not close at night; they may stay open and the stigma may be receptive for 3 days (Randhawa et al. *1963*).

PN-3829

FIGURE 143.—Peach blossoms.

Pollination Requirements

Considering the economic importance of the peach crop, surprisingly little has been done about its pollination requirements. There are many references to fruit production (for example, Cullinan *1937*, Hedrick *1917*, USDA *1967*), which usually state that most cultivars are self-fertile and a few are self-sterile (Kanato et al. *1967*, Lagasse *1926*). Many self-sterile cultivars have been largely or completely eliminated from the market, regardless of their other good qualities, because interplanting of cultivars and insect pollination are necessary in their production. These include 'Alamar', 'Candoka', 'Chinese Cling', 'Hal-berta', 'J. H. Hale', 'June Elberta', 'Mikado', and a few others. Unfortunately, the references to the self-sterility of such cultivars has tended to draw attention away from the "self-fertile" cultivars and the possibility that they might not be capable of fertilizing themselves without the aid of an outside agency.

GLASSHOUSE POLLINATION STUDIES

Grieve (*1879*) discounted the need for or value of bees in a glasshouse. Conners (*1922b*, *1926*) reported that peaches in a glasshouse failed to set unless pollinated by hand or bees because of a lack of air currents to sway the blossoms and cause the stamens to come in contact with the stigma. Coote (*1895*) also showed that when trees were grown in the greenhouse with bees to visit the flowers a heavy set resulted. Vermeulen and Pelerents (*1965*) obtained 84 fruits per tree in a glasshouse with bees but only five per tree with bees absent. Thompson (*1940*) reported on the value of bees to peaches in greenhouses in England.

BAGGING AND WIND POLLINATION STUDIES

Conners (*1917*) reported that trees of 'Belle', 'Early Crawford', 'Elberta', and 'Greensboro' cvs. caged to exclude insects set fruit readily. Later, he (*1922a*) mentioned the 'Susquehanna' as being self-sterile and that he discarded three other selections for that reason. Crandall (*1920*) found that more than twice as many bagged flowers set fruit if they were hand pollinated than if bagged only. Detjen (*1945*) performed a similar experiment with similar results, that is, flowers bagged and hand pollinated set more fruit than did open flowers, but flowers bagged only, without additional pollination, set fewer flowers. He felt that buffeting of the flowers by wind was sufficient to dislodge the pollen and transfer it to the stigma. Sharma (*1961*) reported that while bagged peach flowers "gave a commercial set without pollination insects," the set was higher on unbagged branches. Kerr (*1927*) bagged branches of 27 cultivars and found that 19 were "sufficiently self-fruitful, 5 did not set enough and 2 were unfruitful." Both Chandler (*1951**) and Langridge (*1969*) reported that there is little airborne peach pollen.

INSECT POLLINATION STUDIES

Factual tests on the relation of insects to pollination of peaches are woefully inadequate although numerous tests have given indications, and conclusions have been drawn, on the relation of insects to set of fruit on peaches. For example, MacDaniels and Heinecke (*1929*) stated: "Most peach varieties are self-fertile and present no pollination difficulties except that attributable to lack of sufficient insects at blooming time to accomplish self-pollination."

Bulatovic and Konstantinovic (*1962*) obtained better set on various species with exposed flowers than with selfed flowers, and they concluded that there was slightly more fruit set on all cultivars when visited by bees.

Rather thorough studies were conducted by Marshall et al. (*1929*) who summarized their findings with the statement, "Enough has been written to show that satisfactory crops from either self-sterile or self-fertile varieties of orchard fruits cannot be obtained unless there are plenty of honey bees or other pollen-carrying insects working in the orchard at the time the trees are in bloom." Murneek (*1937*) also stated that "Whether a variety is self-sterile or self-fertile insects are equally necessary for proper pollination and setting of fruit." Chandler (*1951**) stated that the pollen must be applied to the stigma by insects that visit the flowers. Jorgensen and Drage (*1953*) listed peaches as "largely self-fruitful," but "bees are necessary" in their pollination. Khan (*1930*) also concluded that cross-pollination is necessary to obtain good yields and that bees are the chief agents for cross-pollination.

Boller (*1953*) stated that "Some pollination occurs without the help of bees, probably by shaking of the

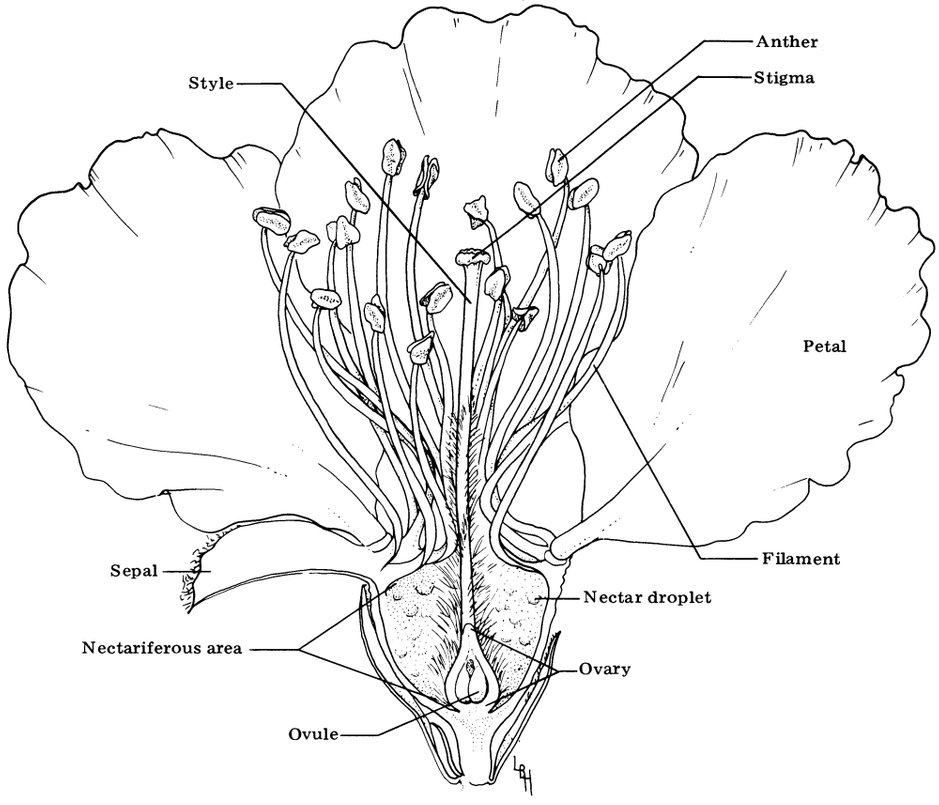

FIGURE 144.—Longitudinal section of 'Babcock' peach flower, ×4.

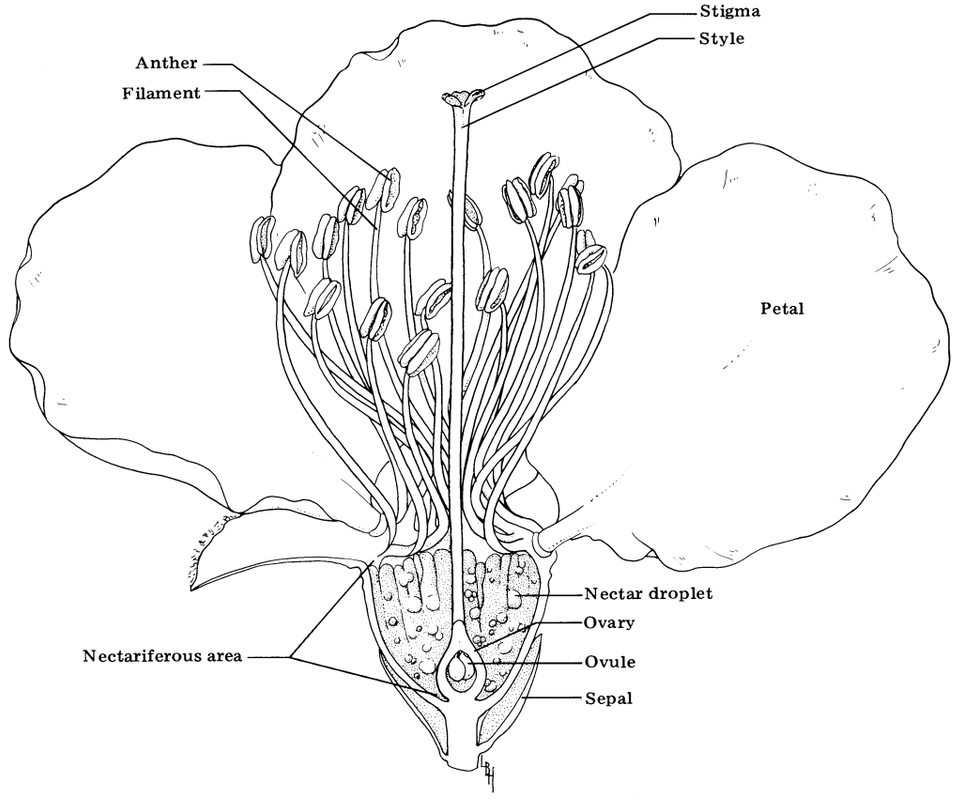

FIGURE 145.—Longitudinal section of 'Perfection' nectarine flower, ×4.

flowers by the wind. Whether we get enough self-pollination by this means is unknown. We do know that a small number of bees can do a lot of self-pollinating since almost every visit to a flower results in self-pollination."

H. W. Fogle (personal commun., 1971) stated that the flowers are receptive to pollination 4 to 7 days, depending upon the weather, but the set is unlikely "unless a bee or similar insect enters the flower and spreads the pollen around."

These references indicate that, although the actual data are sparse, pollinating insects are of value even for the self-fertile cultivars of peaches.

Some growers consider thinning of a heavy set of fruit to be a greater problem than pollination (Snyder et al. *1952*); however, thinning the fruit after flowering is easier than getting fruit to set if the flowers are gone and the set is inadequate.

Pollinators

The degree of pollination actually accomplished by wind as compared to insects is unknown. Also, if, as some references indicate, wind alone is insufficient and insects are needed, the number of visitors is unknown. If the weather is clear and mild, the bees will visit the flowers throughout much of the day; however, if the weather is cold or wet, bees may be absent. In visiting the nectaries in the base of the flower, the bee either pushes one or more anthers against the stigma or rubs against it. In either case, pollen is transferred to the stigma. If the cultivar is self-fertile, a high population of bees would not be needed to set an adequate crop (Boller *1953*). Should the population of bees in the area be inadequate, honey bees can be transported and placed in the orchard. The evidence indicates that their presence in the orchard is important. Randhawa et al. (*1963*) considered the honey bee most important as a pollinator of peaches. Yokozawa and Yasui (*1957*) reported that when the weather was generally cloudy and rainy the Diptera were the most common floral visitors, but during clear weather the Hymenoptera were more frequently observed on the flowers.

Pollination Recommendations and Practices

Numerous horticulturists have indicated that bees are beneficial to peaches, and most State bulletins recommend to growers that action be taken to increase the number of insect pollinators in the orchard. The growers are fortunate in that the peach flowers are attractive and ample pollination is obtained free when conditions are favorable, with bees coming long distances.

Newell (*1903*) urged the keeping of honey bees near peach orchards. Jorgensen and Drage (*1953*) considered bees necessary. Kelly (*1964*) made a study relating to cost of peach growing in Pennsylvania and found that an average of only one hive per 16 acres was used.

Benner (*1963*) recommended one strong colony of honey bees for each three to five acres of orchard just coming into bearing but stated that in older orchards one good colony of bees for each acre might be needed.

Several hundred colonies of honey bees are rented annually for pollination of peaches in New Jersey (J. C. Matthenius, Jr., personal commun., 1970). Most growers, however, take no action in relation to pollination of the crop.

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PEANUT

Arachis hypogaea L., family Leguminosae

Peanuts are also known as goobers, groundnuts, and pinders. Approximately 1.5 million acres were planted to peanuts in 1969, and the value of the crop was $311.3 million. This frost-sensitive plant is grown in the southeastern and southern States, primarily for its seed, the peanut, which is a pea and not a true nut. The foliage is sometimes used for livestock feed.

Plant

The peanut plant is an erect to spreading branched annual, 10 to 20 inches tall, that is cultivated in rows about 1½ to 3 feet apart. The seeds are planted in the spring after all danger of frost is past, and the crop is usually harvested before frost in early fall. The plant has a primary taproot with weak laterals that permit easy removal of the entire plant from the soil. The leaves have four leaflets, 1½ to 2½ inches long. The seeds develop just below the surface of the soil, but they are attached to the branches near the base of the plant.

Inflorescence

The first flowers appear near the base of each branch, 4 to 6 weeks after planting. Flowering continues along the branch for 6 weeks or more. The peanut flower is yellowish and about one-half inch in size. There may be one to several flowers in an inflorescence on the plant, but only one opens on one day, and there is an interval of one to several days between the opening of successive flowers. Smith (*1950*) stated that the peanut flower has a recurved beaked keel, with two petals fused along the dorsal edges to the apex but open ventrally at the base. There is a club-shaped stigma on a tortuous style extending beyond the eight functional and two sterile stamens (fig. 146).

The flower opens at sunup and pollen shedding occurs at once, the pollen accumulating between the anthers and stigma. Fertilization occurs 8 to 9 hours after pollination (Oakes *1958*). After pollination, the flower fades (Beattie and Beattie *1943*), and the ovary elongates to become the peg, which pushes into the soil (fig. 147). In 7 to 10 weeks, the peg matures into the reticulated pod of one to five edible seeds separated by slight constrictions (Gregory et al. *1951*).

The value of peanut flowers to bees is not clear. Apparently, there is no functional nectary within the flower although some references indicate (erroneously) that bees collect peanut nectar (Graham *1941**, Pellett *1947**). Pollen is collected by honey bees although

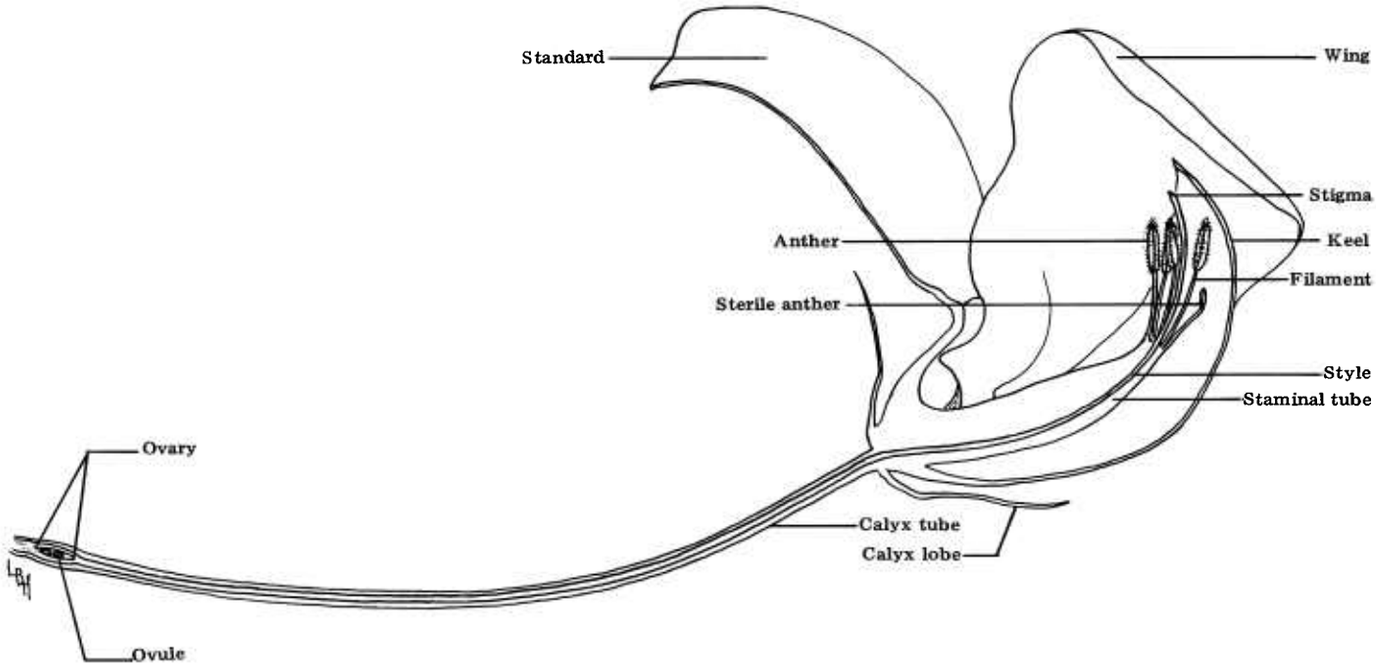

FIGURE 146.—Longitudinal section of peanut flower, × 5.

peanut plants are not considered to be a major pollen source by beekeepers.

Pollination Requirements

There is no doubt that peanuts are largely self-fertilized. The question is whether an increase in the set of seed is caused by cross-pollination. Some selections have a structure that impedes selfing and facilitates cross-pollination by bees. Reed (*1924*) reported that cross-pollination between cultivars occurs. Kushman and Beattie (*1946*) and Balhuis (*1951*) reported finding hybrids in peanuts. Stokes and Hull (*1930*) pointed out that the stigma of the mature flower " . . . *usually* lies buried among the dehisced anthers in the tightly closed keel petal so that self-fertilization is assured except for visitation by insects." Srinivasalu and Chandrasekaran (*1958*) noted that varietal differences exist for cross-pollination in relation to the protrusion of the stigma out of the keel. Leuck and Hammons (*1969*) reported that two cultivars have a structure in the flower that impedes self-pollination but which facilitates cross-pollination by bees. Leuck and Hammons (*1965a*) obtained no hybrids from caged plants but got a significant number from plants not caged. Later, they (*1965b*) reported that at least 80 percent of the peanut flowers in the open were actually tripped for pollen by bees.

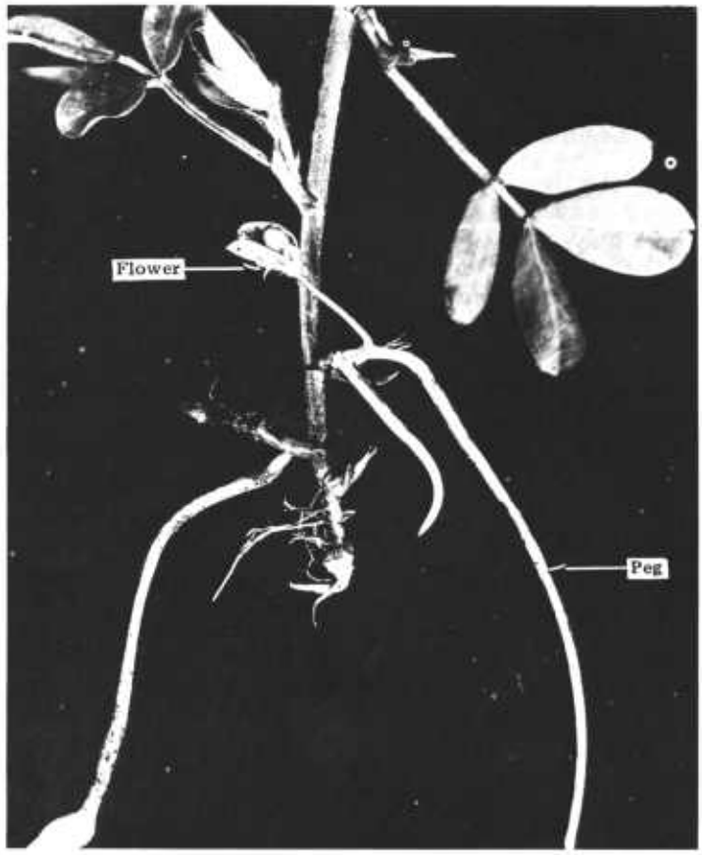

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FIGURE 147.—Flower and pegs of a peanut plant.

Girardeau and Leuck (*1967*) showed that caged flowers not manipulated in any way produced 4 to 10 percent fewer fruits than hand flexed or water-drip manipulated flowers. Also, their open plots produced a significant 6 to 11 percent more than plots caged to exclude bees. Culp et al. (*1968*) recorded differences in the amount of crossing that occurred in different areas and in different cultivars but made no mention of the relation of pollinating insects to these differences. Shibuya et al. (*1955*) associated one-seededness with insufficient pollen on the stigma.

Pollinators

There seems to be no doubt that the peanut flower may be cross-pollinated and that crossing is primarily by

bees. Hammons and Leuck (*1966*) showed that thrips are vectors of peanut pollen but that halictid bees were the principal visitors to peanut flowers at Tifton, Georgia. Hammons (*1963*), at the same location, noted that *Lasioglossum*, *Megachile*, *Bombus*, and *Apis* species worked peanut flowers. Hammons et al. (*1963*) and Leuck and Hammons (*1969*) added *Anthidium* and *Melissodes* species to the list of visitors but gave major credit for cross-pollination to species of halictids and megachilids. Diwan and Salvi (*1965*) stated that *Apis cerana* generally ignored peanut flowers, but Heide (*1923*) stated that the flowers were visited "actively and persistently" by *A. cerana*, and that *A. cerana* visited the flowers from 7 to 9 p.m. Gibbons and Tattersfield (*1969*) reported that *A. m. adansonii*, *Nomia* spp., and *Megachile* spp. visited the flowers in the Malawi area of Africa.

Leuck and Hammons (*1965b*) stated, "We conservatively estimate that in 1964, at least 80 percent of the peanut flowers were actually tripped for pollen each day by species of the combined bee complex." Unfortunately, they gave no indication of the bee population density, floral visitation, or bees per unit of flowers that provided this tripping. Hammons et al. (*1963*) noted that the halictids and megachilids were most abundant during the cool morning hours when most efficient pollination of peanuts occurs, whereas honey bee activity was spread over the day. No consideration was given to changing the degree of honey bee visitation by concentrating their numbers in the area.

If the 6 to 11 percent increase, which Girardeau and Leuck (*1967*) attributed to bee pollination, can be consistently obtained, it is of sufficient importance that consideration should be given to building up the bee population of large peanut plantings. This could be done by "saturation pollination" with honey bees if their use could be proven practical.

Pollination Recommendations and Practices

None.

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PEAR

Pyrus spp., family Rosaceae

All of the important pears growing in the United States, referred to as the French or European types, belong to *P. communis* L., except a few hybrids such as the 'Kieffer' and 'Le Conte', which are crosses between *P. communis* and the fire blight resistant Chinese sand pear (*P. pyrifolia* (Burm. f.) Nakai) (Davis and Tufts *1941*).

The estimated production of pears in 1971, was 701,120 tons, almost half of which (309,000 tons) were produced in California. Production in Washington was 165,400 tons and in Oregon, 174,000 tons. Production in other States was relatively insignificant. The total value of the crop was $63 million.

Plant

The pear tree may live 100 years or more and if unpruned may reach a height of 50 feet. When grown in orchards, however, the trees are usually pruned to 10 to 20 feet. Its general appearance is similar to the apple although its limbs are usually somewhat less gnarled and more upright. It flowers in the springtime about the same time that apples flower or slightly earlier. The fruit is consumed fresh, canned, preserved, or pickled. The trees are usually spaced 20 feet apart in the orchard, except for dwarf trees, which are sometimes as close as 12 feet (Davis and Tufts *1941*).

Although Hedrick (*1921*) stated that thousands of cultivars of pears are grown in Europe and the United States, the 'Bartlett', 'Williams', or 'Williams Bon Chretien', a European cultivar, is probably the most widely grown pear in the world (Griggs and Iwakiri *1954*). Other important European cultivars are: 'Anjou', 'Bosc', 'Comice', 'Hardy', and 'Winter Nelis' (Magness *1937*). According to Hedrick (*1938**), the Europeans have listed more than 5,000 pear cultivars; the Americans, more than 1,000 cultivars. Hedrick considered the 'Kieffer' next in importance to the 'Bartlett', the 'Le Conte' about like the 'Kieffer' in quality but not quite as good. Today, 'Kieffer' is important only in the Eastern and Southern States where better quality pears cannot be grown because of fire blight (Batjer et al. *1967*). The 'Winter Nelis', which was the standard winter pear in the United States, has been replaced in many places by the 'Anjou'. The relatively unimportant 'Pound' is grown primarily for its monstrous fruit (3 to 4 pounds each). Auchter and Knapp (*1937**) showed a production of 210 bu/acre for 'Kieffer' pears versus 140 to 160 for 'Bartletts'.

Inflorescence

Pear flowers are at least 1 inch in diameter, pure white, and in simple clusters (fig. 148). The flower is protogynous (the stigma of an individual flower is receptive to pollen before its anthers release pollen). The flowering on a tree usually lasts about a week. The flowers produce abundant pollen, which is highly attractive to bees (Tufts and Philp *1923*), but the nectar is low in sugar content (Vansell *1946*) and frequently fails to attract bees. When the flower opens, the style stands erect, the stigma is receptive, and the stamens are so bent inward that the unripe anthers are crowded together around the style but below the stigma (fig. 149). Later, they extend to the full height of the style and release their pollen. Unlike the plum and nectarine,

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FIGURE 148.—Branch of pear tree in full flower.

the pear does not have a deep cup lined with nectar tissue, but only five small, slitlike openings in the flat top surface or disk area between the petals and stamens (Vansell *1942**). Vansell showed that the percentage of sugar concentration of pear nectar was quite low, for example, apple, 46.2 percent; peach, 28.9; plum, 25.8; sour cherry, 23.5; 'Winter Nelis' pear, 9.9; and 'Bartlett' pear, 7.9. He observed that bees frequently visited other blossoms for nectar but visited pear blossoms only for pollen.

Brown and Childs (*1929*) stated that a full-bearing 'Anjou' tree at 15 years of age may have as many as 8,000 fruit buds, each of which contains a cluster of at least seven perfect flowers. A single tree may therefore produce as many as 56,000 flowers, all of which are potential fruit producers. They estimated that 1.96 percent of the flowers could set and produce a satisfactory crop. Powell (*1902*) stated that if 6 percent of a moderately blooming tree set fruit, a heavy crop would result. Brown and Childs (*1929*) showed that a 7.1 percent set resulted in production of 12,851 lb/acre over a number of years.

Pollination Requirements

The classic research by Waite (*1895*, *1899*) established the principles of fruit pollination and clarified the need for pollinating insects on fruit. In particular, he showed that the 'Bartlett' pear was self-sterile in Virginia and only set good crops when other cultivars were grown nearby so that bees could bring compatible pollen to its flowers. This basic pollination principle for pears was shown by Swayne (*1824*) (see also, Chittenden *1914*), but it was largely forgotten until Waite's

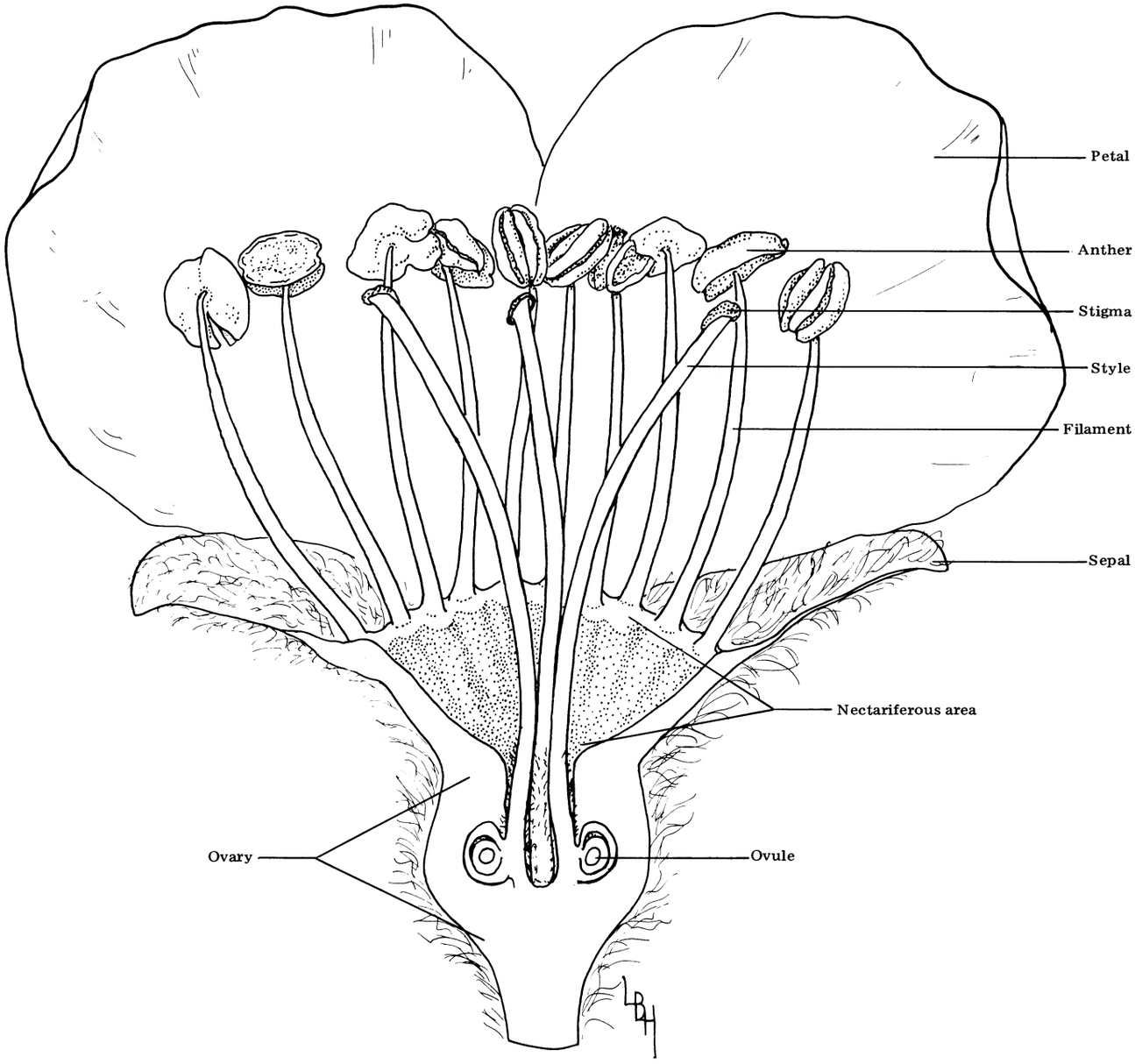

FIGURE 149.—Longitudinal section of 'Bartlett' pear flower, ×9.

research. Close (*1903*) also showed that neither 'Kieffer' nor 'Angouleme' set fruit on bagged flowers. Fletcher (*1907*, *1911*) showed that both 'Kieffer' and 'Bartlett', if planted in solid blocks in West Virginia and Michigan, yield poorly if not properly pollinated. Florin (*1925*) found that 'Bartlett' were self-sterile in Sweden. Powell (*1902*) recommended the interplanting of pollinizer cultivars with the 'Kieffer'. Kraus (*1912*) advised growers in Ohio to plant 'Anjou', 'Clairgeau', 'Howell', or 'Kieffer' with 'Bartletts' for cross-pollination.

Luce and Morris (*1928*) reported that the 'Bartlett', 'Bosc', 'Anjou', and 'Winter Nelis' were partly or entirely self-sterile in the Wenatchee, Wash., area. However, rumors began to develop that 'Bartletts' might not require cross-pollination and considerable controversy developed on the subject. Weldon (*1918*) reported that large solid plantings of 'Bartletts' in California produced satisfactory crops. Tufts (*1919*), after a study of fruit production from hand-crossed flowers and from commercial orchards, concluded that all 'Bartlett' orchards should be provided with facilities for cross-pollination, that is, supplied with other varieties and bees. Westwood and Grim (*1962*) showed that 'Bartlett' yields were inversely related to distance from the pollenizer.

Kinman and Magness (*1935*) stated that the setting of fruit by all important pear varieties is aided by cross-pollination under some if not all conditions in the Pacific States. Magness also admitted that in some areas in some years 'Bartlett' sets good crops where no provision was made for pollination but that in other years heavier crops might be expected if pollination were provided. Davis and Tufts (*1941*) also considered the 'Bartlett' varying from almost completely self-sterile in the Sierra Nevada foothills of California to only partially self-sterile under interior valley and coastal conditions. Under these latter conditions, orchards planted solidly usually produce satisfactory crops. Griggs and Iwakiri (*1954*) finally showed that it was not the area where 'Bartletts' grew but the conditions under which they grew that determined their fruitfulness. They showed that the inclination of 'Bartletts' to produce parthenocarpic fruit determines its need for cross-pollination. This was supported by Bulatovic and Konstantinovic (*1962*); Wellington (*1930*); Reinecke (*1930*); Griggs and Vansell (*1949*); Konstantinovic and Milutinovic (*1968*); and Griggs et al. (*1951*).

If the orchard is well cared for, it will set a commercial crop of parthenocarpic fruit in many of the main pear-growing areas. If conditions are not good for parthenocarpic set, cross-pollination by bees will insure set of the crop. Parthenocarpic fruit, being seedless, is more desired by the consumer, although Reinecke (*1930*) showed that such fruit does not keep as well as pollinated fruit.

Stephen (*1958*) showed that when 'Bartlett' trees were caged for several seasons, the amount of fruit that set declined rapidly in succeeding years whether the tree was caged without bees or with bees alone without a bouquet of blooms from other varieties. The first year, there was no apparent difference. The second year, production in the cage containing only bees declined 58 percent. The following year, production was down by 92 percent. Stephen believed that the ability to produce fruit-set parthenocarpically decreased as time increased after the tree was cross-pollinated. These studies indicate that parthenocarpic fruit may be produced satisfactorily in some parts of Western United States, although, as Griggs (*1970**) indicated, fruit set could be increased by interplanting pollinizers and using an ample supply of bees.

In other parts of the United States, 'Bartlett' should be interplanted with other cultivars and provided with bees. Evidently insect cross-pollination is essential for some cultivars in all areas (Hutson *1925*, van Laere *1957*) and for all cultivars in some areas. Where 'Bartletts' produce fruit parthenocarpically, the presence of other cultivars and bees can be an insurance in marginal seasons, and, during favorable seasons, tend to increase the number of seeded fruit. Lewis (*1942*) showed that parthenocarpy can be induced in some cultivars by frost. Steche (*1959*) showed that cross-pollination by honey bees trebled the crop when compared to the weight of fruit from self- or non-pollination.

Pollinators

Waite (*1895*, *1899*); Johnston (*1927*); Overholser et al. (*1944*); and Vansell (*1942**, *1946*) mentioned numerous species of insect visitors to the pear flowers, including hymenoptera, diptera, coleoptera, and other major groups. Like the other observers, Vansell (*1942**) found that the honey bee was the most important visitor of all. In an orchard adjacent to uncultivated brush and timberland, which should have provided an abundant supply of insect visitors, honey bees accounted for more than 62 percent of the visitors to the flowers over two seasons even though there were few colonies of honey bees in the area. Vansell pointed out that although blowflies accounted for 23 percent of the visitors, they were of little value as pollinators, and concluded that honey bees were "practically the only distributors of pear pollen." He noted also, as did Scullen and Vansell (*1942*), Smith and Bradt (*1967**), Stephen (*1958*), and Tufts and Philp (*1923*), that the bees showed a strong preference for pear pollen but weak interest in the nectar, which had a concentration of only 4 to 25 percent sugar, and which influences the bee foraging behavior (Free and Smith *1961*).

Pollination Recommendations and Practices

Most growers of 'Bartlett' pears in California make no attempt to interplant pollenizer cultivars or to increase the local pollinating insects although the evidence indicates that they would benefit at times by doing so. Growers in other areas, and of most other cultivars should provide for cross-cultivar pollination and arrange to some degree for placement of honey bee colonies in or near their orchards. The colonies should be strong, sheltered from cold wind, exposed to the warm sun, provided with clean water, and protected from pesticides—a standard operation in the pollination of most fruit crops.

The number of visits by insect pollinators to pear

flowers for optimum cross-pollination has not been determined. The pollinator population should be sufficiently heavy on cultivars that require cross-pollination that the bees are forced to forage on many blossoms to obtain a load of food. Waite (*1895*, *1899*) recommended that there be honey bees in the neighborhood or at least within 2 or 3 miles, and that each large orchardist should keep bees. Root (*1899*) recommended that hives should be within one-half mile of the orchard. Fletcher (*1900*) stated that the keeping of bees by the grower might become necessary. Hooper (*1935*) advised growers to have one or more hives of bees in the vicinity of the orchard. Tufts (*1919*), Davis and Tufts (*1941*), Stephen (*1958*), Brown and Childs (*1929*), Vansell and DeOng (*1925*), and various others recommended that one colony of honey bees per acre be scattered throughout the orchard. Batjer et al. (*1967*) and Luce and Morris (*1928*) recommended one strong colony per two acres. Corner et al. (*1964*) recommended two colonies per acre of pears.

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PEPPER, GREEN

Capsicum spp., family Solanaceae

The green garden vegetable or bell peper (*C. annuum* L.) comprises the major acreage of peppers in the United States. The well-known small and burningly pungent tabasco type (*C. frutescens* L.) is grown principally in Louisiana (Boswell *1937*). (See also "Black Pepper.")

Green peppers were grown on an estimated 50,350 acres in 1971, the crop having a valuation of $52.3 million. Florida was the leading State with 13,700 acres, followed by New Jersey (8,100), North Carolina (8,100), California (7,100), and Texas (6,800). Various other States produced less than 2,000 acres of this crop. Boswell et al. (*1952*) stated that about 50,000 acres were devoted to production of sweet or bell peppers (fig. 150) and 12,000 to 15,000 acres to the hot or pungent cultivars, so the acreage seems relatively stable.

The fruit is consumed, according to its pungency, in salads, cooked dishes, pickled or powdered, or in sauces.

Rosengarten (*1969**) defined *paprika* (fig. 151) as the dried, ground pods of ripe (red) pepper without the central placenta; *chili powder* as ground ripe pepper with oregano, cumin, garlic, etc.; and *cayenne pepper* as ground, whole, small, ripe fruits. *Capsaicin*, obtained from pepper, is used in the manufacture of ginger ale.

Plant

Pepper is a perennial woody plant, but because it is easily killed by frost it is usually cultivated in rows, as an herbaceous annual. The plant is 2 to 4 feet tall, erect, but many-branched and compact. The fruit is picked each few days as the individual pods approach mature size but before they ripen.

Inflorescence

The pepper flower, 3/8 to 5/8 inch across, is usually

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FIGURE 150.— 'California Wonder' bell pepper, with flowers and fruit.

PN-3833

FIGURE 151.—Type of sweet pepper often used in making paprika or ornamental strings of dried pepper.

whitish but may be tinged with purple. It is usually solitary in the axils of the branches or leaves, but occasionally there are small clusters of flowers. It has five stamens with bluish anthers (not united as in the tomato) and a single stigma that may vary from slightly shorter than the anthers to much longer (fig. 152). The corolla is somewhat bell- to wheel-shaped and white in *C. annuum*, but greenish white in *C. frutescens* (Smith and Heiser *1951*).

The flower opens within the first 2 hours after sunrise and is open less than 1 day (Erwin *1931*). The anthers may open from 1 to 10 hours after the flower opens, but frequently they fail entirely to dehisce (Murthy and Murthy *1962*). Hirose (*1957*) stated that tabasco pepper flowers dehisce more slowly than other peppers. Nectar is produced and accumulates in the nectary at the base of the ovary. The quantity depends on many factors, an important one being the cultivar involved (Martin et al. *1932*). The flowers are visited by bees for both the nectar and the pollen (Erwin *1932*, Markus *1965*, Odland and Porter *1941*), but the attractiveness of the flowers to bees is comparatively low, and visitation is influenced by relative attractiveness of competing plants.

Pollination Requirements

The pollination requirements for maximum production of the different cultivars of pepper is not clear. Jones and Rosa (*1928**) stated that "Self-pollination takes place, in general, but there appears to be a considerable percentage of cross-pollination also, for many hybrids have been noticed as a result of growing different varieties near each other." Hawthorn and Pollard (*1954**) implied the same thing. Cobley (*1956**) concluded that both self and cross-pollination occurred for which he gave credit to ants. Dempsey (*1961*) found no difference in set of open flowers and those caged in special cone cages. Cochran (*1936*) stated that flowers emasculated and bagged set fruit as well as open-pollinated flowers, which without qualifications is difficult to accept. Later, however, he (*1938*) conceded that cross-pollination takes place more frequently than is generally supposed. Martin and Crawford (*1951*), Peterson (*1958*), and Shifriss and Frankel (*1969*) reported male sterility in peppers, which is accentuated by higher temperatures (Bashir *1953*). Hirose (*1959, 1962*) reported that high temperatures 13 to 17 days before anthesis causes pollen abortion and the deterioration of pollination efficiency. Odland and Porter (*1941*) found that none of the varieties tested were entirely self-fertilized and concluded that there is more cross-pollination than is generally realized.

Erwin (*1932*) measured the effect of pollination on set of fruit. He found that only 46 percent of self-pollinated flowers set compared to 71 percent that were left to open pollination by bees. Nagarathnam and Rajamani (*1963*) obtained only 6 to 11 percent set of the flowers present. Angeli (*1957*) reported that hybrid pepper ripens earlier, produces more, and is more disease resistant than the parents. He also stated that production of seed by open pollination was unsatisfactory because of the lack of insect pollinators.

Cochran (*1932*) reported that high nitrogen and low soil moisture at flowering time increase set, but high nitrogen and high moisture increase production.

The period of receptivity of the stigma has not been too well determined, but apparently it functions only the first day the flower opens.

Smith (*1932*) noted that few tomato flowers with elongated styles develop normally and set fruit. As previously mentioned, the pepper style varies in length also. Quite conceivably, in the absence of pollinating insects, the long style would prevent pollen from the anthers reaching the stigma, and fruit setting would be prevented or reduced. Markus (*1965*) noted that crossing occurred primarily between 7 and 11 a.m.

The evidence indicates that pepper flowers do not always release their pollen, or if it is released, it may not come in contact with the stigma. Under such conditions, the transfer of pollen between flowers by an outside agency is essential.

Pollinators

Boswell (*1937*) stated that peppers are cross-fertilized to a considerable extent but did not state what agencies were responsible. Although ants are frequently mentioned in relation to pollination of peppers, their type of activity, the lack of a dense coat of hairs on their body, and their limited number in relation to the blossoms present in a commercial planting, would indicate that they have received more credit as pollinators of pepper than they deserve. Honey bees and other bees visit the flowers of pepper on warm bright days (Hawthorn and Pollard *1954**) or during dry

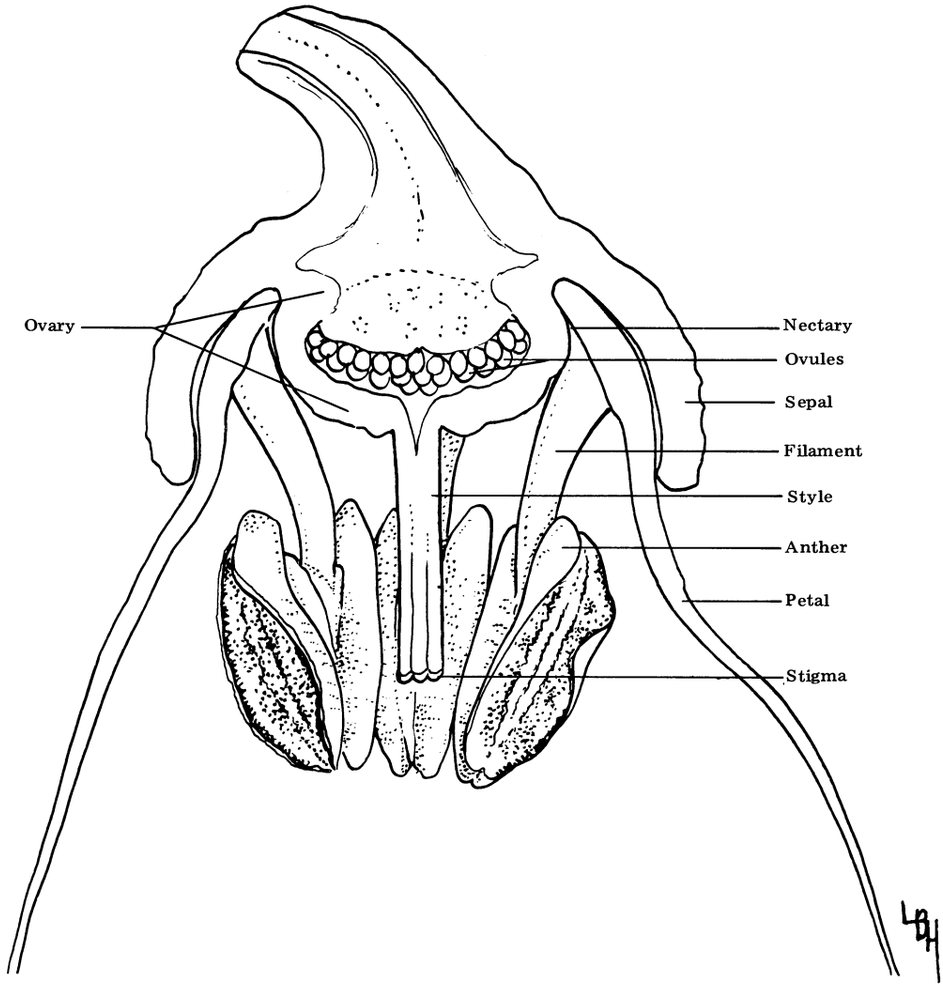

FIGURE 152.—Longitudinal section of flower of bell pepper, × 12.

periods (Erwin *1931*, *1932;* Markus *1964;* Odland and Porter *1941*; Pammel and King *p. 605*, *1930**).

Other members of the family Solanaceae are noted for their low attractiveness to bees, for example, potatoes, tobacco, eggplants, and petunias, although when other sources of nectar or pollen are scarce these plants may be visited. This would appear to apply to peppers also. Wind, rain, and other insects appear to be of little or no value in the pollination of peppers.

Pollination Recommendations and Practices

None.

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PERSIAN CLOVER[31]

Trifolium resupinatum L., family Leguminosae

Persian clover is an annual legume adapted to the heavy low-lying soils of the Southern States from Tennessee southward. It is grown for pasture, for hay, and as a green manure crop. The area, volume, or value of production is not large as compared to other clovers. Not too much has been published on this plant (USDA *1960*).

Plant

The seeds are planted in the fall, and a rosette of leaves is formed during the winter. When spring comes, the upright stems appear and grow rapidly to 8 to 24 inches. They flower and produce seeds in late spring or early summer, then the entire plant dies—somewhat earlier in the season than white clover. The stems do not root at the nodes or creep on the surface, as do many other species of *Trifolium*, but because they are hollow they lodge badly. Once established, reseeding is unnecessary as seeds are produced in abundance, many of which shatter.

Inflorescence

The heads are small, pink to light purple, and somewhat flat. They are about the size of those of wild or small white clover and are borne in the leaf axils on ½- to 2-inch stems. Honey bees work Persian clover flowers for nectar and pollen (Hollowell *1943*). Weaver and Weihing (*1960*) stated that plants reaching full bloom about April 15 on the gulf coast of Texas still had a considerable amount of bloom on May 7. The flowers of one cultivar were fairly attractive to bees, whereas those of another were seldom visited.

Pollination Requirements

Lancaster (*1949*) indicated that Persian clover is not dependent on bees. Hollowell (*1943*) stated that the flowers are self-fertile and self-pollinating, but honey bees work the flowers for nectar and pollen and undoubtedly help in increasing seed production. Weaver and Weihing (*1960*) also stated that Persian clover does not require insect pollination, but their caged plots that included bees yielded about nine times as much seed as plots caged without bees. Wheeler and Hill (*1957**) also indicated that bees increase seed production. The degree of help is not clear, but the small amount of data available indicate that bees are highly beneficial and that they should be used if maximum seed production is desired.

Pollinators

The meager evidence available indicates that honey bees are the principal pollinators of Persian clover. Weaver and Weihing (*1960*) stated that Persian clover yielded "little nectar per blossom, but the bees foraged from the individual florets very rapidly," which helped to compensate for the small amount of nectar.

Pollination Recommendations and Practices

The number of colonies per acre or bees per square yard of Persian clover to provide maximum benefit has not been determined. The desired concentration of bees is probably similar to that for crimson clover.

[31] See "Clovers, General."

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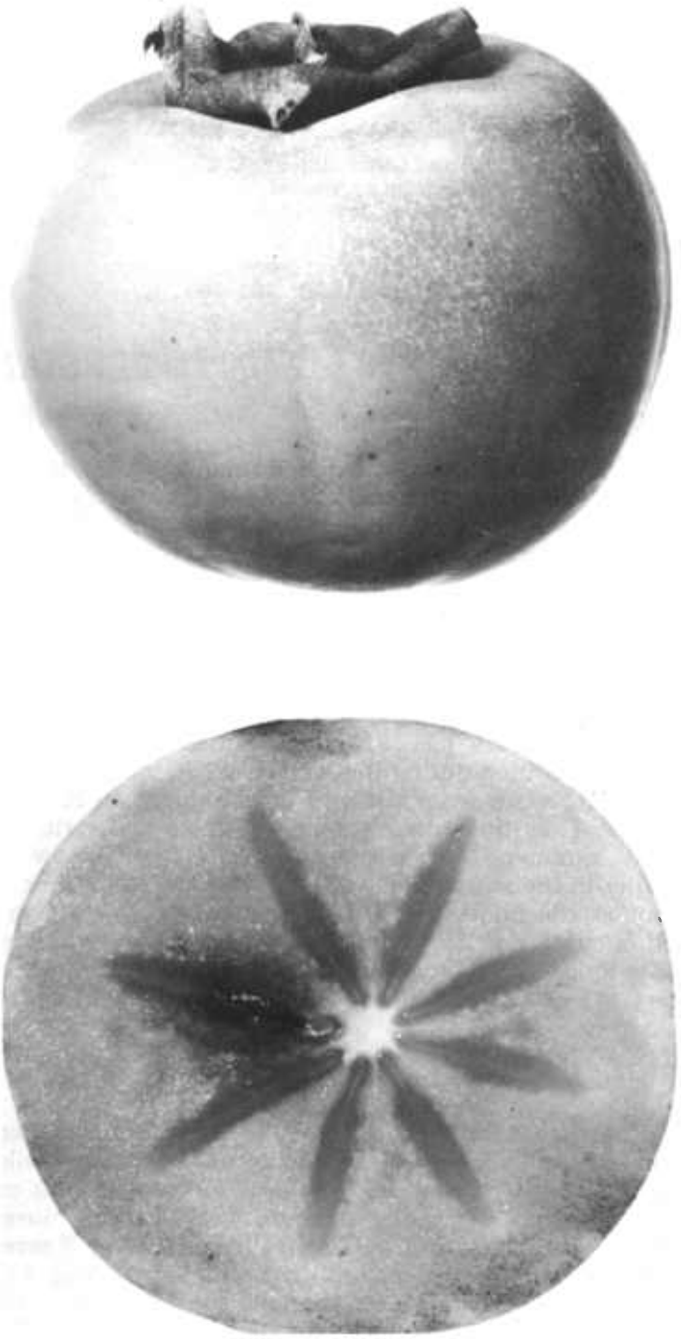
PERSIMMON (ORIENTAL OR KAKI)

Diospyros kaki L. f., family Ebenaceae

The Oriental or Kaki persimmon (fig. 153) is cultivated for its delicious, highly nutritious, pale-orange to red, 1- to 5-inch, zero- to eight-seeded fruit that may be eaten out of hand or used in culinary dishes ranging from appetizers to yogurt.

It is grown on about 500 acres in California (Swedberg and Nelson *1970*) and to a lesser extent in several other Southern States. It is hardy as far north as Pennsylvania (Griffith and Preston *1961*).

The Oriental should not be confused with the smaller-fruited but edible American persimmon (*D. virginiana* L., and *D. texana* Scheele) (fig. 154), which are common forest plants but rarely cultivated except as dooryard ornamentals (Pape *1957*). The fruits of *D. virginiana* also contain up to eight large seeds. The trees are generally dioecious, with single pistillate flowers and usually three staminate flowers in a group. The pollen is generally carried from the staminate to the pistillate flowers by insects, but Fletcher (*1942*) stated that wind may also contribute. The flowers are a good source of nectar and are visited throughout the day by bees for nectar and pollen (Pellett *1947**). Oertel (*1939*) listed *D. virginiana* as a major source of nectar in five States and of some value in 22 States, indicating that in acres it is far more common than the Oriental one. (See also Condit *1919*, and Preston and Griffith *1966*.)



PN-3834
FIGURE 153.—Complete and sectioned fruit of kaki persimmon.

Plant

The Oriental persimmon is a round-topped, usually deciduous, tree to 20 feet high unless it is competing with other trees for light, when it might reach 40 feet. It has 3- to 7-inch elliptic glossy leaves and ¾-inch long, yellowish-white flowers. The fruit is variable in shape—oval, round, globular, or elongated—and ribbed with brownish pulp surrounding the seed, if any are present. Cultivation is similar to that of citrus or stone-fruit trees grown in warmer areas. Camp and Mowry (*1945*) reported 14 to 18 percent total sugars in the mature fruit.

Inflorescence

The campanulate flowers are three-quarters of an inch long and yellowish white, with outfolded, prominent green sepals extending beyond the corolla. The staminate ones have 16 to 24 stamens, the pistillate ones have eight staminodia (Bailey *1949**) (fig. 155). Nectar secretion is probably similar to that of the American species. The blossoms hang downward, with the stigma

rarely exposed beyond the petals, which offers little opportunity for wind pollination. Hume (*1913*) stated that no crosses between *D. kaki* and *D. virginiana* had ever resulted in production of viable seed.

Pollination Requirements

Ryerson (*1927*) stated that Oriental persimmon trees may be staminate, pistillate, or both, but that pollination is not essential for fruit setting. He believed that ample crops of seedless fruits could be obtained without pollination. Hodgson (*1938*) confirmed that Oriental plants produce seedy fruits if pollinated but set a few of the preferred seedless fruit if no pollen is available. Later, Hodgson (*1939*) stated that there was a high degree of parthenocarpy, and that various cultivars of Orientals contained the following types of plants: (1) Pistillate; (2) pistillate, sporadically monoecious; (3) monoecious; (4) monoecious, sporadically staminate or pistillate; and (5) staminate.

Gould (*1940*) concluded there are pollination prob-

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FIGURE 154.—Fruiting branch of American persimmon.

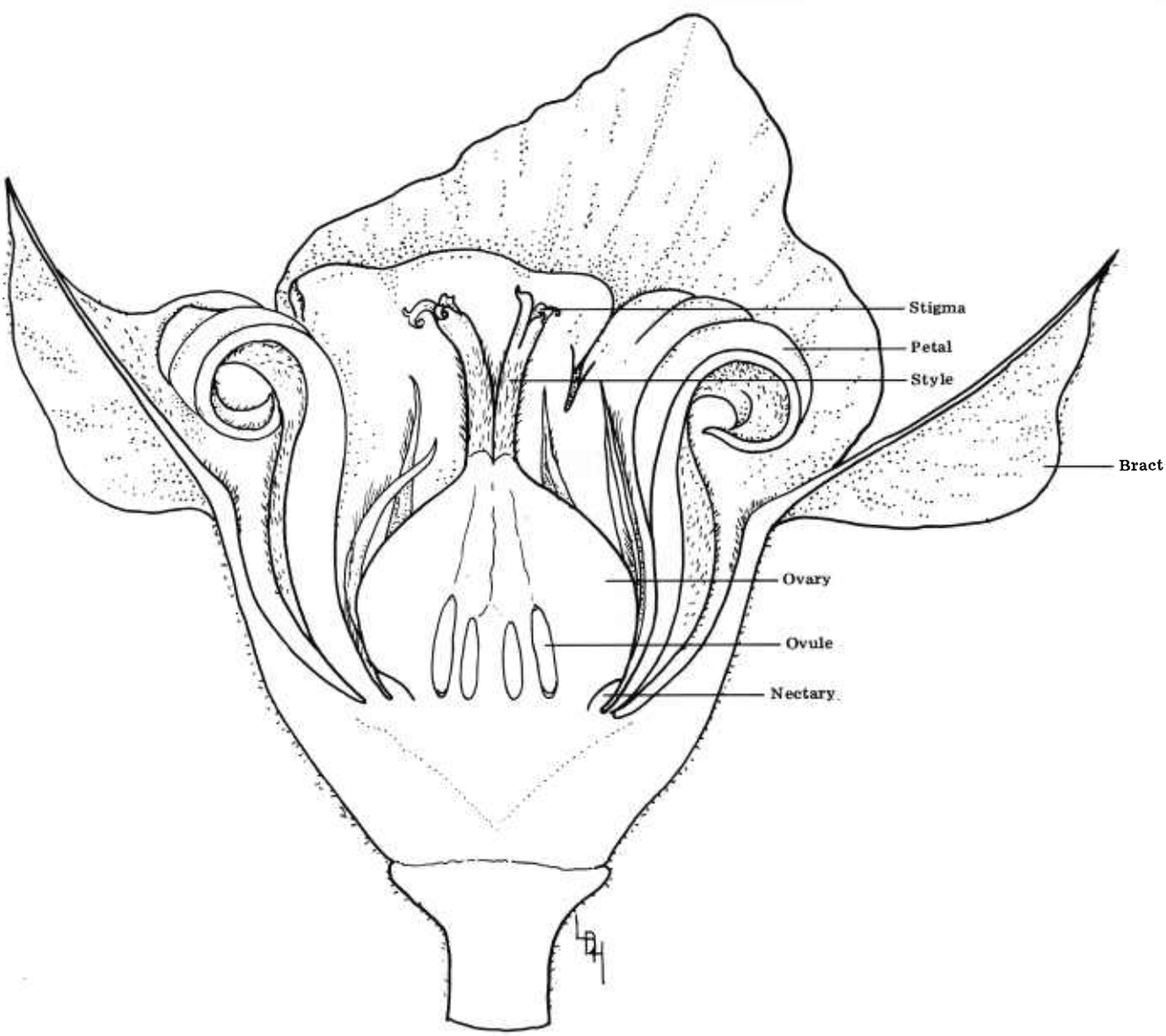

FIGURE 155.—Longitudinal section of 'Fuji' kaki persimmon blossom, × 5.

lems with Oriental persimmons just as there are with many other fruits. Some cultivars will develop some fruit to maturity without pollination, whereas other cultivars drop their fruit prematurely or fail entirely to set without pollination. The length of time to flower opening and the actual time of pollination of individual flowers has not been determined.

Pollinators

Honey bees and bumble bees visit persimmon blossoms freely for nectar and pollen and would appear to be dependable agents in the transfer of pollen. Fletcher (*1942*) stated that pollen is generally distributed by bees although wind can carry the pollen great distances. The effectiveness of wind on the downward hanging campanulate flower would appear to be minor. Abbott (*1926*) stated that pollen from our native species does not cause Oriental persimmon fruit set, but the pollen must come from staminate Oriental plants.

Pollination Recommendations and Practices

None.

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PIGEONPEA

Cajanus cajan (L.) Millsp., family Leguminosae

The pigeonpea or cajan is adapted to the tropics and subtropics where it is one of the most valuable legumes. It is cultivated as an annual for both forage and its edible beans, which are produced in abundance (Graham *1941**). It is common in India, Hawaii, and Puerto Rico and has been tried extensively in Florida and some other southern stations on an experimental basis but is not grown commercially within the continental United States (McKee and Pieters *1937*). Killinger (*1969*) conducted tests with 'Norman' cv. in Florida and concluded that it shows promise as a seed, hay, cover, grazing, or windbreak crop.

Plant

Pigeonpea is a pubescent, many-branched shrub (but cultivated as an annual), 4 to 10 feet or more tall, with yellow or orange papilionaceous flowers that produce brown, hairy, four- to seven-seeded, long-beaked pods, 2 to 3 inches long by ½ inch thick.

Inflorescence

The 1½- to 5-inch terminal and/or axillary raceme bears several flowers that resemble the common sweet pea in shape, but the color is yellow, red, or yellow-purple with a brownish back. The filaments elongate in the bud, and pollen is shed the day before the flower opens. Whether actual pollination of the stigma occurs before the flower opens is not clear. The majority of the flowers open between 1 a.m. and 3 p.m., and often remain open for only about 6 hours (Purseglove *1968**). Bees visit the flowers in great numbers (Wilsie and Takahashi *1934*), but whether they do so to collect pollen, nectar, or both has not been reported.

Pollination Requirements

Krauss (*1932*) and Wilsie and Takahashi (*1934*) considered the pigeon pea to be a normally self-pollinated species. However, a high degree of cross-

pollination, ranging from 5 to 40 percent, has been observed (Wilsie and Takahashi *1934*, Purseglove *1968**, Matta and Dave *1931*, Krauss *1927*, Shaw *1932*, Abrams *1967*).

There is no information on the need for pollinating agents in the production of seeds. Apparently, seeds can be produced when insects are excluded from the flowers (Abrams *1967*), but whether production by plants where pollinating insects are excluded is equal to open pollinated plants has not been determined.

Pollinators

Abrams (*1967*) stated that bees visit the flowers in large numbers. He also indicated that thrips might be of some significance. Purseglove (*1968**) stated that the flowers are visited by "bees and other insects," and Wilsie and Takahashi (*1934*) stated that bees visit the flowers in great numbers. These references indicate that, if insect pollination is beneficial in pigeonpea seed production, there should be no problem in building up a high bee population on the crop.

There is no proven value of pollinating insects to pigeonpeas, even though the evidence indicates these insects might be of value.

Pollination Recommendations and Practices

None.

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PIMENTO OR ALLSPICE

Pimenta dioica (L.) Merrill, family Myrtaceae

Pimento is a semiwild crop in Jamaica and the nearby islands where most of the world's supply is produced (Chapman *1966*). Deliberate planting of pimento in Jamaica is negligible (Chapman and Glasgow *1961*).

Plant

The plant is an aromatic tree to 40 feet tall, with 6-inch oblong leathery leaves that shed twice a year. The dried, unripe fruit is a dark-brown, round berry, one-fourth inch across, known as allspice. Its flavor is considered to be a combination of the flavors of cinnamon, cloves, and nutmeg; hence the name allspice. Oil extracted from the dried berries is a stimulant carminative (Purseglove *1968**). Although the trees superficially appear to be hermaphrodite, some of them actually function as male and others as fruiting female trees. The differences in the two types are recognizable at harvesttime. Chapman (*1966*) suggested planting or budding male trees as alternate trees in alternate rows to provide pollination for the bearing trees.

Inflorescence

The inflorescence consists of a cluster of several dozen white flowers, 2 to 6 inches long, each flower having four tiny petals, a single style with one ovary, two ovules, and a cluster of anthers. As the flower opens, the style straightens, and although the stigma is raised above the anthers, the flower appears to be hermaphrodite. However, there are differences in flowers between trees. The barren or male-type tree has many flowers, each of which has 75 to 100 anthers per flower. These flowers produce much pollen. Most of the flowers shed, but one or two per tree may produce one-seeded fruit. The bearing or female-type tree has fewer flowers, and the flowers have fewer anthers. The small amount of pollen produced is nonviable but may serve to lure pollen-coated bees from other trees. A bearing tree may produce 20 pounds of berries per year but yields of 150 pounds for one tree have been recorded. The flowers are attractive to honey bees and some other pollinators (see Chapman *1964**, *1966*).

Pollination Requirements

Ward (*1961*) bagged inflorescences and obtained only 19 berries as compared to more than a thousand obtained from a similar number of flowers that were not bagged, which established that the flower must be cross-pollinated. Chapman and Glasgow (*1961*) considered the barrenness physiological.

Pollinators

Ward (*1961*) believed that wind was the primary pollinating agent. Chapman (*1966*) considered the plant to be cross-pollinated by bees.

Pollination Recommendations and Practices

Chapman (*1966*) recommended the placement of honey bee colonies in the plantings to transfer the pollen to receptive stigmas. The relative concentration of colonies was not indicated.

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PLUM AND PRUNE

Prunus spp., family Rosaceae

Prunes are basically plums that because of their high sugar content can be dried successfully without removal of the stone. More than 2,000 varieties of plums and prunes, comprising 15 species, have been grown in the United States. Some are native to America; however, all commercially grown cultivars in California, the major producer of plums and prunes, belong to the European plum (*P. domestica* L.), the Japanese plum (*P. salicina* Lindl.), or the hybrids of the latter (Allen *1929*). The best known and most important are the European plums and prunes of which the Italian prune is the most widely grown in the world. Of the numerous species of native plums (*P. americana* Marsh.) (fig. 156), only a few are commercially less important. These include the 'Damson ' (*P. insititia* L.), myrobalan or cherry plum (*P. cerasifera* Ehrh.) and the Simon type (*P. simonii* Carr.) (Allen *1929*).

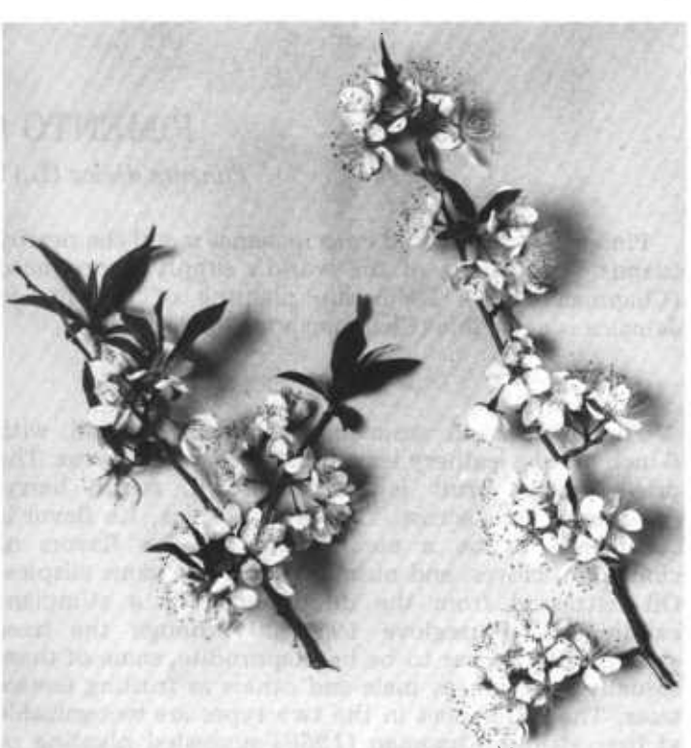
In 1971, California produced an estimated 101,000 tons of plums and 131,000 tons of prunes, while Idaho, Michigan, Oregon, and Washington, produced a combined total of only 63,500 tons. The total value of the crop in all of these States was $62 million. The 1969 acreage in California was 21,770 acres of plums (producing 3.08 tons per acre) and 97,560 acres of prunes (producing 1.33 tons of fruit per acre) (Henderson and Swedberg *1970*).

Plant

The deciduous trees of plums and prunes (fig. 157) are spaced in orchards 16 to 24 (average 20) feet apart, depending upon species, soil type, and other factors (Kinman *1943*). The Japanese types are in general smaller than the European types, but, depending upon vigor and type, the height may vary from 10 to 20 feet. In California, the numerous white flowers appear ahead of the leaves from late February to mid-March, and the fruit is harvested from May to July.

Inflorescence

The numerous white to cream-colored, 1 inch or smaller flowers occur in clusters of one to three along the new growth of the branches of the plum. The Japanese types bloom about the time almonds bloom. The European types bloom about the time peaches bloom. Buchanan (*1903*) stated that the anthers are about level with the two-lobed stigma, but Brown



PN-3836

FIGURE 156.—Flowers of the native plum.

PN-3837

FIGURE 157.—Closeup of prune flowers.

(*1951*) noted that the stigma of 'President' cv. was twice the length of the stamens (figs. 158 and 159). He also referred to the "long-styled low-nectared 'Jefferson' cv." Knuth (*1908, p. 344*) stated that the stigma of *P. domestica* projects beyond the inner stamens but is at the same level of the outer ones, but in *P. insititia* it exceeds the longest stamen in length. The style leads to one ovary with two ovules, one of which rarely develops. Considerable nectar is secreted by the fleshy lining of the receptacle at the base of the stylar column (Buchanan *1903*), and, although quite dilute in the early morning, it becomes more concentrated as the day advances. Vansell (*1934*) reported the sugar concentration of only 6.2 percent at 7 to 8 a.m. when the relative humidity (R.H.) was 100 percent and the weather was foggy; 8.1 percent at 9:40 a.m., when the R.H. was down to 85 percent; and 25.8 at 2 p.m., when the R.H. was down to 53 percent. Later, Vansell (*1942**) reported that the sugar concentration in the nectar of the 'Gos' plum blossom increased from 20 percent at 8:30 a.m. to 37 percent at 4 p.m.

Brown (*1951*) found considerable differences in the amount of nectar produced per flower, with one cv. ('Kea') producing 1.7 ml per 100 flowers—more than 10 times as much as the lowest nectar-yielding cultivar. He reported a close correlation between nectar volume per flower and the number of bees present. Vansell (*1942**) also observed bees that in one case shifted their activity from plums at about 10 a.m. to more attractive manzanita (*Arctostaphylos* sp.) but shifted back to plums in the midafternoon. Roberts and Congdon (*1955*) considered that plum pollen was not sufficiently attractive to pollen-gathering insects to insure effective pollination.

The flower is open for 5 days according to Knuth (*1908, p. 344*) with the stigma being receptive almost 2 days before the anthers dehisce. How long it is receptive is not clear. Backhouse (*1911*) said that if the flowers are not pollinated, they shed in 3 or 4 days.

As a source of pollen and nectar for honey bees, plums are considered of stimulative value but because of the short flowering period and low sugar content of the nectar little surplus honey is obtained.

Pollination Requirements

Rather thorough studies have been made to determine the pollination requirements of the different species of plums (Backhouse *1911, 1912*; Hendrickson *1916, 1918, 1919a, 1919b, 1922, 1923, 1930*; Luce and Morris *1928*; Marshall *1920*; MacDaniels *1942*; Philp and Vansell *1932, 1944*; Waugh *1898*). These studies established that plum cultivars vary from completely self-incompatible, in which they set no fruit with their own pollen, to complete self-compatibility, where a full crop is set from the plants' own pollen. Some are also cross-incompatible—not receptive to pollen of certain other cultivars. The majority are self-incompatible (Backhouse *1911*; Griggs *1970**; Griggs and Hesse *1963*). Pollinating insects are necessary on all cultivars to transfer the pollen from the anthers to the stigmas (Alderman and Angelo *1933*). Thompson and Liu (*1972*) concluded from their tests that the Italian prune is fully self-fruitful and bees are not necessary for pollen distribution. Dickson and Smith (*1953*) stated that except for the Italian prune and Stanley, all European cultivars in Canada are self-unfruitful and require mixed plantings, and those two benefit from cross-pollination in many orchards. They also stated that the 'Burbank' and the 'Shiro', the main Japanese cultivars are also self-unfruitful and concluded that insect pollination is necessary for all cultivars, both European and Japanese. Luce and Morris (*1928*) also noted that most cultivars are self-sterile. Dorsey (*1919*) concluded that pollen abortion was not the cause of sterility, but rather it was associated with genetic factors in embryo development.

To provide pollen within the orchard, Griggs and Hesse (*1963*) recommended that in every fourth tree location in every fourth row there should be planted a compatible cultivar that flowers consistently at the same time as the primary cultivar flowers. Free (*1962*) showed that fruit set on plum trees decreased sharply with increased distance from the pollenizer tree. Trees adjacent to pollenizer trees had a greater set on the sides facing the pollenizers than on their far sides, indicating that the pollen was not thoroughly distributed over the tree.

Pollinators

The honey bee has been recognized as the primary pollinating agent of plums and prunes by numerous workers since Waugh (*1898, 1900*) stressed its importance (Buchanan *1903*; Free *1962*; Hendrickson *1916, 1930*;

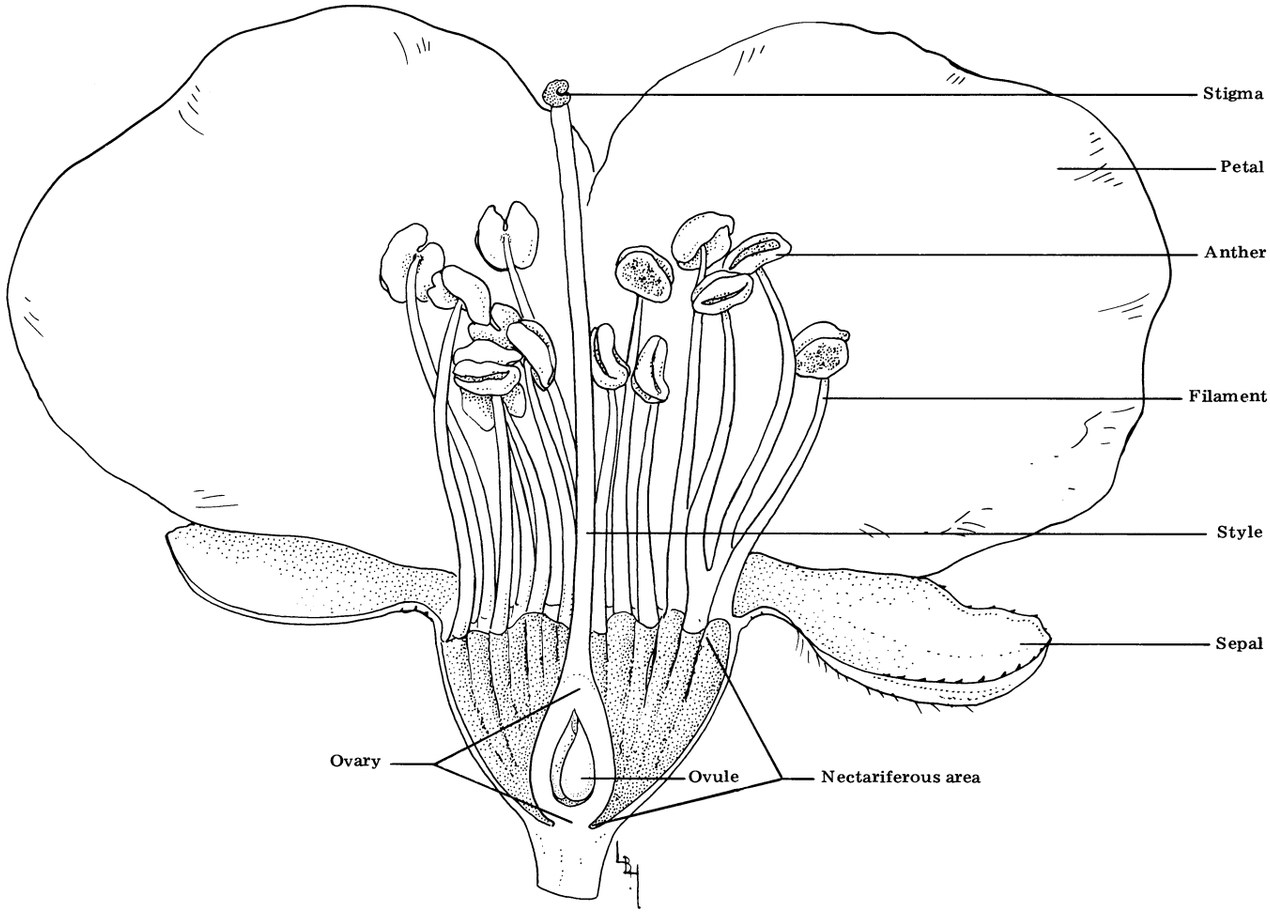


FIGURE 158.—Longitudinal section of French prune flower, ×7.

Hooper *1936*; Kinman *1938*, *1943*; MacDaniels *1942*), although bumble bees and other wild bees and blowflies and other flies are given some credit by Backhouse (*1912*) and Brown (*1951*). Wind is not a factor (Backhouse *1912*, Waugh *1900*). Hooper (*1936*) pointed out that the honey bee was best because of its strong tendency to continue foraging from one source. As with many other deciduous fruit trees, plums and prunes bloom early in the spring when few pollinating agents are active. Also, large plantings have more blooms than local pollinators can service. Kinman (*1924*, *1938*, *1943*) warned that crop failures can be expected if no bees are present. Honey bees are easy to transport and establish in the orchard at flowering time, and are essential in the commercial production of both plums and prunes. The blooms are usually attractive to bees all day but more so in the morning. The plums and prunes, like other stone fruits, require that only one viable pollen tube reach the ovary to produce a fruit, but this pollen grain must, in most cases, arrive from another compatible blossom and at the right time. To assure that such pollen reaches the maximum number of flowers to produce the plum or prune crop desired, a heavy population of pollinators is required.

Hendrickson (*1916*, *1918*) indicated that although the number of blooms on a tree varies greatly from year to year, a set of 15 to 20 percent results in massive crops. This only occurs when proper pollenizers are interplanted and bees are present in large numbers.

Pollination Recommendations and Practices

Hendrickson (*1916*) concluded that best pollination would result " . . . if the bees were brought in from some outside district and scattered about the orchard, about one hive to the acre, during the blossoming period, and then removed." Philp and Vansell (*1932*) stated that bees were rented for plum pollination during World War I at $5 to $7 per colony.

Allen (*1929*) recommended one colony per acre, but believed that a centrally located apiary might serve one or even more small orchards. Roberts and Congdon (*1955*) said that the groups of colonies should be no further than 150 yards apart. Philp and Vansell (*1944*) suggested one colony per acre, the colonies in groups of 10 to 20. The Great Britain Ministry of Agriculture, Fisheries, and Food (*1958*) also recommended strong colonies be placed in the orchard. Roberts (*1956*) stated that the number of colonies per acre necessary to insure good pollination will vary (in New Zealand), but in most circumstances one vigorous colony per acre will meet all requirements. Stephen (*1961*) also recommended one colony per acre, with the bees to be moved in at one-third bloom stage.

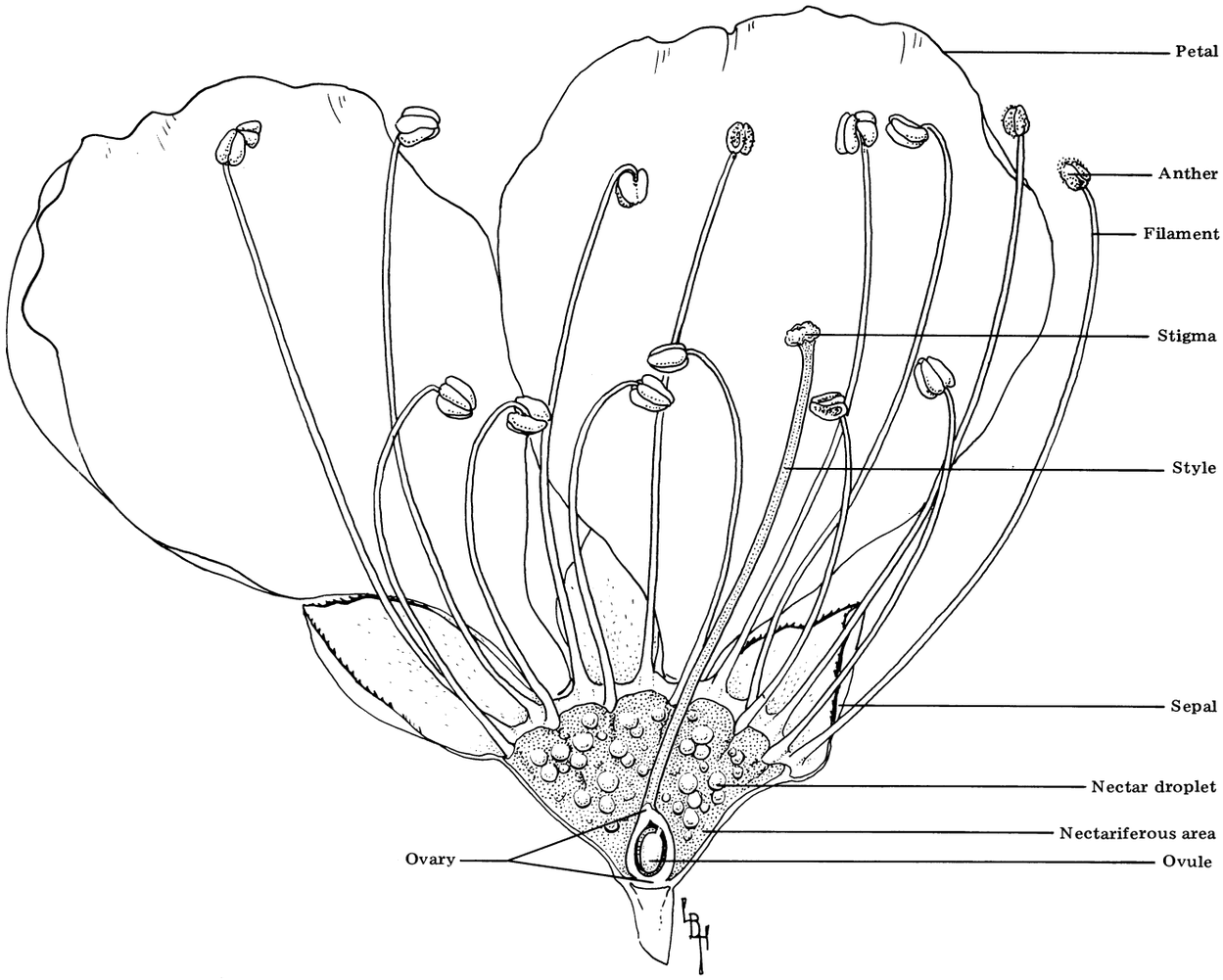


FIGURE 159.—Longitudinal section of 'Mariposa' plum flower, ×8.

Griggs and Hesse (*1963*) recommended for each acre at least one strong colony of honey bees with four or five frames of brood and enough bees to cover eight frames, the colonies to be placed in the orchard in groups of 5 to 10.

Most growers take some steps to see that bee colonies are in or near their orchards.

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POMEGRANATE

Punica granatum L., family Punicaceae

Pomegranates were grown in 1970 on 1,220 acres in California, the leading State in the production of this delicious fruit (Henderson and Kitterman *1971*). The largest single planting was 120 acres (Larue *1964*). The estimated value of the crop is less than one-half million dollars. Average production per acre is about 5 tons of fruit. Only one cv., 'Wonderful', is grown commercially in California. It grows best in areas of cool winters and hot dry summers (Purseglove *1968**).

Plant

The plant usually grows as a bush or shrub 6 to 15 feet in height and is deciduous in the cooler areas of its range. Spacing in the orchard is 12 to 15 feet, or the plants are doubleset in hedgerows with more space between rows.

The fruit is a large, globose berry, red-green or violet when ripe (fig. 160). Its pulp is eaten out of hand and in salads, or its juice is used in a refreshing drink or sirup. A jet-black ink is made from the rind. Kihara (*1958*) stated that normal fruit contains an average of 667 seeds. Evreinoff (*1953*) stated that vegetative growth starts from mid-March to mid-April and flowering is primarily in May.

Inflorescence

From one to several flowers may be borne on a twig, one being terminal, the others lateral and solitary. The odorless but colorful flowers are large, 1½ to 3 inches in length, campanulate or cylindrical, and generally reddish but sometimes yellow to white. There are five or more petals, some of which may be doubled. The stamens are numerous, erect to slightly curved at the apex, and red (fig. 161). The anthers are yellow. The ovary is many celled, each cell with numerous ovules. The style is yellowissh red and roughly an inch long. The stigma is

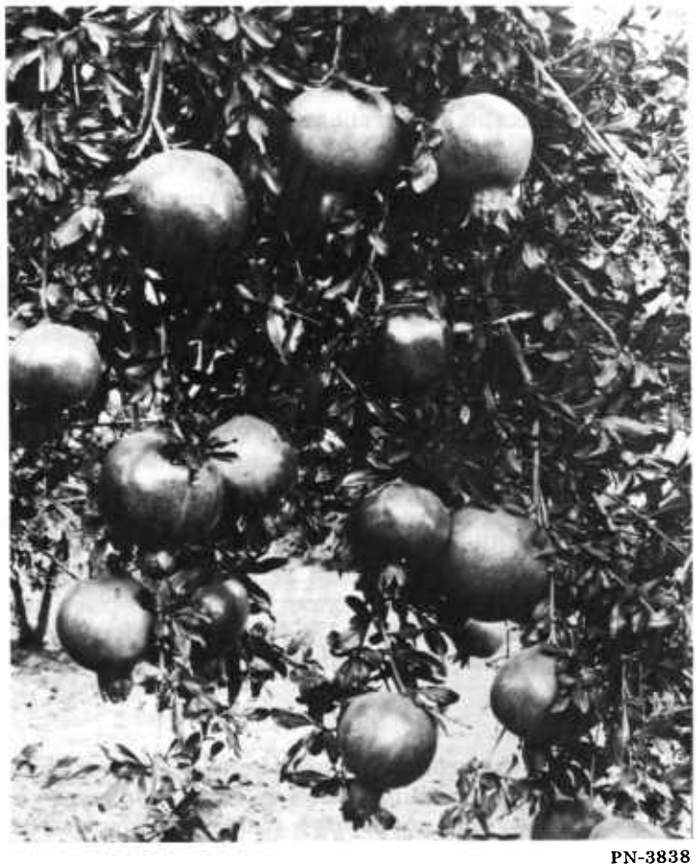

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FIGURE 160.—Mature pomegranate fruit on the tree.

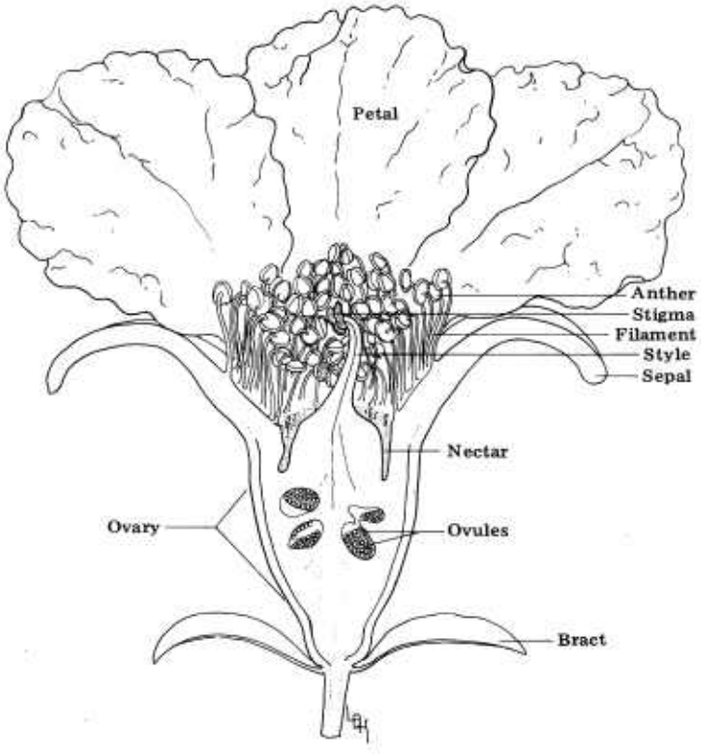

FIGURE 161.—Longitudinal section of 'Wonderful' pomegranate flower, × 2.

globose or truncate and yellowish green (Bailey *1916**, *v. 5., pp. 2750–2751, 2861–2862*; Knuth *1908**, *p. 440*; Ochse et al. *1961*).

The pomegranate flower has been referred to as nectarless; however, flowers of cv. 'Wonderful', grown in Tucson in 1973, contained several drops of nectar with 27 percent soluble solids (sugars).

The flowers are primarily of two types: the *fruitful*, large, long-styled, long-stamened, colorful flowers, in which the anthers and the stigma are at about the same height; and the smaller, *barren*, short-styled, short-stamened flower, in which the stigma is far below the anthers. Occasionally, "intermediate" flowers have styles that may equal the length of the long-styled flowers or be as short as the short-styled ones. Those with long styles occasionally become fertilized, but only rarely does such fruit mature and then it is malformed and defective. On the contrary, short-styled flowers are never fertilized and soon shed. The petals of these are a dull, pale rose, and the pollen is defective (Hodgson *1917*).

The long-styled flowers usually develop on old wood, whereas the short-styled flowers develop on new growth. The relative proportion of each is influenced by many factors. The best fruit is obtained from the early flowers, probably because they develop during more favorable meteorological conditions (Evreinoff *1953*).

Pollination Requirements

Little is known about the pollination of pomegranates. Knuth (*1908**, *p. 440*) stated that beetles belonging to the genera *Cetonia* and *Trichodes* effect both cross- as well as self-pollination, while devouring the flowers. The ability of the plant to self-pollinate or its need for transfer of pollen either within its own flower, between flowers, or between plants is unknown.

Kihara (*1958*) reported the discovery of a "seedless" pomegranate in which the pollen was sterile but the fruit developed. It had only half (307) of the normal number of developed embryos. These were not viable seeds; however, the size of the fruit was normal.

Pollinators

Where no nectar is produced, only pollen-collecting insects would be of value to the blossom. If beetles contribute to the pollination of this plant, as Knuth (*p. 440, 1908**) indicated, the visitation by pollen-collecting bees would appear to be much more valuable. No information is available on the degree of benefit such flowers may derive from beetles or, if bees are beneficial, how many bee visits would be desired.

Pollination Recommendations and Practices

There are no recommendations for the use of pollinating agents on pomegranates, but some growers in California arrange for honey bee colonies to be placed in or near their fields, believing that their presence benefits pomegranate fruit production.

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PUMPKIN AND SQUASH

Cucurbita spp., family Cucurbitaceae

There is no satisfactory association between the common and scientific names of pumpkin, squash, summer squash, winter squash, vegetable marrow (primarily a British term), cushaw (Louisiana French for "big pumpkin"), and ornamental gourds. Four species of *Cucurbita* of economic importance are involved: *C. maxima* Duch., *C. mixta* Pang., *C. moschata* Duch. ex Poir., and *C. pepo* L. Botanical identification of the specimens is according to the type of stem (trunk) or peduncle (flower stalk). To the general public, however, a plant, or its fruit, may be known as a squash or pumpkin to one individual and as a cushaw or gourd to another. Botanical classification is further complicated by the fact that all cultivars of the species will readily intercross (Tapley et al. *1937*, Whitaker and Bohn *1950*, Whitaker and Davis *1962**). The proposal by Whitaker and Davis to separate the species according to culinary usage has not been accepted.

From the pollination standpoint, the four species and their types and cultivars are subsequently treated herein as a unit, and are collectively referred to as "pumpkin and squash."

In addition to the use of pumpkin and squash as human food, they are also used as livestock food, some cultivars much more than others. Also, the seeds are eaten whole as a confection or crushed to extract the oil, which is about equal to peanut oil production on a per-acre basis. This oil is used as a high-quality liquid vegetable fat and as a sandwich spread (Curtis *1948*). The fruit of plants more frequently known as gourds is used for containers, musical instruments, and ornamentation (Whitaker *1964*).

Although the USDA, Agricultural Statistics, 1971, does not show the acreage devoted to these four species of cucurbits it gives the acres devoted to seed production and the volume of seed produced in 1969 as follows:

Crop	*Acres*	*Lbs. seed X 1,000*
Pumpkin	226	109
Squash:		
Summer	1,039	551
Winter	500	210

This amount of seed should be sufficient to plant several hundred thousand acres (Jones and Emsweller *1931*, Thompson et al. *1955*, Whitaker and Davis *1962**).

Pumpkin and squash are grown throughout the country, with Illinois, New Jersey, California, Florida, and Texas having the greatest acreage, although State positions vary from year to year because of season and market conditions (USDA *1964*). Individual plantings usually range from home-garden size to about 40 acres.

Plant

All of the *Cucurbita* spp. are annuals. Most of them are prostrate with trailing branches, reaching a length of 40 to 50 feet, but some have short, semierect stems (Castetter and Erwin *1927*). The leaves are large, sometimes exceeding 12 inches across, and are borne on petioles up to 24 inches in length. The plants are susceptible to frost but do well in relatively cool climates. If the fruit is consumed in the immature stage, it must be harvested at frequent intervals. Otherwise, it is left to mature on the vine. The fruits vary greatly in size, from a few ounces to more than 100 pounds, and in shape from globular and oval to gooseneck, crookneck, and other grotesque shapes.

Inflorescence

The flowers are large (to 3 inches), solitary, showy, creamy white to deep orange-yellow, and are open for only 1 day. Plants are normally monoecious, but hermaphroditic flowers occur (Jones and Rosa *1928**). Battaglini (*1969*) recorded 10 staminate flowers for each pistillate one. Staminate flowers are at the end of a thin stem, and have three anthers producing relatively large pollen grains (fig. 162). The morphology of the staminate flowers was described by Chakravarty (*1958*). Pistillate flowers are on a short peduncle, the style is thick, and the stigma two-lobed. The showy corolla of the pistillate flower is attached to the end of the easily recognizable ovary (Whitaker and Jagger *1937*). Tapley (*1923*) recorded 24 to 34 pistillate blooms per squash plant with 5.5 to 43.7 percent set. Both pollen and nectar are produced in the staminate flowers and nectar in pistillate flowers. Verdieva and Ismailova (*1960*) stated that most bees visit the squash flowers for nectar only. Nectar is secreted from a ring of tissue surrounding the style and just inside the perianth tube. The ovary is divided into three to five carpels. Eisa and Munger

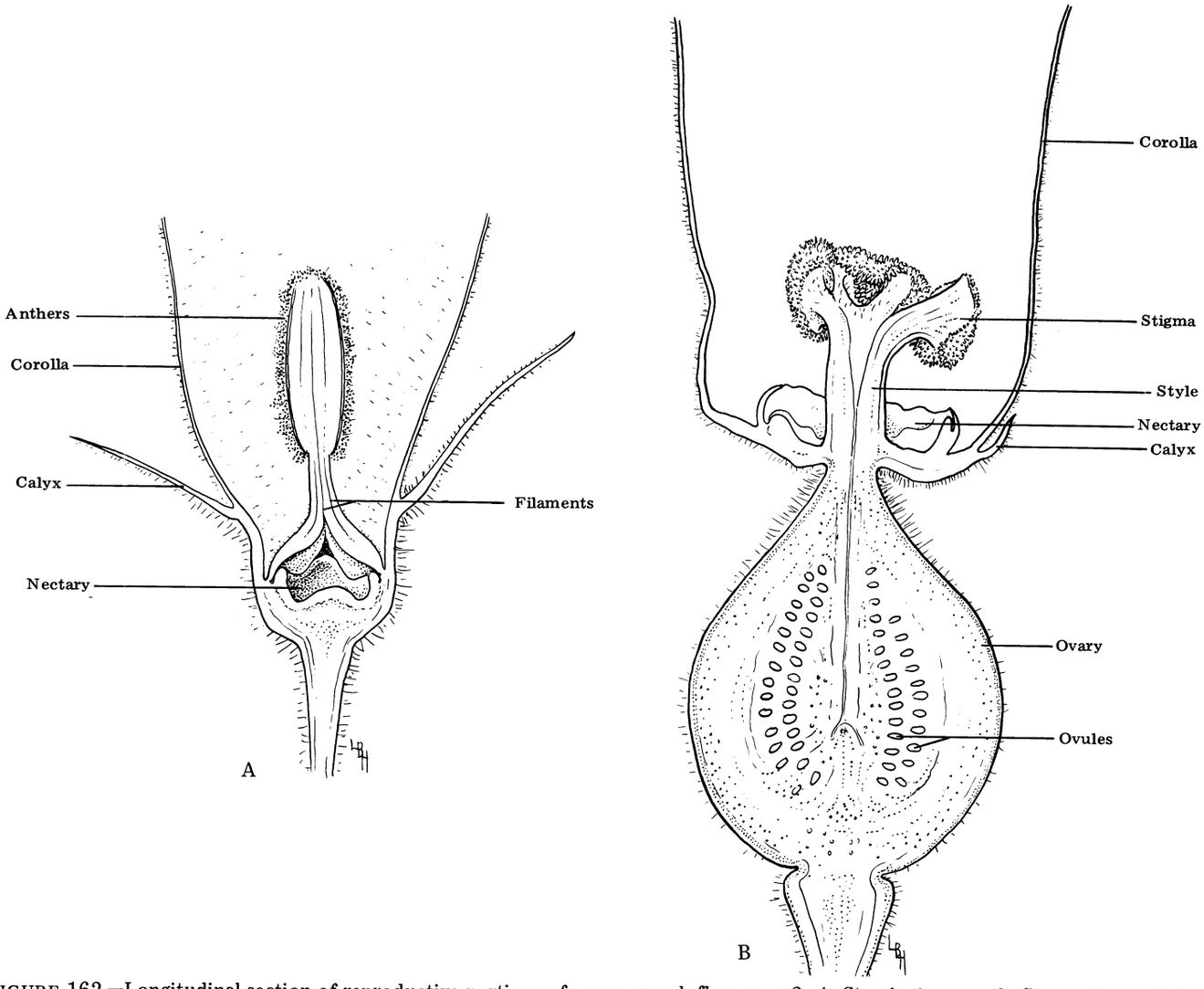

FIGURE 162.—Longitudinal section of reproductive portions of acorn squash flowers, × 2. *A*, Staminate, or male flower; *B*, pistillate, or female flower.

(*1968*) reported that male and female sterility have been observed in *C. pepo*, and Scott and Riner (*1946*) reported male sterility in *C. maxima*.

The squash blossom is the emblem of fertility to the Hopi Indians of the Southwest, whose more expensive pieces of jewelry include the squash blossom necklaces.

Pollination Requirements

Because the anthers are in one flower and the stigma is in another, the mechanical transfer of pollen is essential to fruit set. Hayase (*1953*) stated that the seed number and fruit weight was increased in proportion to the amount of pollen deposited on the stigma. The period of receptiveness has not been thoroughly worked out. Sanduleac (*1959*) observed that honey bees worked the flowers most intensively from 6 a.m. to noon with maximum activity from 8 to 9 a.m. Amaral and Mitidier (*1966*) stated that the flowers of *C. pepo* open before sunrise and close by 11 a.m. Atwal (*1970*) recorded that pollinating insects visited the flowers from 7 to 10:30 a.m., "when the flowers began to close." Hurd (*1966*) noted that, depending upon the weather and season, the flowers of the host (cucurbits) open some time before daylight or shortly thereafter, and in hot weather they wither and close by 8 to 9 a.m., otherwise they may stay open until noon. Hawthorn and Pollard (*1954**) also stated that the flowers open about 5 a.m. and close about noon. Pollination, therefore, is most effective in the early morning—primarily before 9 a.m.

Bailey (*1890*) indicated that "squash" and "gourd" were self-sterile, but Bushnell (*1920*) stated that the 'Hubbard' squash was not self-sterile, and if there was sterility apparently it no longer existed. Bailey (*1937*) further stated that in "gourds" it is doubtful whether there is ever impregnation between two flowers on the same plant because experimental efforts to do so are unsuccessful. He felt, therefore, that seeds of the "gourds" are always produced from crosses between two plants.

Pollinators

Practically all authorities give primary credit to the

honey bee in pollinating *Cucurbita* (Pammel and Beach *1894*, Jones and Rosa *1928**, Jones and Emsweller *1931*, Thompson et al. *1955*, Whitaker and Davis *1962**, Battaglini *1969*, Langridge *1952*, Nevkryta *1953*, Robinson *1952*, Sanduleac *1959*, Verdieva and Ismailova *1960*, Wolfenbarger *1962*). Michelbacher et al. (*1964*) and Hurd (*1966*) credit both honey bees and wild bees. Some species of wild bees are most efficient pollinators of *Cucurbita*, but they are frequently so limited in number or in range as to be of no great economic significance. Durham (*1928*) gave some credit to the cucumber beetle; Tontz (*1944*) to ants; and Fronk and Slater (*1956*) to the wild bees, *Peponapsis* spp. and *Zenoglossa* spp., with a minor role played by *Diabrotica* spp. beetles. Hurd (*1966*) stated that "other insects are involved such as cucumber, scarab and meloid beetles, and flies and moths but to a lesser extent than are bees."

Michelbacher et al. (*1964*) concluded that even though honey bees are poorly adapted as pollinators of squash, pumpkin, and gourd, because of the small size of the insect and the relatively large pollen grains, still the importance of honey bees as pollinators of these crops should not be minimized. Langridge (*1954*) stated that if pollination was inadequate, the introduction of honey bees was the only solution.

For commercial production of Cucurbits, there seems little doubt that the honey bee is the only effective pollinator that can be provided in sufficient numbers for adequate pollination. Wadlow (*1970*) reported that with only about 1,000 colonies, at $10 per colony, he provided pollination for squash and other crops valued at over $1 million.

The value of bees as pollinators has been shown in terms of fruit produced. Wolfenbarger (*1962*) showed the following correlation between colonies per acre and increased production in baskets of squash per acre: No colonies provided, 148 baskets; one-half colony per acre, 155 baskets; one colony per acre, 161 baskets; two colonies per acre, 168 baskets; and three colonies per acre, 173 baskets. In open plots, he obtained 4.20 squash per yd^2; whereas in plots caged to exclude bees, he produced only 0.82 per yd^2. Verdieva and Ismailova (*1960*) reported 47 to 57 kg squash from plants pollinated by honey bees compared with 25 to 30 kg from plots pollinated by other (unspecified) methods. Nevkryta (*1953*) increased cucurbit production 3.0 to 3.4 times with increased bee activity, attributed to stimulative feeding of the bees. Battaglini (*1969*) recorded a set of 61.2 percent of pistillate flowers exposed to bees in comparison with a set of 6.8 percent of caged flowers. The agent responsible for the set of the caged flowers was not given.

Not only are bees largely responsible for the fruit set on standard cultivars, but their value is enhanced on plants in which hybrid vigor has been demonstrated. Curtis (*1939*) obtained 59 fruits from a hybrid compared to 25 and 27 from the two parents.

Hutchins and Croston (*1941*) also obtained significantly greater yields from 7 out of 10 crosses, and production of all crosses was significantly earlier than in the parental lines. With male sterility now available in *Cucurbita* (Eisa and Munger *1968*), techniques involving the crossing of inbred lines by honey bees provide plant breeders with the opportunity to develop improved hybrid cultivars.

Pollination Recommendations and Practices

Unfortunately, concrete data are scarce on the pollination of crops of the genus *Cucurbita*. As a result, most publications merely generalize with such statements as " . . . largely insect pollinated" (Thompson et al. *1955*), "Transfer of pollen is usually accomplished by insects, chiefly honey bees" (Jones and Rosa *1928**, Purseglove *1968**), "Honey bees are the usual agents . . . " Hawthorn and Pollard (*1954**), or "insect pollinated" (Whitaker and Davis *1962**). The "one colony of honey bees per acre" recommended for cantaloups (McGregor and Todd *1952**) might be expected to apply to *Cucurbita* also, but proof should be established.

Sanduleac (*1959*) reported one to two colonies per 25 acres in the area of his test. Eckert (*1959**) suggested that one strong colony per 2 acres of squash may be enough under irrigated conditions in California. Jaycox (*1969*) listed pumpkins and squash along with many other crops and generalized without supporting data that most crops require one strong colony per acre. Wolfenbarger (*1962*) showed continued increase in squash production in Florida up to three colonies per acre without hitting a peak in production.

Available evidence shows that the plants must be insect pollinated, and that honey bees are the chief pollinators. Detailed studies, correlating bee visits to flowers with yield, quality, and related factors have not been carried out. Where yields are low, an additional one to three colonies per acre should be provided for at least 3 years to determine their value. The literature indicates that colonies nearby are most effective.

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PYRETHRUM

Chrysanthemum cinerariifolium (Trevir.) Vis., family Compositae

Pyrethrum is grown for the insecticidal material, pyrethrins, that is found primarily in the flower head. It is grown in numerous countries but Kenya, Tanzania, Ecuador, and Rwanda produced an average of 34.2 million of the 35 million pounds produced per year during 1966–70 (Fowler and Mahan *1972*). Pyrethrum has been tested experimentally but has not been grown commercially in the United States (Drain and Shuey *1934*, McClintock *1929*) although, if mechanical harvesting of the flower heads could be perfected and the hand labor reduced, its growth in certain areas might be feasible.

Plant

Pyrethrum is a tufted, slender, pubescent perennial 12 to 30 inches high with daisylike flower heads 1½ inches across, on long slender stems. It is adapted to a temperate climate with 45 to 50 inches of rainfall. The seeds are sown in special beds. Four months later the 4- to 5-inch-high plants are transplanted into the field (fig. 163).

In another 4 months, harvest of the just-opening flower heads begins and is repeated every 2 or 3 weeks for several months. After three annual harvests, the plants decrease in productivity and are plowed under and another crop planted. Maximum productivity (800 to 1,000 pounds dried seed heads per acre) may be obtained the second season (Purseglove *1968**).

Inflorescence

The flower head consists of 18 to 22 white, pistillate ray florets almost an inch long and a tightly packed cluster of 40 to 100 yellow, short, bisexual disk florets (fig. 164).

The flower is not considered highly attractive to honey bees, which seem to collect pollen primarily and only at certain times. The main insect visitors were reported by Kroll (*1961*) to be adult coleoptera and diptera, and their presence was seasonal. Kroll (*1961*) and Smith (*1958*), however, indicated that bees increased production of pyrethrum, so presumably the flowers were visited by these insects.

FIGURE 163.—Pyrethrum plants cut with a grain binder and curing in shocks. Experimental production at Glenn Dale, Md.

PN-3839

FIGURE 164.—Pyrethrum flowers in different stages of development.

Harvest begins when the florets on a head are about three-fourths open (Hartzell *1943*). The pyrethrin content of the flower increases as the flower stage increases: Buds unopened, 0.84 percent; one row of disk flowers open, 1.83 percent; and overblown and ripening, 1.21 percent (Kroll *1964*). A similar variation from 0.23 to 1.36 percent pyrethrin was also obtained from different plant sources by Hoyer and Leonard (*1936*).

Pollination Requirements

The pollination requirements of pyrethrum are not too clear, probably because of differences obtained in tests with different cultivars or under different environmental or ecological conditions. Culbertson (*1940*) stated that seed formation seemed to be the result of self-fertilization or apomyxis because flower heads bagged and with the anthers removed set seed. Delhaye (*1956*) stated that pyrethrum is highly self-fertile although a higher set of seed, and seed with higher viability, are obtained when the pollen comes from another clone. Kroll (*1961*) discussed a test comparing production of plants in cages with bees present, with bees excluded, and open plots. He reported that the analysis of the data was not quite conclusive but gave strong indications that production of pyrethrum is increased by insect pollination, and that fertilized embryos contain more pyrethrin than unfertilized embryos.

Purseglove (*1968**) stated, without supporting data, that pyrethrum is self-sterile and must be cross-pollinated to produce viable seeds. He stated that it is insect-pollinated mainly by coleoptera and diptera. Kroll (*1961*) stated that the percentage of unfertilized and nonviable seeds in the field is very high. This, he concluded, seemed to indicate that the number of insect visitors was never large enough to effect satisfactory fertilization, and, at the same time, it provided a strong

argument in favor of the predominance of cross- as opposed to self-fertilization.

The fertile achene was shown by Chandler (*1956*) to contain 1.05 percent pyrethrin compared to only 0.71 percent of barren achenes, which shows the value of having pollinated flowers for highest pyrethrin production.

Parlevliet and Contant (*1970*) stated that most clones are highly self-incompatible. Smith (*1958*) reviewed a test by L. A. Notcutt which showed that the yield of seeds was greatest from cages with bees, least from cages excluding pollinating insects, and intermediate in open plots.

A United Nations (FAO) (*1961*) report stated that pyrethrum is a cross-fertilized plant that requires insects for cross-pollination, the main pollinators being bees and other hymenoptera.

Brewer (*1968*) stated that the floret's own pollen cannot reach the receptive surfaces of the style (the stigma) because the stylar lobes are closed when they extrude through the anther tube. He concluded that by the time the style becomes receptive, the germination of the floret's own pollen is about past. Delhaye (*1956*) tested the effect of selfing and crossing on the germination of pyrethrum seed. He found the following: Selfed without bees, 0.0 to 1.0 percent; selfed with bees present, 1.7 to 22.7 percent; crossed without bees, 5.2 to 8.3 percent; and crossed by bees, 17.7 to 27.7 percent. Brewer (*1968*) concluded:

> The flower morphology and the flower morphogenesis of Pyrethrum resembles closely the classical concept known in the Compositae. The flowering rhythm of the inflorescences encourages cross-pollination through:—
>
> (1) The individual floret discharges the ripe pollen before it unfolds the receptive surfaces of the style.
>
> (2) When insects visit the inflorescence their path follows the development of the flower, i.e., from the margin to the centre, in order to collect pollen and nectar. Thus they deposit the foreign pollen they carry on fully opened styles.
>
> (3) By sticking together, the pollen mass encourages transport by insects.
>
> (4) Pollen does not germinate on genotypically identical styles. Strong evidence exists that the incompatibility system is sporophytically determined.
>
> (5) The limited life of the pollen after anthesis reduces the chance for own pollen to germinate on styles of the same floret.
>
> Lower germination percentages of the pure seed (P.G.S.) are due to rainfall during the maturing period of the seed.

Pollinators

The previous references indicate that honey bees are not overly attracted to pyrethrum flowers, as compared to beetles and flies. There has been no attempt to concentrate honey bee colonies near the crop. A test should be conducted to determine the practicality of supplying honey bee colonies to pyrethrum fields for pollination purposes. The use of leafcutter and other wild bees and different species of flies should also be investigated.

Pollination Recommendations and Practices

There are no recommendations on the use of pollinating insects on pyrethrum, even though the evidence indicates they are beneficial.

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QUINCE

Cydonia oblonga Mill., family Rosaceae

The common quince is closely related to the apple and pear but is of much less importance in the United States, where possibly 1,000 tons are produced commercially each year (Magness et al. *1971*). In Europe, the fruit is more highly esteemed and more extensively grown than in the United States. This species should not be confused with the flowering quinces (*Chaenomoles* spp.) grown primarily as ornamentals, but whose fruit is occasionally utilized also. Chandler (*1951**) stated that the Chinese quince (*Chaenomoles sinensis* (Thouin) Koehne) makes nearly as good jams and jellies as the common quince.

Plant

The quince is deciduous, about as hardy as the peach, but is less tolerant to warm weather. The plant is 10 to 20 feet tall, spineless, and similar in appearance and growth habits to the apple. The trees are usually set 6 to 12 feet apart. The fruit is smaller than the average apple and has a pleasant odor but may contain more than 50 seeds.

Inflorescence

Quince trees may bloom from February to May depending upon the species and geographical area. Blooms on a tree may last 11 to 20 days with full bloom lasting 6 to 10 days.

The quince flower is similar to the apple, but in general it is coarser and more colorful. It develops on first year growth and therefore appears later in the season than the apple blossom. It may be as much as 2 inches across, with five cup-shaped petals that vary, according to cultivar, from white to scarlet. It bears 20 or more stamens and five styles leading to a five-carpel ovary that, as a fruit, may produce the more than 50 seeds (fig. 165). The stamens and pistils are fully twice as large as and thicker than those of the apple (Waite *1899*). A nectary at the base of the styles is half-concealed by the closely spaced filaments, and only honey bees or larger insects can push in between the petals and stamens to reach the nectar.

Nectar secretion and pollination of the common quince was studied by Stancevic (*1963*) and Simidchiev (*1967*) who found that the amount secreted by a blossom in 24 hours varied from 0.851 to 1.634 mg on an average in the different cultivars with sugar concentration varying from 41.3 to 49.9 percent. Nectar secretion continued day and night for 5 days but was highest around noon each day. The flowers are freely visited by pollen and nectar collecting insects.

Pollination Requirements

The stigma of the quince is receptive even before the flower opens. When it opens, the outer anthers are first to dehisce, the inner ones remaining closed and beneath the receptive stigma. Because most insects settle on the flower center, crossing is effected before selfing is possible. Later, the inner anthers dehisce in contact with the stigma, but whether it remains receptive seems to be unknown. The question then deals with the effectiveness of this self-pollination. Chandler (*1951**) stated that the flowers of the quince varieties seem self-fruitful enough, but he did not indicate whether he referred to self-compatibility or self-fertilization. Waite (*1899*) cross-pollinated several cultivars and observed no striking benefit to be derived from pollinating insects bringing pollen from other cultivars. Gardner et al. (*1952*) and Shoemaker and Teskey (*1959*) also concluded that quinces were self-fertile. Mace (*1949*) stated that insects cross-pollinate the flowers shortly after they open, but if this is not accomplished the flowers self later. He did not indicate how he arrived at this conclusion.

Ershov (*1966*) conducted fertility studies on quince varieties from different places over a 5-year period. Of 23 varieties tested, only five were self-fertile. The others were partially to completely self-sterile. He concluded that for all practical purposes the quince is a self-sterile crop. Where mutual pollination exists, a good harvest can be obtained.

There seems to be no question that pollinating insects are needed when the flower first opens. In apples and numerous other plants, pollination at the earliest possible time is highly desirable. This would appear to be the case with quince.

Pollinators

The most thorough study of pollinating agents on quince was made by Simidchiev (*1967*) on five cultivars of the common quince. He showed that quince is highly attractive to honey bees throughout the day for both nectar and pollen. This activity is highly conducive to transfer of pollen from anther to stigma between cultivars as well as within the individual flower. Simidchiev (*1967*) noted that under favorable conditions for bee flight, when bees visited the blossoms from morning to night, 5 percent gathered only nectar, 11 percent gathered only pollen, and 84 percent gathered both. The flowers are highly attractive to honey bees, therefore, where needed they should be satisfactory pollinating agents.

Pollination Recommendations and Practices

None.

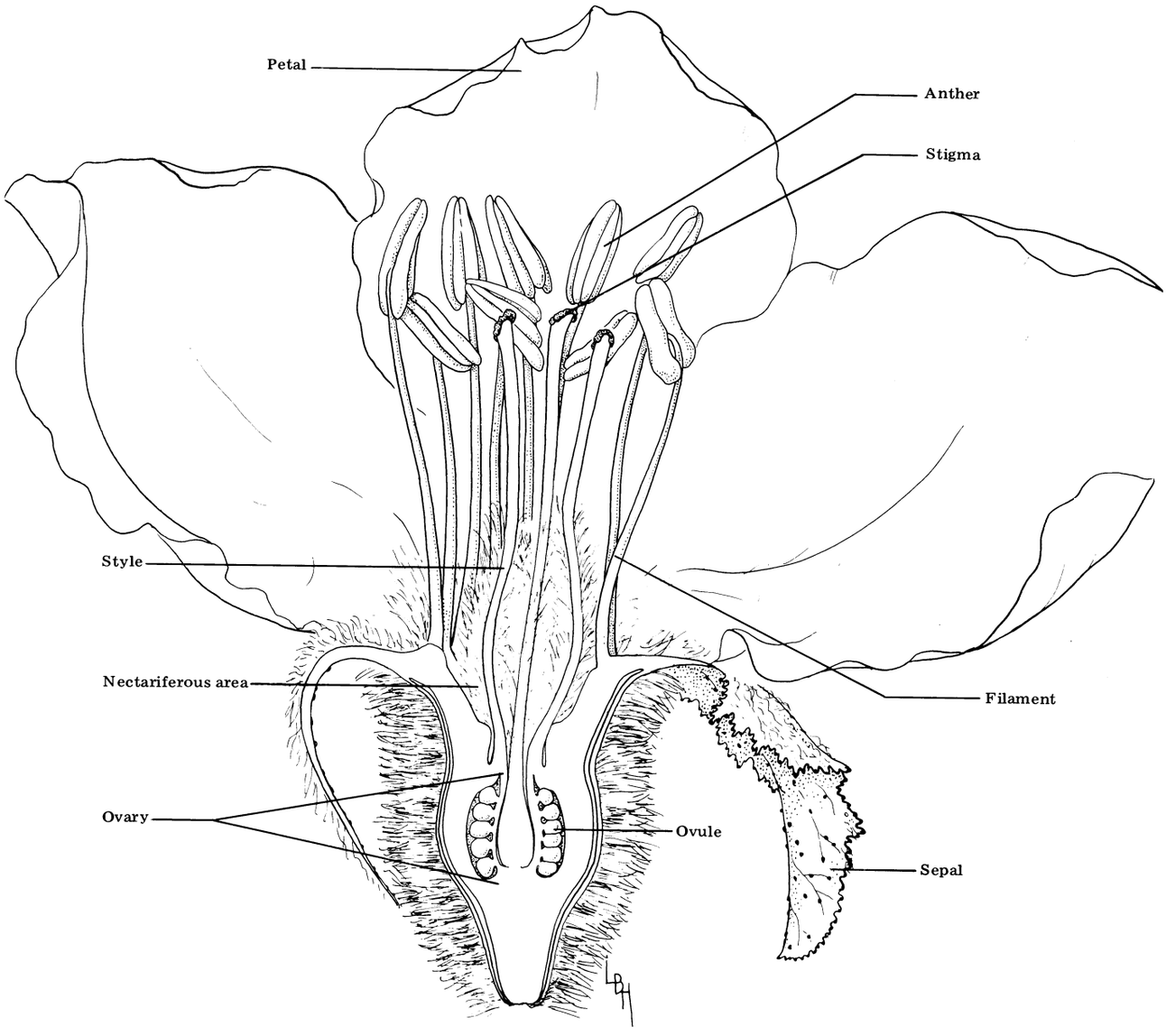

FIGURE 165.—Longitudinal section of 'Smyrna' quince flower, ×4.

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RADISH

Raphanus sativus L., family Cruciferae

Radish is grown almost entirely for the use of its succulent root as a green salad vegetable. It is a popular home garden vegetable because it is ready to harvest 3 to 6 weeks after planting. Radishes grow best in rather cool weather—fall and spring of the Northern States and late fall, winter, and early spring of the warmer areas.

An estimated 1.9 million pounds of radish seed was produced on 1,347 acres in 1971. Production was largely in California, although some was produced in Idaho, Montana, and Wyoming. Seed yields per acre range from 500 to 1,200 pounds. In most years, more acres of radish are grown for seed and more seed is produced in the United States than of any other cruciferous vegetable crop (Hawthorn and Pollard *1954**).

Plant

The radish grown in the United States is primarily an annual, although biennial types occur. The plant first produces a relatively small rosette of leaves, compared to the cole crops, mustard and rape, the leaves being only 6 to 18 inches long, and a succulent fleshy taproot ½ to 2 inches thick and 1 to 12 inches long, depending upon the type and cultivar. After the root growth is completed, the flowering stem elongates to a height of 2 to 3 feet. The root is harvested as soon as possible after it reaches market size. The longer it remains in the soil afterwards, the less tasty it becomes.

There is no problem of shattering in the harvest of radish seed, as the pods do not dehisce. The seeds are usually harvested with standard or all-purpose combines (Hawthorn and Pollard *1954**).

Inflorescence

The white to lilac cruciferous flowers are smaller and less showy than those of mustard or rape.Each day of flowering three florets usually appear on the tip of each branch of the panicle (fig. 166). Each flower is capable of producing a pod 1 to 3 inches long and containing one to six seeds (Bailey *1949**) or possibly up to 12 seeds. (See "Cole Crops" for details of the cruciferous flower.)

Kremer (*1945*) stated that the flower opens during the morning with the corolla remaining fresh throughout the day or into the second day. He indicated that pollen receptivity of the flower was limited to a few hours of the day. Radish is the source of some nectar and pollen, but Kremer (*1945*) stated that honey bee

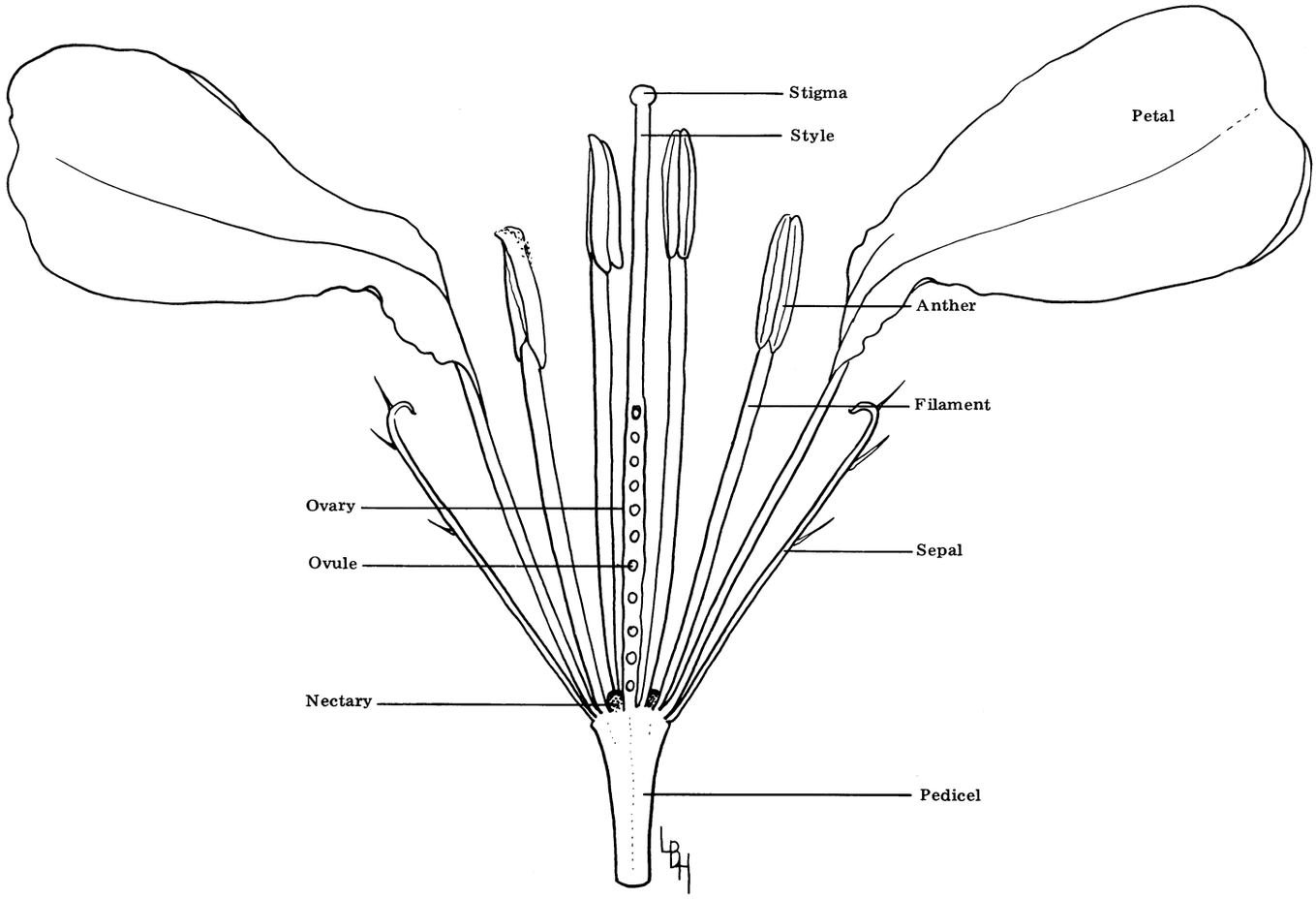

FIGURE 166.—Longitudinal section of radish flower, × 8.

flight volume in radish fields was less than half that in clover fields, with little activity in the afternoons.

Pollination Requirements

The pollination of radish was studied by Crane and Mather (*1943*), Kremer (*1945*), and Radchenko (*1966*). The cross-pollination of radish was the main object of the study by Crane and Mather (*1943*) who found that the 'Icicle' and 'Scarlet Globe' cvs. were self-incompatible and that crossing decreased from 30 to 40 percent at 9 inches, to 1 percent at 15 feet, and 0.1 percent at 240 feet. Radchenko (*1966*) stated that pollination was primarily by honey bees (77 to 94 percent of the total) and that bee pollination increased the seed crop by 22 percent and enhanced seed quality. All seemed to agree with Jones and Rosa (*1928**) that the radish is almost entirely insect-pollinated.

Pollinators

Honey bees are the most important agents in the pollination of the radish. The studies by Kremer (*1945*) indicate that the seed yield is largely influenced by the number of honey bees visiting the radish flowers. Radchenko (*1966*) also reported that honey bees were the main pollinators of radish flowers, accounting for 77 to 99 percent of the total, increasing the crop by 22 percent, and enhancing the seed quality. Crane and Mather (*1943*) also accredited honey bees with effectively setting the seed crop, noting that the seed set was especially heavy near 25 colonies of honey bees.

Pollination Recommendations and Practices

Kremer (*1945*) indicated the need for honey bees, only stating that the nearer the hives to the plants the better. He cautioned that when colonies are not nearby, or when major honey-producing plants flower between the apiary and the radish field, many of the radish flowers are not visited by bees, pollination does not occur, and seed yields are reduced. He suggested renting colonies of honey bees if none are close by at radish flowering time.

Although the number of colonies or units of bees per unit of blossoms has not been indicated, the relatively short length of time the flower is receptive and its relative unattractiveness would indicate that a higher population of bees might be necessary than the one or two colonies per acre mentioned for rape pollination.

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RAPE[32]

Brassica spp., family Cruciferae

Two species of *Brassica* are known as rape, a word derived from the Latin word "rapum" meaning turnip. *B. napus* L. is known in Canada as the Argentine type of rape, and elsewhere as summer rape, winter rape, colza, colza-oil rape, or swede rape. *B. campestris* L. is known as field mustard, summer turnip rape, Polish rape, toria, and sarson. Sarson is somewhat different from toria for it has both yellow-seeded and brown-seeded cultivars.

Rape is not extensively grown in the United States, but there are about 4 million acres in nearby Canada. About 80 percent of this acreage is planted to *B. campestris*; 20 percent to *B. napus*. The oil, pressed from the seed, is used in margarine and shortenings and in salad and cooking oil. The quality of rape oil is equal to or better than soybean oil. Rapeseed meal has found wide acceptance as a food for many classes of livestock. The protein in rape is considered equivalent to that in soybean on a pound-for-pound basis (Downey et al. *1970*). Yields reported from Canada range from 1,560 to 2,220 pounds seed per acre.

Plant

Young rape plants look somewhat like young cabbage plants, with basal leaves 4 to 12 inches or more long and half as broad as long. The flower stalk of *B. napus* grows to a height of 2½ to 4 feet, whereas *B. campestris* reaches only 1½ to 3 feet. Rape is a cool-season crop but is susceptible to frost. The seeds of rape are drilled into the soil, just like wheat, either late in the fall (making it a sort of biennial) or early in the spring as an annual.

Inflorescence

The plant is topped by a mass of golden yellow flowers that in bloom give the field a bright golden appearance.

The flowers are in elongated terminal racemes. There are the four characteristic cruciferous petals and, usually, six stamens, four projecting above the stigma and two shorter than the style. There are four partly concealed nectar glands, two on the inner side of the short stamens, the others between the insertions of each pair of long stamens (Knuth *1908*, p. 96*). The latter nectaries become more accessible to bees as the flower matures (Meyerhoff *1958*). The fruit is a slender silique or pod 2 to 4 inches long. Knuth (*1908*, p. 76*) stated that when the flower of *B. napus* opens, the anthers are

[32] See also, "Cole Crops," and "Mustard."

still unripe, and those of the four long stamens lie close to the already mature stigma. Before the corolla has fully expanded, the anthers make a half turn and dehisce so the pollen-covered sides are turned outward. The anthers of the short stamens, 2 to 3½ mm below the stigma, remain with their pollen-covered sides toward the style, but they lean outward. When the flower fades, the long stamens recurve, so that automatic self-pollination may occur if the plant is self-compatible. Flowering extends from 22 to 45 days (Gerard and Cronan *1963*, Radchenko *1964*).

Rape produces nectar sufficiently to be considered a better honey plant than white or red clover (Hammer *1966*). The nectar can be seen glistening in the bottom of the flower all day, and a colony of honey bees may store 15 to 33 pounds of honey per day (Palmer *1959*). This, of course, would depend upon the strength of the colony, the number of flowers present, and weather conditions.

Pollination Requirements

There seems little doubt that *B. campestris* or Polish rape requires insects for cross-pollination and seed production. Koutensky (*1958*) showed that production in fields with apiaries beside them was 2,095 kg/ha (1,844 lb/acre), but with apiaries 2.4 km (1.4 miles) distant the production was only 1,275 kg/ha (1,511 lb/acre). Pritsch (*1965*) studied the pollination of *B. campestris* in cages with bees compared to cages with bees excluded, although smaller insects had access to both cages, and obtained significantly greater production with bee pollination. Downey and Bolton (*1961*) reported that the yield of seed in fields stocked with bees was at least 30 percent higher than fields not supplied with bees. Downey et al. (*1970*) stated that *B. campestris* is almost completely self-sterile and bees must be provided. White (*1970*) reported that summer turnip rapes are almost completely cross-pollinated, the "true" rapes about one-third cross-pollinating and two-thirds self-pollinating.

In the case of *B. napus* or Argentine rape, there is some question about the degree of benefit from insect pollinators. Knuth (*1908*, p. 98*) reported that "according to some authors the plant is self-sterile," and insect visitation will increase seed production. According to Free and Nuttall (*1968*), Fujita (*1939*) reported that *B. napus* plants caged with bees produced 25 percent more seed than plants caged without bees. Von Rhein (*1952*) cited other workers who showed that bees caused 17.4 percent more seed per pod and 9.7 percent heavier seeds than were produced on plants not visited by bees. Louveaux and Verge (*1952*) reported a 50 percent increase in seeds per pod on plants growing near a large apiary as compared to plants caged to exclude bees.

Jenkinson and Jones (*1953*) reported that although the relationship of anthers to the stigma in individual flowers favors self-pollination, the presence of bees resulted in increased yields, for example, 8.8 seeds per pod with bees present versus 5.3 seeds per pod with bees excluded.

Downey et al. (*1970*) stated that *B. napus* is largely self-pollinated, and thus a good uniform set of seed can be obtained without bees. Turnip rape, however, is almost completely self-sterile and requires cross-pollination to set seed. Wind can carry pollen from one plant to another, but insects, particularly bees, are important. Experiments show that when fields of turnip rape (*B. campestris*) are stocked with bees, earlier and more uniform maturity results. Downey (*1964*) indicated that when bees were excluded from 'Arlo' cv. of rape only two-thirds as much seed set as when bees were present at flowering. Even so, he indicated that neither native bees nor honey bees were available in sufficient quantities for effective pollination of the large acreages of rape in Canada. Nothing was mentioned about transporting colonies to the fields that had low pollinator populations. The ratio of seeds per flower with bees present was 6.7 compared to 2.8 without bee visitation.

Koutensky (*1959*) reported that bee pollination increased seed yields of *B. napus* v. *arvensis* by 64 percent. Vesely (*1962*) reported that bee activity increased *B. napus* v. *oleifera* seed production by 25 percent and that cross-pollinated plants set the crop of seed and ceased flowering earlier than plants not visited by bees. Pritsch (*1965*) also reported significantly greater yield of seed in cages with bees than with bees excluded. Free and Nuttall (*1968*) reported a 13 percent increase in seed yield from cages with bees compared to cages without bees—an amount they did not consider of significance.

Downey et al. (*1970*) indicated that *B. napus* was 70 percent self-pollinated. Mohammad (*1935*) stated that in toria and brown-seeded sarson 12 and 20 percent of bagged pods set, whereas 91 percent of yellow-seeded sarson in bags set. He also stated that plants from cross-pollinated seeds were more productive.

Meyerhoff (*1954*) conducted five tests over 3 years with 'Lembke's' winter rape. He concluded that honey bees increased the number of pods per plant by 53.2 percent, pod length by 6.1 percent, and seeds per pod by 12.6 percent. Zander (*1952*) also studied 'Lembke's' winter rape in one cage with bees, in one without bees, and an open plot. In mid-May, the plants in the cage with bees had set their seed crop and had ceased flowering, whereas the plants in the cage without were still in full bloom; the stage of the plants in the open was between that of the others.

Latif et al. (*1960*) showed that rape seed production in fields with bees was more than double that in fields where bees (*Apis cerana* F.) were absent. Olsson (*1955*) also showed that rape was about one-third cross-pollinated in open fields, whereas white mustard was almost completely self-pollinated. The presence of bees in cages of white mustard doubled the number of seeds per pod and increased the pod set by 50 percent.

Vasil (*1964*) and Hasler and Maurizio (*1949, 1950*) have shown that boron, in some unknown way, influences the pollination of *B. napus* and other plants. More information in this area would be most helpful in understanding the pollination and fruit setting not only in the *Brassicas* but also in the pollination and fruit setting of other plants.

The above tests showed a benefit from bee polli-

nation ranging from 13 to 64 percent more seeds per pod, and with earlier cessation of flowering. This would indicate that the crop is considerably benefited by insect pollination.

Olsson (*1955*) gave wind pollination some credit in the setting of rape seed, but most other researchers consider wind as only a minor factor.

Pollinators

Rahman (*1940*) studied the pollinators of *B. napus* in India. He concluded that the dwarf honey bee of India (*Apis florea* F.), the wild bees (*Andrena ilerda* Cam. and *Halictus* sp.), and the fly (*Eristalis tenax* (L.)) were the most important pollinators.

Free and Nuttall (*1968*) studied the activity of honey bees on *B. napus*. They reported that all bees that visited the flowers collected nectar although some collected pollen also. All became covered with pollen, but some removed and discarded it. Those that collected the pollen did so primarily during the morning hours.

Honey bees are the primary pollinators of rape (Belozerova *1960*, Nikitina *1950*, Radchenko *1964*, Vesely *1962*). The plant is highly attractive to honey bees, providing both nectar and pollen, and the honey bee is of appropriate size for effective transfer of pollen from anthers to stigma. Hammer (*1952*) reported as many as 20,000 bees per hectare of rape in fields 3½ to 4 km from the apiary. Each bee was returning to the hive with 30- to 60-mg loads of nectar, roughly half the weight of a worker bee.

Belozerova (*1960*) noted that *B. napus* had 2.326 mg nectar per flower at the beginning of bloom, 1.950 mg during the peak, and 1.350 mg per flower toward the end of blooming. He noted that 96.3, 95.3, and 72.9 percent of the floral visitors at the three different periods were honey bees. Other pollinators in India include *Apis florea*, *A. dorsata*, *A. cerana*, and *Andrena ilerda* (Kapil et al. *1969*).

Pollination Recommendations and Practices

Hammer (*1963*, *1966*) recommended three colonies per hectare (1.5 colonies per acre); Radchenko (*1964*), two colonies per hectare (0.8 colony per acre); Downey and Bolton (*1961*), one colony per acre; White (*1970*), two colonies per acre; and Vesely (*1962*) three to four colonies per hectare (1.5 to 2 colonies per acre). Downey et al. (*1970*) stated that it is not necessary to provide bees to produce good seed yields, which is puzzling when it is remembered that 80 percent of the rape in Canada is *B. campestris*, which is largely self-sterile. White (*1970*) said that both summer turnip rapes and true rapes depend on bees for maximum production. The data indicate that a heavy bee population on rape would be beneficial, but no data establish the maximum floral visitation desired. Until more concrete data are available, the one to two strong colonies of honey bees per acre cited above would appear to be a logical usage.

The ideal pollinator population and proper distribution of colonies for most efficient pollination of rape needs to be determined.

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RASPBERRY

Rubus spp., family Rosaceae

The commercial cultivated raspberries include the red raspberry of Europe (*R. idaeus* L.), the red (*R. strigosus* Michx.) and black (*R. occidentalis* L.) wild raspberries of North America, and the purple raspberry, which was developed here as a cross between *R. strigosus* and *R. occidentalis* (Darrow *1937*).

In 1971, the estimated production of raspberries in frozen commercial pack was 28 million pounds, most of which came from Oregon, Washington, and the northern Midwest. This does not include production in home gardens for fresh use or for frozen food lockers. Production in the above two States from 8,730 acres in 1969 amounted to 39 million pounds valued at $11.2 million (USDA *1971*).

Plant

Raspberry roots may live for years, but the "cane" or stem lives only 2 years. Usually, the cane growth is attained the first year, then the fruit is produced the second year, after which the cane dies. Some kinds produce a fall crop on the terminals of current season canes (Magness et al. *1971*). Red and purple raspberry canes may reach a height of 8 feet. They are upright or semierect. Black raspberries, or black caps, have arched canes that reach 4 to 5 feet and form roots at the tips. Hybridization of the species has produced many variations in the growth habits of these plants. The thorns or spines on the stems vary from strong and sharp to scattered weak prickles or none. The leaves are usually deciduous (USDA *1967*).

The fruit, a berry, consists of many one-seeded drupelets or carpels on the receptacle. When the fruit is harvested, the receptacle remains on the plant, leaving the fruit as a more or less hollow cap (Bailey *1949**).

Inflorescence

The raspberry flower is about 1 inch in diameter and has five whitish petals, many stamens inserted on the

calyx, and many ovaries, each with a slender terminal style usually remaining on the drupelet. The flowers are mostly bisexual (Eaton et al. *1968*).

When the flower opens, the anthers are immature, with the filaments bent over the immature styles (fig. 167). Subsequently, the outer stamens bend back toward the petals and their anthers dehisce. As dehiscence progresses toward the center of the flower, the receptacle expands, the styles grow, and the receptive stigmas appear at their tips; later, the anthers nearest the stigmas dehisce, and, if cross-pollination has not already been brought about by insects, some selfing may result. The degree of such selfing seems to vary with species and cultivar, but most of them are largely self-sterile.

A day or so after the flower opens, the petals begin to shed. Flowering on a plant may occur over 1 to 3 weeks. Nectar is secreted abundantly by a fleshy ring on the margin of the receptacle (inside the ring of stamens) (Knuth *1908*, p. 351*). The rich and copious nectar (13 mg per flower) (Haragsimova-Neprasova *1960*, Petkov *1963*) as well as the pollen are highly attractive to insects. Commercial production of a high quality, much sought after raspberry honey occurs in some Northern States and Canada.

Pollination Requirements

Wellington (*1913*) and Hardy (*1931*) concluded that the raspberry is self-fertile, and that the pollen fertilizes the stigma before the flower is open. Other research has shown that they reached erroneous conclusions. Johnston (*1929*) showed that only 16 to 70 percent of the flowers produced berries when insects were excluded, as compared to 64 to 98 percent that set when the blossoms were exposed to pollinating insects. Couston (*1963, 1966*) compared production of a few plants caged to exclude pollinating insects with plants exposed to insect visitation. Fruit developed on plants of both treatments, but on the caged plants the size of the berries was so small (half the size of those on the open plants) and the volume of fruit produced was so low (one-third less) that it was not worth harvesting commercially. When the 'Malling Jewel' cv. was caged against insects, it produced almost no berries, but plants caged with a colony of honey bees yielded better than those in the open. Couston concluded that raspberries can be pollinated by honey bees alone, without other insects if necessary.

Shanks (*1969*) used cages over raspberries with and without colonies of honey bees enclosed. He found that the fruits had 71 to 82 percent fewer drupelets in the absence of bees, and that wind was not a factor in raspberry pollination. The fruit that set in the beeless cages was distinguished by a tuft of unpollinated pistils on the end of each berry. He considered the honey bee of primary importance in the pollination of raspberries in Washington. Allen (*1937*) stated, without supporting data, that raspberry bushes "... bear but little fruit unless there are some bees in the neighborhood." Likewise, Smith and Bradt (*1967**) stated without supporting data, that raspberries and blackberries are self-fruitful but require bees for pollen transfer.

In a well-conducted test, Eaton et al. (*1968*) showed the value of repeated bee visits in producing more and larger red raspberries. They emasculated the flowers, treated the stigmas to different pollen applications, and recorded the results in terms of fruit set and drupelets per fruit. Their results are shown in table 15.

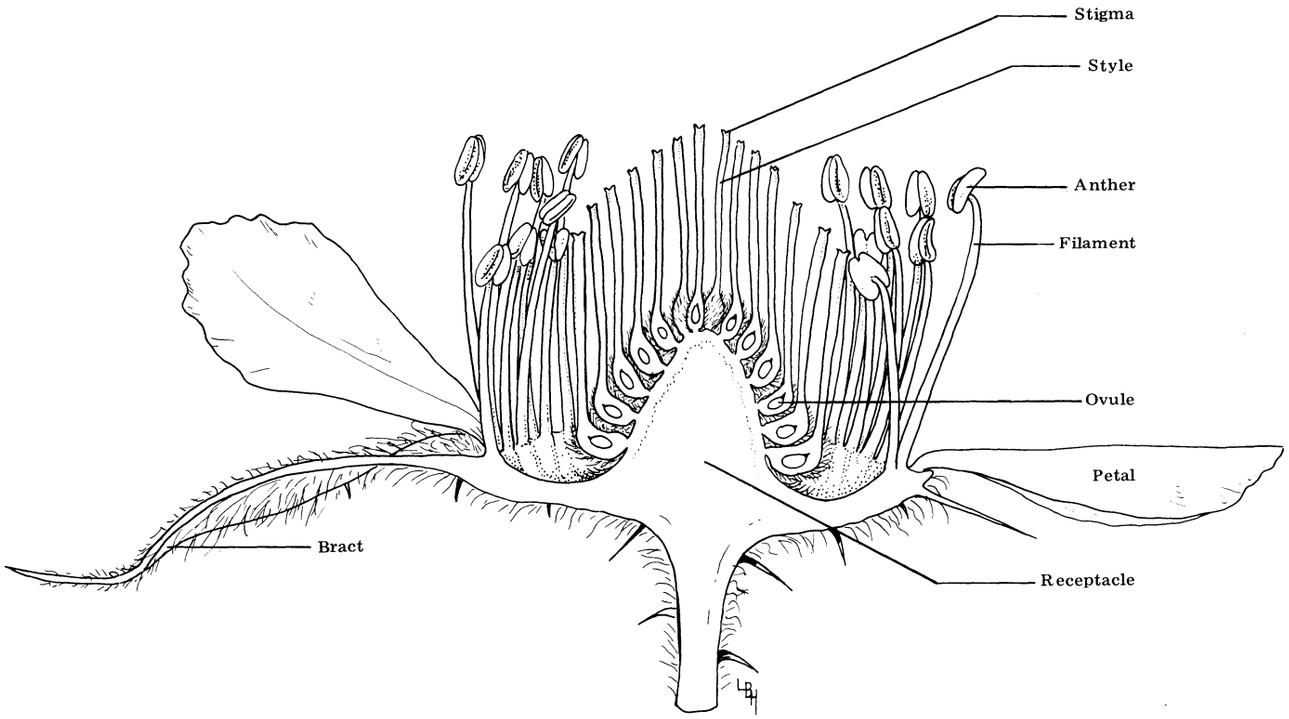

FIGURE 167.—Longitudinal section of 'Willamette' raspberry flower, ×10.

TABLE 15.—Value of repeated bee visits in producing red raspberries

Fruit set and size	Treatments				
	1[1]	2[2]	3[3]	4[4]	5[5]
Mean number of fruits set of 5 flowers	1.0	2.7	2.8	3.8	4.2
Mean number of drupelets per fruit	5.3	21.5	35.0	38.3	40.0

[1] No pollen applied to stigma.
[2] Pollen applied once, immediately after emasculation.
[3] Treated same as treatment 2, then pollen was applied again on the following day.
[4] Treated same as treatment 3, then pollen was applied again on the 3d day.
[5] Treated same as treatment 4, then pollen was applied again on the 4th day.

The results showed that for the largest number of berries with the most drupelets, each flower should be repeatedly visited by bees for at least 4 days.

Pollinators

Honey bees are the best pollinating agents of raspberries. Because honey bees and raspberries are mutually benefited, these insects should be given major consideration as pollinators of raspberries.

Pollination Recommendations and Practices

None of the research workers who have studied the pollination requirements of raspberries have recommended that steps be taken to increase the pollinator population on the raspberry since Hooper (*1913*) made the general statement that raspberries need insect pollination. He recommended one colony for each 2 acres. The evidence is plain that the plant requires or at least is greatly benefited by such pollination. Where the crop is grown commercially with its vast numbers of blossoms calling for insect transfer of pollen from anthers to stigmas, whether on the same flower, flowers of the same plant, or between plants, bees should be supplied to the plantings. The grower is interested in the largest possible berries as well as maximum production. This can only be obtained with ample insect pollinators.

No studies have been made on the number of bee visitors per flower that result in maximum pollination, although Eaton et al. (*1968*) showed that the flowers should be visited for at least 4 days. The anthers are not all open at the same time nor are all of the stigmas receptive at once. Thus, repeated bee visits are quite probably necessary if all of the ovules are to be cross-pollinated and a well-formed berry is to be harvested. Until real evidence is available, one can only compare bee activity and floral structure of other plants in estimating the bee activity desired. By this method, a desired bee population of about one bee visitor for each 100 open blossoms would appear logical. The colonies per acre necessary to supply this visitation would depend on the acreage of berries involved, competing plants, colony strength, and many other factors. The importance and value of the bees is so great that quite likely several colonies per acre would be justified.

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RED CLOVER[33]

Trifolium pratense L., family Leguminosae

Red clover is a highly important forage legume, although much of the acreage formerly in red clover has been diverted to alfalfa growing. The acreage in red clover seed production has dropped from over 2 ½ million acres in 1950 to about ½ million acres per year for 1967-71.

The principal seed-growing area is the Central and North Central States, although highest per acre production is in the Western States. In 1969, production in the four Western States, California, Idaho, Oregon, and Washington, ranged from 305 to 410 pounds per acre, with Oregon fourth in total production of clean seed. Michigan (5.5 millions pounds), Indiana (5.2 million pounds), and Illinois (5 million pounds) lead in total seed produced. These seven States produced more than half of the 43.9 million pounds.

E. A. Hollowell (personal commun., 1971) expressed the belief that red clover will be used more in the future than it is at present. This, he believed, was because farmers had concentrated on production of high-priced corn and soybean crops and had long neglected a crop rotation program to replenish the soil. He believed that with the inevitable return to such a program, red clover will regain its popularity.

PN-3840

FIGURE 168.—Red clover blossoms.

Red clover is a short-life herbaceous perennial plant that grows to a height of 15 to 36 inches. It is easily recognized by its fine leafy stems, its trifoliate leaves, and rose-pink oval flower heads that are 1 to 1 ½ inches in diameter (fig. 168). When the crop is harvested for hay, the plants are cut during early bloom. If seed is desired, the plants are usually left after a first cutting, until all of the seed heads are mature.

Inflorescence

The compact flower head, borne on the tip of the branch or stem, is made up of 55 to 275 florets (Williams *1930*), which open over a period of 6 to 8 days from the base toward the top (Pammel and King *1911*). An acre of red clover in full bloom will have an estimated 300 million florets (Hollowell and Tysdal *1948*). (There are 250,000 or more seeds per pound.) Depending on the vigor of the plant, the floret may be ¼ to ½ inch long (7.5 to 12.4 mm) but only 1/12 inch in diameter (1.6 to 2.5 mm) (Akerberg *1953*, Dennis and Haas *1967b*). Within the ovary of the floret are two ovules, but rarely more than one develops. Dijkstra (*1969*) showed that when two-seededness occurred it had no influence on total seed yield. The staminal column, with its 10 stamens and the slightly longer stigma, extends to the mouth of the corolla tube, but is enclosed within the keel petals. When the bee exerts pressure with its head on the keel petals, the stigma and the anthers are excerted or "tripped" and come in contact with the bee, usually on the posterior part of the head (Woodrow *1952b*). When the pressure is removed the staminal column returns to its former position within the keel, but can be tripped repeatedly.

Nectar is secreted at the base of the corolla tube but only extends 1.35 to 1.47 mm up the tube. Tetraploid red clover produces more nectar per floret than diploid, but because of the longer corolla tube the nectar is no more accessible to the honey bee (Dennis and Haas *1967b*), which has a "tongue" or proboscis length of only 5.90 to 6.25 mm (McGregor *1938*). Thus, only with the shortest corolla tube (7.5 mm) filled to the highest (1.5 mm) would the 5.90 to 6.25 mm honey bee tongue reach the red clover nectar. Hawkins (*1969*) stated that the honey bee can reach to a depth of 7 mm in the corolla tube. Dennis and Haas (*1967b*) stated that the honey bee is able to push its head about 1.4 mm into the corolla tube thereby increasing the effective length of the tongue (fig. 169). It is well known that the corolla tube of late-season red clover is usually much shorter than at the first flowering. Although surplus red clover honey production is uncommon, beekeepers frequently report that bees work red clover late in the season. Holm (*1972*) caused a reduction in corolla tube length by spraying the plants with a growth retarding chemical. This resulted in a higher frequency of honey

[33] See "Clovers, General."

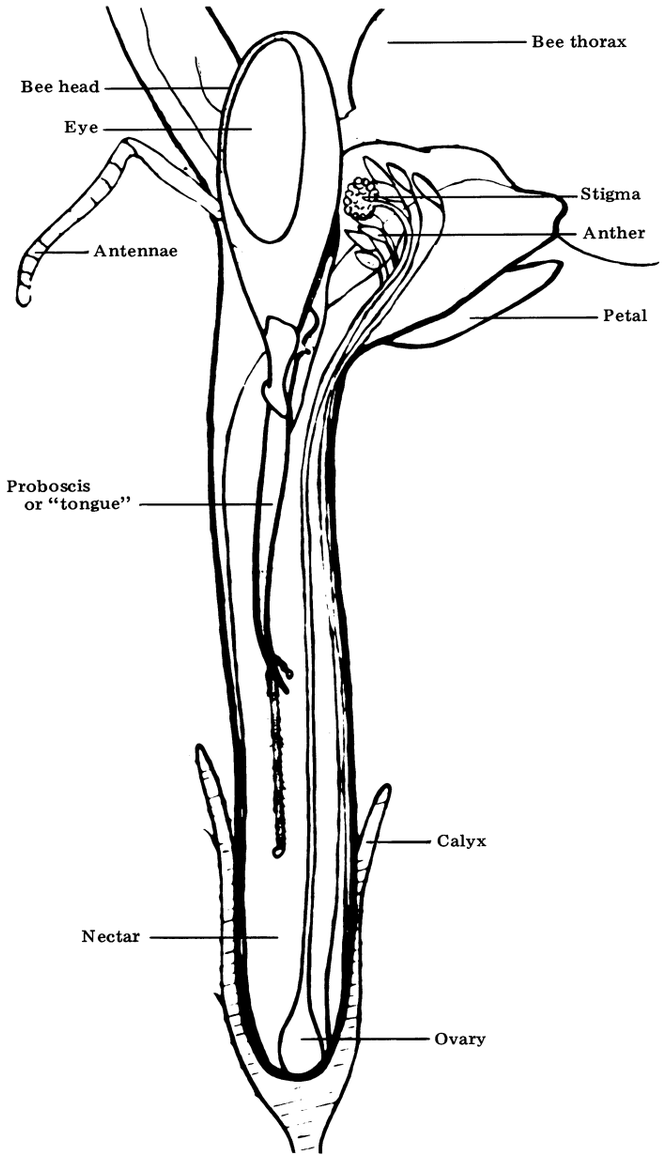

FIGURE 169.—Bee head (enlarged) with proboscis extended into red clover bloom.

bee visits and increased seed production on the treated plants.

Bukhareva (*1960*) showed that nectar secretion was influenced by plant nutrients. Plots treated with 8 oz boron and 3 oz ammonium molybdate showed a 53 percent increase in nectar secretion, 7 to 11 percent increase in sugar concentration, 17 to 32 percent increase in bee visitation, and 14 to 15 percent increase in seed production. Killinger and Haynie (*1951*) associated lack of boron with low seed yields in Florida. Unfortunately, too little attention has been paid to the influence of soil nutrients on floral attractiveness of red clover as well as on many other plants.

MacVicar et al. (*1952*) obtained no benefit from spraying plots with dilute honey to attract honey bees, and, in general, the baiting of bees into the field has not proven practical in the United States.

Hawkins (*1969*) showed that the corolla varied considerably in length, and he believed that the development of either short corolla strains of red clover or long-tongued bees might be feasible. He also believed that breeding clover cultivars with more nectar would contribute to better pollination. Akerberg et al. (*1966*) found that, in general, the corolla tubes were shorter towards southern Europe than to the north, an indication that location of growth might influence bee visitation.

There seems to be no question that some species of bumble bees can reach the red clover nectar with ease. Under certain conditions, all species of bumble bees and honey bees can reach the nectar (Bond *1968*, Bond and Fyfe *1968*).

Woodrow (*1952a*) concluded that the "depth of the red clover corolla in relation to the length of the honey bee's tongue appears to be unimportant to mechanics of the pollination act," because the tongue plays no part in the transfer of pollen. The question then becomes one of the degree of visitation by the honey bee if it were not rewarded with nectar. Woodrow (*1952a*) believed that most of the honey bee visits to red clover were for pollen, although some bees collected nectar also. Bond (*1968*) showed that tetraploid red clover produced more nectar than related diploid cultivars, but the nectar was lower in the corolla tube and more difficult for honey bees to reach.

Specific races of honey bees have been mentioned by various writers as being better pollinators of red clover than other races (Alpatov *1946*, *1948*; Smaragdova *1956*; and Hammer *1950*). There is no agreement as to which race is superior in this regard, and no recent attempt has been made to breed such a bee. In the late 1890's, beekeepers made attempts to select superior red clover honey-producing bees but failed. However, Stahlin and Bommer (*1958*) concluded that breeding clover to suit the bees would be more profitable than breeding bees to fit the clover. Starling et al. (*1950*) concluded that short corollas alone offered no advantage for increased seed production.

Woodrow (*1952b*) described in detail the method the honey bee follows in pollinating red clover. He stated that the length of the tongue of the bee need be no handicap in pollination of this flower because the sexual parts of the flower are at the tips, and the bee's tongue is not used in transferring pollen from flower to flower.

Pollination Requirements

The pollination of red clover has probably been more extensively studied than that of any other plant, not only in the United States but also in many other countries. Excellent reviews have been made by Bohart (*1957*, *1960**), Dennis and Haas (*1967a*, *b*), Free (*1970**), Gubin (*1947*), Stahlin and Bommer (*1958*), and Umaerus and Akerberg (*1959*). The discussion on red clover pollination by Free (*1970**) is extensive and thorough. Krishchunas and Gubin (*1956*) also devoted about 25 pages of their book to this crop.

Self-sterility in red clover has been known since Darwin (*1889**) showed that caged plants would not set seed unless they were cross-pollinated. The pollen must

come from another plant if commercial production of seed is anticipated (Williams *1931*, Westgate and Coe *1915*). Martin (*1913*) demonstrated that self-pollen tubes penetrated the style toward the ovary more slowly than foreign pollen (from another red clover plant). Whether or not this time factor is critical has not been demonstrated, but the floret must be pollinated within 2 to 4 days after it opens (Free *1965*, Umaerus and Akerberg *1959*). The appearance of the flower heads is a strong clue to the adequacy of pollination. If pollination does not occur, the florets remain turgid, the head is soon covered with the colorful florets, and the field takes on a flower-garden appearance.

If pollination is adequate, an individual head in flower will have the lower florets pollinated and wilted, with the position of the florets changed from upright to drooping, the color changed from rose-pink to rusty brown, those in the center of the head attractive to pollinators, and the uppermost ones still in the bud stage (Woodrow *1952a*). When this situation exists, the field takes on a greenish-brown cast. Naturally, the seed-grower should strive for this situation and should be concerned if the field has the flower-garden appearance.

Pollinators

The relative value of the pollinating insects on red clover has been debated for decades. Many references attest to the value of bumble bees. Others support honey bees, and some support other genera of bees. Hawkins (*1962a*) found a correlation between bumble bee populations and red clover seed production in England 2 years out of 3, but no correlation between honey bees and seed production. He (*1962b*) proposed that an organization be formed to make annual counts of bumble bees, similar to bird counts, to stimulate public interest in these insects. Bird (*1944*) also considered bumble bees much more important than honey bees.

Lindhart (*1911*) concluded that honey bees occasionally aid in red clover pollination. This evaluation of honey bees has consistently increased over the years in many subsequent papers. For example, Anderson and Wood (*1944*) obtained one seed per head of red clover where bees were excluded but 56 seeds per head where honey bees were caged on the plants.

Butler (*1941*), Valle (*1959*), and Valle et al. (*1960*) after thorough studies gave credit to both honey bees and bumble bees. The other genera of bees that have been mentioned, but in general considered of little importance, include *Andrena* (Benoit et al. *1948*), *Eucera* (Yamada and Ebara *1952*), *Halictus* (Maurizio and Pinter *1961*), *Megachile* (Akerberg et al. *1966*), *Melissodes* (Folsom *1922*), *Osmia* (Maurizio and Pinter *1961*, Akerberg et al. *1966*), *Psithyrus* (Scullen *1930*), and *Tetralonia [Synhalonia]* (Folsom *1922*).

Dennis and Haas (*1967b*) also observed the action of bumble bees on red clover and learned that *Bombus terrestris* (L.), with a short (6.8 mm) tongue, obtained red clover nectar only by cutting a hole in the base of the corolla tube. *B. lapidarius* (L.), with an 8-mm tongue, collected nectar normally from diploid red clover. *B. distinguendus* F. Morawitz, with an 8.8-mm tongue, and *B. hortorum* (L.) (11.1 mm) were more frequent on tetraploid red clover.

Bohart (*1957*) and van Laere and Martens (*1962*) concluded that bumble bees, except for a few nectar-thieving species, are ideal pollinators of red clover although their populations are unpredictable and usually insufficient to adequately pollinate all the blossoms in a large field. Bohart (*1957*) considered honey bees satisfactory if they are sufficiently concentrated in the area and the competing pollen and nectar sources are kept at a minimum. In Canada, Peterson et al. (*1960*) also concluded that honey bees were best. In Russia, Gubin (*1947*) considered bumble bees to be the best pollinators of red clover on a bee-for-bee basis but that overall they provided only 3.5 percent of the pollination service. The value of honey bees was expressed by Hopkins (*1896a*, *b*), Pieters (*1924*), and Stapel (*1934*) and demonstrated by Richmond (*1932*), Dunham (*1932*, *1939a*, *b*, *c*), and Armstrong and Jamieson (*1940a*, *b*).

Bumble bees were considered of such importance that they were transported from England and established in New Zealand for the express purpose of pollinating red clover (Belt *1876*, Hopkins *1914*). However, Forster and Hadfield (*1958*) showed that 35 colonies of honey bees placed adjacent to a 10-acre field of Montgomery red clover in New Zealand provided 77 percent of the pollinating insects in 1954 and 89 percent in 1955. They stated that this was a fair cross-section of pollinator activity on red clover crops in South Canterbury. Morrison (*1961*) found inconsistencies over the years between the efficiency of honey bees and bumble bees in New Zealand and considered both groups of value. Hills (*1941*), Palmer-Jones et al. (*1966*), and Palmer-Jones (*1967*) considered honey bees of greater value than bumble bees. Bond and Fyfe (*1968*) showed that seed production in a cage with one strong colony of bees was more than twice that in a cage with a weak colony.

Hollowell (*1932*) proposed the introduction of additional honey bee colonies into clover fields to increase seed production. This action has now become a common practice. Walstrom et al. (*1951a*, *b*) proposed 400- to 600-foot intervals as an economical distance between groups of colonies used for red clover pollination. Jamieson (*1955*) showed that only 63 lb/acre of seed were obtained with local wild bees, but 307 lb/acre were obtained with two colonies of honey bees per acre.

The production of red clover seed is directly proportional to pollinator activity. Everly (*1950*) associated reduced native pollinators with decreased seed yields in Indiana, and stated that red clover pollen-collecting honey bees were effective in setting a good crop of seed. Walstrom et al. (*1951a*, *b*) showed that seed production decreased 6.4 lb/acre with each 100 feet of distance from the apiary. Walstrom (*1958*) showed that differences in seed yields at 100-foot intervals from apiary sites were significant at the 1-percent level of probability. Zivov and Skvorcov (*1951*) also showed that seed production decreased with increased distance: 246 lb/acre when the field was only 0.5 km from the bee source, 158 lb/acre at 1 to 1.5 km,

and only 90 lb/acre beyond 1.5 km. Jamieson (*1955*) obtained 307 lb/acre with two colonies per acre but only 63 lb/acre when honey bees were not provided. Thomas (*1951*) and Braun et al. (*1953*) obtained similar results.

The data leave little doubt that if bumble bees are not sufficiently abundant (and they usually are not), their services can be supplemented and seed production stabilized by the use of honey bees. Other pollinators are of little significance.

Pollination Recommendations and Practices

Hogborg (*1966*) considered pollinators in terms of "positive bee pollinating units," and calculated that adequate pollination would be given by 20,000 units per hectare (using the value of 2.5 units for one bumble bee). This amounts to about one bumble bee or two nectar-collecting honey bees per square yard. Akerberg (*1947*) calculated that 1,100 bumble bees per hectare (about 0.1 bee/yd^2) were sufficient to produce 300 kg alfalfa seed per hectare (about 300 lb/acre). These estimates are below the amounts specified in the formula of Stanley Roadfeldt (McGregor *1966*) of one honey bee per 4 yd^2 per minute equals 300 pounds red clover seed, or one bee per square yard per minute equals 700 pounds red clover seed.

Dennis and Haas (*1967a*) used a numerical rating on the values of bees on diploid red clover, based on the bees' working speed, as follows:

Apis	1.0
Short-tongued *Bombus*	1.5
Long-tongued *Bombus*	2.5

However, their remanipulated data gave the following values:

Nectar-collecting honey bee	1.0
Pollen-collecting honey bee	1.3
Nectar-collecting bumble bee	1.6
Pollen-collecting bumble bee	1.9

By this method, they considered pollen-collecting, long-tongued bumble bees to be about twice as efficient as honey bees.

The pollination recommendations for red clover revolve around bumble bees and honey bees. The presence of bumble bees can be encouraged by providing them with domiciles, by protecting them from pesticides (Fye and Medler *1954*, Hobbs *1967*, Holm *1966*), and by planting off-season flowering plants to provide nectar and pollen. Honey bee colonies can be transported and placed in or adjacent to red clover fields in any number desired and when desired. This is a more dependable practice than "encouraging" the bumble bees.

In most cases, the number of colonies of honey bees that has been recommended per acre has ranged from one to three, but a few recommendations have mentioned four, five, six, and up to 10 colonies per acre. Some urge that the colonies be placed adjacent to the field, others recommend that the colonies be placed within the field in groups of 10 or more 100 to 400 yards apart. Some recommendations stress bees per square yard, the number of bees ranging from 1 to 18. The use of strong colonies is urged. E. A. Hollowell (personal commun., 1971) stated that two bees per square foot (18 per square yard) should set an abundant seed crop. This may require the use of several strong colonies per acre.

If visitation in the field is adequate, the field will have a rusty-brown hue instead of the rose-colored flower-garden appearance. The number of colonies of honey bees per acre necessary to provide this visitation will vary with condition of the colonies, placement pattern, climate, crop, and competing plants. The important point to remember is that there should be sufficient bees on the flowers to keep the florets tripped as rapidly as they appear.

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ROSE CLOVER[34]

Trifolium hirtum All., family Leguminosae

Rose clover is grown primarily in California, where it is used for seeding brush burns, cleared brushland, and dryland pasture. It will grow in dry "sterile" fields, on slopes, sandy steppes, or roadsides, and in waste places. Cattle and sheep, as well as such wildlife as deer, doves, and quail feed upon it even when it is completely dried up (Arkley et al. *1955*, Holland *1964*, Love and Sumner *1952*, Williams et al. *1957*).

Plant

Rose clover is a reseeding annual winter legume. The leaflets usually have a small reddish mark near or slightly above the center (Strang and Broue *1958*). The leaf stalks are ½ inch to 2 inches long. The seeds germinate with the first substantial fall rain and the plant grows slowly as a rosette of leaves until late winter. Then, as spring temperatures rise, it grows rapidly into an upright many-branched plant 3 to 18 inches tall. It blooms and sets seed in May. The plant then becomes dry and casts its seeds, which ripen 4 to 6 weeks after flowering starts. The seeds remain dormant in the soil until fall rains begin (Bailey *1966*, Williams and Leonard *1959*). Rose clover provides a high-quality forage pasture under a wide variety of climatic conditions in California. Plantings succeed in areas with as little as 10 inches of rainfall. Foliage of rose clover is much less profuse than most other clovers. It has the ability to produce some seeds under extremely unfavorable conditions (fig. 170).

PN-3841

FIGURE 170.—Rose clover in full bloom.

Inflorescence

The pink flower head of rose clover is spherical, about three-quarters of an inch across, and profusely covered with stiff white hairs. These blossoms are highly attractive to bees for both nectar and pollen. When a floret is visited by a bee, the staminal column protrudes, then withdraws after the bee departs. From four to six bees per square yard have been seen on this plant. There is one seed per floret, and there are 40 florets per head.

Pollination Requirements

Bohart (*1960**) stated, "In California, honey bees are sometimes placed by fields of rose clover to ensure pollination, but apparently the practice is not based on any known requirement." This would indicate that experience may have convinced growers that, despite lack of experimental evidence, bee pollination is beneficial to this crop. The subject should be explored and the true pollination requirement of this important western forage determined.

Pollinators

Evidence indicates that honey bees can be satisfactory pollinators of rose clover.

Pollination Recommendations and Practices

There are no recommendations for the use of pollinating insects on rose clover, although the reference by Bohart (*1960**) indicates that growers believe they obtain some benefit from bee pollination.

[34] See "Clovers, General."

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SAFFLOWER

Carthamus tinctorius L., family Compositae

Safflower is grown principally in California and Arizona, but has been grown successfully in every State west of the 100th meridian (USDA, *1961*, Dennis and Rubis *1966*, Shaw and Joppa *1963*, Klages *1954*, Knowles and Miller *1960*). The acreage varies from year to year according to the demand for safflower oil, which is obtained from the crushed seed. The oil is used in paints and in margarine and other human food. In 1963, a peak acreage of around 301,000 acres was grown. Production of seed per acre on irrigated soils has varied from 2,500 to 4,000 lb/acre; on dryland soils, from 500 to 2,500 pounds (Knowles and Miller *1965*).

Safflower is frequently planted instead of barley. Although safflower is slightly more costly to produce, the same culture and harvesting equipment can be used on each. When grown in cotton-producing areas, the cotton oil mills process the seed. The residue after the oil is removed is used for livestock feed (Knowles *1955*, Halloran and Kneeland *1961*). The price has relatively stabilized at $80 to $90 per ton, which also amounts to about $80 to $90 per acre.

Plant

Safflower, like other such related plants as artichoke, thistles, and star thistles, has spine-tipped leaves that make contact with the plant unpleasant. It is an upright annual, 2 to 6 feet high (fig. 171), with a coarse stem and numerous branches, each of which terminates in a yellow or orange (rarely white to red) flower head (fig. 172) from ½ inch to 1½ inches across (Knowles *1958*). It may be planted in rows 18 to 40 inches apart, drilled or broadcast in the field with two to six plants per square foot (Knowles and Miller *1965*). The seeds ripen and are harvested 120 to 150 days after planting.

Rubis[35] reported the discovery of a thin-hull mutant that produced seeds with about 10 percent more oil than earlier cultivars. The florets in this selection have delayed anther dehiscence (see "Inflorescence"), which lets the plant serve as a male-sterile line and provides a means for producing hybrid safflower.

Inflorescence

There may be 15 to 150 flower heads on a plant, each head enclosed in layers of spine-tipped bracts. The head that terminates the main axis of the plant flowers first, then flowering proceeds downward with those flower heads on the lowest branches opening last. On an individual plant, flowering may extend 10 to 40 days.

There may be 20 to 100 florets in a head (Claassen *1950*). Those florets on the outside open first, and opening proceeds centripetally for 3 to 5 days. Within the floret, the style is enclosed by five fused anthers attached at the base by short filaments (fig. 173). The floret begins to elongate by sunrise of the day it opens. Anther dehiscence normally occurs within the fused anther tube shortly after sunrise while the style is elongating. If dehiscence occurs *before* the style elongates, the stigma pushes through a mass of pollen, becomes coated with pollen, and becomes self-fertilized. If dehiscence occurs *after* the style elongates so that the stigma passes through the anther tube without becoming pollen coated, self-sterility results. Such flowers must be visited by bees that either bring pollen from other pollen-coated stigmas or transfer pollen from within the tip of the anther tube to the stigma. The thin-hull cultivar has this delayed dehiscence and is therefore functionally male-sterile.

Nectar is secreted at the base of the filaments and is highly attractive to bees, although the quality of honey it produces is poor.[36] The bee collects this nectar at the base of the anther tube from the outside rather than through the tube.

Safflower pollen is also highly attractive to bees and

[35] RUBIS, D. D. SAFFLOWER BREEDING AND GENETICS IN ARIZONA. Safflower Conf. Proc., 5pp. University of Arizona, Tucson. 1963. [Mimeographed.]

[36] MCGREGOR, S. E., LEVIN, M. D., and RUBIS, D. D. BEE POLLINATION OF SAFFLOWER. Safflower Conf. Proc., 2 pp. University of Arizona, Tucson. 1963. [Mimeographed.]

is considered an excellent source by beekeeping standards.

Pollination Requirements

Safflower is usually considered to be a self-pollinated crop. Claassen (*1950*), however, reported cross-pollination ranging from zero to 100 percent, although in most of the plants he used, the detectable crossing ranged from 5 to 40 percent. Knowles (*1955*) reported that some selections give more vigorous progeny if open-pollinated rather than selfed. The necessity for pollen transfer by insects depends largely upon the growth characteristic of the style. If it elongates and thrusts the stigma through and beyond the anther tube before dehiscence of the pollen, then bee visitation to that stigma is necessary for maximum production (Rubis et al. *1966*). If, on the other hand, dehiscence occurs before the style elongates, the stigma usually emerges thoroughly coated with pollen, and self-fertilization can result. This condition is most common in current cultivars; however, the description of the "normal" floret in India by Howard et al. (*1915*) indicates that delayed dehiscence, such as occurs in the thin-hull selection, may have been much more common in earlier cultivars.

PN-3842

FIGURE 171.—Safflower plant showing branching habit, spiny leaves and flowering heads.

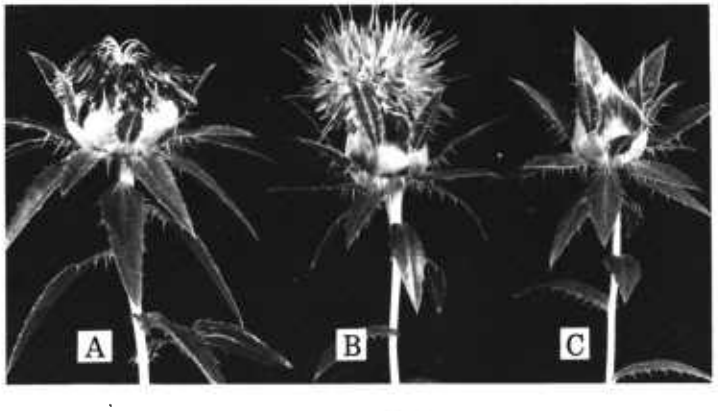

FIGURE 172.—Safflower heads in different stages of development. *A*, Head after flowering has ended; *B*, head in full Flower; *C*, bud just before first florets appear.

Rubis (*1970b*) proposed a novel way to use bees to create isolation by overstocking the area with honey bee colonies that would so intensively forage an area that outside pollinators would not enter; therefore, no cross-pollination would occur. This has not been tested in practice.

The few reports on the measured value of pollinating insects to safflower are inconsistent. An extensive review of the literature on safflower by Larson (*1962*) revealed little on its pollination requirement. Plessers[37] reported that absence of insect pollinators caused a reduction of 47.7 and 36.5 percent in two Indian cultivars and 31.8 percent in the American cv. 'WO-14'. At least some of this reduction might be attributed to cage effect. Eckert (*1962*) reported lower production from plants caged to exclude bees than from open plots for one cultivar that was "somewhat self-sterile" but no difference between treatments in the "self-fertile" cultivar. Boch (*1961*) reported that during flowering he obtained twice as much seed from plots to which bees had access, as from plots caged to exclude pollinating insects, but again cage effect might have been a contributing factor. Patil and Chavan (*1958*) found that both temperature and humidity affected seed setting of bagged flowers. Kursell (*1939*) was reported by Claassen (*1950*) to have found extensive self-sterility in different lines, which, if true, would indicate that pollinating insects would have had a beneficial effect. McGregor and Hay (*1952*) gave a brief nod of approval to the value of pollinating insects. Rubis (*1970a*) indicated that commercial cultivars are from 75 to 95 percent self-fertile, indicating that their production could be improved with an ample pollinator population.

Pollinators

Not only honey bees but various other bees and other nectar and pollen-feeding insects visit the blossoms. These may contribute in various degrees to pollination of the flower (Levin et al. *1967*, Levin and Butler *1966*, Butler et al. *1966*, Kadam and Patanker *1942*), but, in relative numbers, honey bees are by far the most

[37] PLESSERS, A. G. THE EFFECTS OF INBREEDING ON SAFFLOWER. Safflower Conf. Proc., 3 pp. University of Arizona, Tucson. 1963. [Mimeographed.]

important. No differences have been observed in attractiveness of different cultivars to honey bees. All seem to be attractive.

Probably, the best test of the value of pollinating insects to safflower was conducted at Tucson, Ariz. (Rubis et al. *1966*). In this replicated test with two cultivars, the plots exposed to insect pollinator visitation during the flowering period were compared with plots caged under plastic screen. Pollinating insects were excluded from plants of some cages, whereas a functioning colony of honey bees was added to plants of other cages. Two lines of safflower were used: Line A was a selection from the 'Gila' cv., which normally showed about 5 percent outcrossing; line B was a composite of multiple crosses of the thin-hull selection (Rubis *1962*), which normally showed about 80 percent outcrossing. The production of line A was increased about 5 percent by bees, whereas production of line B was approximately doubled.

Dennis and Rubis (*1966*) concluded that the benefits of honey bees or other pollinating insects to commercial cultivars depended on the amount of self-sterility or crossability in a cultivar. They stated that 'Frio' cv. was lower in self-fertility than 'Gila' cv.; therefore, yield increase from pollinating insect activity on the former would be expected to be greater. They concluded that production of 'Gila', even though it was considered to be self-fertile, could be increased 5 percent or more by honey bee pollination. Knowles and Miller (*1965*) apparently were in agreement for they stated that

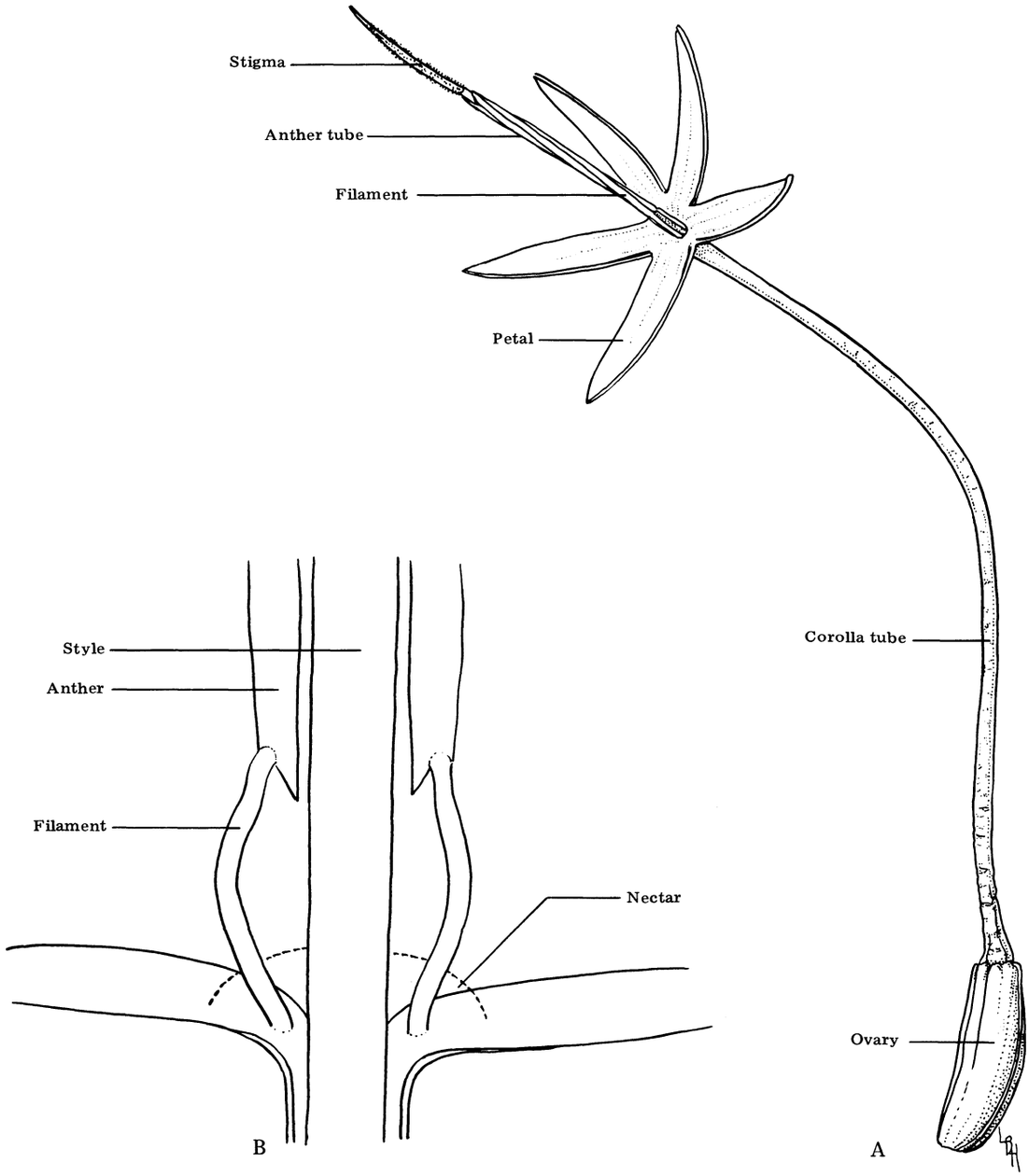

FIGURE 173.—Longitudinal section of safflower floret. *A*, Floret, ×6; *B*, filaments and adjoining area, greatly enlarged.

because safflower is not wind-pollinated, the presence of pollinating insects in abundance was necessary for maximum seed set in types that were deficient in "production" of pollen.

Pollination Recommendations and Practices

Eckert (*1959**) recommended two honey bee colonies per acre of safflower, but few, if any, growers take steps to secure this pollinator population.

Because safflower is an excellent source of nectar and pollen, beekeepers frequently place their colonies near safflower plantings, but not in the density recommended by Eckert (*1959**). The data indicate that although the safflower has a high degree of fertility, the grower would profit more than the beekeeper would by having a high population of honey bees visiting his safflower blossoms.

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SAINFOIN

Onobrychis viciifolia Scop., family Leguminosae

Sainfoin is sometimes called esparcet or holy clover. The crop is limited to a few acres grown in Montana.

Plant

Sainfoin is a perennial with a deep taproot and stout erect stems arising from a many-branched crown. Some plantings in Montana are 60 years old and still used for pasture (Dubbs *1967*). The plant may grow from 15 to 40 inches high. It requires a soil rich in lime. Because it

can withstand temperatures as low as −40° F., it can grow in the coldest parts of the country.

Inflorescence

The pinkish or rose-colored flowers occur on terminal, erect, close racemes at the top of the plant, giving a field in flower a delicate rose color. The flower mechanism is essentially like that of white clover or sweetclover. The weight of a bee on the flower causes the stigma and anthers to protrude from the keel, then return after the weight is removed. The stigma projects beyond the anthers so that cross-pollination is assured should the bee visit occur. Lateral access to the nectar in the flower by the bee is impossible. The calyx tube is only 2 to 3 mm deep, so most melliferous insects can reach the nectar and pollen. The style becomes more and more erect as anthesis progresses, and ultimately projects 1 to 1½ mm beyond the cleft in the keel (Knuth *1908*, p. 319*). Tereshchenko (*1949*) stated that flowers may open throughout the day but mostly in the morning. They usually remain open only 1 day. Flowering begins at the base of the raceme and takes 2 to 3 weeks to reach the tip. The seed develops in a one-seeded pod.

Sainfoin blossoms secrete nectar excessively and are highly attractive to pollinating insects, particularly honey bees. Pollen is also produced in abundance. Dubbs (*1968*) stated that 20 hives placed on 4.78 acres was insufficient for bee saturation. An estimated nine-tenths of all bee visitors were honey bees.

Graham (*1941**), Madoc (*1934*), Alfonsus (*1929*), Dubbs (*1967*), and Pellett (*1947**) reported that sainfoin honey is of the finest quality. Kropacova (*1969*) calculated the total quantity of nectar sugar produced as 32.8 to 130.3 kg/ha or 29 to 155 lb/acre.

Pollination Requirements

Bosca and Hejja (*1963*) stated that self-fertility of the plants ranged from zero to 37 percent. They also found that inbred plants produced only 70 percent as many stems and weighed only 73 percent as much as crossed plants. Knuth (*1908*, pp. 318–319*) indicated that cross-pollination of sainfoin flowers was required because automatic self-pollination does not occur. Kropacova (*1969*) found that seed production of exposed plants was 10 to 25 times as great as that from plants caged to exclude bee visitors (caged plants yielded 9.75 g/m^2), whereas plants exposed to bees yielded 179.13 g/m^2). Sainfoin seed production is primarily dependent upon bee pollination. The most effective time for bees to visit sainfoin flowers has not been determined, nor has the effect of bee pollination on the appearance of the flower. Flowers of many other species of plants begin to fade or wilt shortly after they are pollinated.

Tereshchenko (*1949*) caged plants to exclude bees and obtained only 3.2 percent set of blooms (3.2 g seed) compared to 42.7 percent set (49.2 g seed) of those not caged. He also found a high negative correlation between distance from the apiary and seed set.

Pollinators

The honey bee is doubtless the most populous of insect visitors to sainfoin flowers. Pellett (*1947**) stated that he saw 100 bees on sainfoin for each 10 on white clover, a plant considered highly attractive to bees. Honey bees begin visiting the flowers quite early in the morning and continue to visit them throughout the entire day.

Pollination Recommendations and Practices

Kropacova (*1969*) recommended two to three colonies of honey bees per hectare (about one colony per acre) located close to the field. This seems rather low when we consider Dubbs' (*1968*) statement that 20 colonies placed on a 4.78-acre seed field were insufficient for bee saturation. He calculated that two to three colonies per acre would provide five or six visits to every sainfoin flower. This would appear to be low, thus more colonies may be required.

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SCARLET RUNNER BEAN

Phaseolus coccineus L., family Leguminosae

The scarlet runner bean, or runner bean, native to Mexico or Central America (Graham *1941**) and of major importance in parts of Europe, is of minor importance in the United States, where it is sometimes called the Oregon lima bean.

Plant

The roots of the slender, twining scarlet runner bean are tuberous and live for several years, but frost kills the aerial part; therefore, it is an annual plant above the

ground, but a perennial beneath (Kooistra *1968*). The plant may grow to a height of 10 to 15 feet if staked, but when grown commercially the crop is not staked. It is harvested by the same method used in harvesting lima beans, with yields of 1,200 to 1,500 lb/acre of seed (Hawthorn and Pollard *1954**).

Inflorescence

The showy blossoms are borne on long racemes. They are attractive to various species of bees for both nectar and pollen. Darwin (*1874*) showed that the blossom is ingeniously contrived to insure that insect visitation results in pollination. This is brought about by a pair of nectar holes at the base of the staminal tube, almost covered by a flap on one stamen. When the bee forces this flap aside, it rubs across the staminal column and transfers pollen from anthers to stigma.

Pollination Requirements

Darwin (*1889**) covered scarlet runner beans to exclude pollinating insects and obtained only one-eighth and one-third as many beans as were obtained from open plants. In a more elaborate experiment, Free (*1966*) caged scarlet runner beans with and without honey bees to determine the need for insect pollination. Plants caged with bees set 1,479 g of pods per plant, compared with 180 g per plant where bees were excluded. Other factors varied correspondingly: Pods per plant, 96:11; grams of seed per plant, 356:50; number of seeds, 206:30; and seeds per pod, 3.9 in bee cages compared to 2.7 in cages where bees were excluded. Only the mean weight per seed was unchanged. The pods in the cages without bees could not be harvested until later in the season than those in the bee cages. Tedoradze (*1959*) obtained similar benefits from bees.

Mommers (*1971*) studied the pollination of runner beans under glass and reported that bees had no effect on production of beans. He concluded that varietal differences influenced the results obtained by Free (*1966*), and that this accounted for the differences reported.

Pollinators

Henslow (*1878*) showed that bumble bees pollinated scarlet runner beans. Free and Racey (*1968*) showed that honey bees were as useful as bumble bees in pollination of scarlet runner beans grown in glass houses, although Free (*1968*) found that individual bumble bees worked faster and visited more flowers per plant than did honey bees. Bumble bees often pierce a hole in the base of the flower and steal the nectar without contributing to pollination. Subsequently, honey bees visit this hole and again pollination is bypassed (Jany *1950*).

Pollination Recommendations and Practices

Blackwall (*1964*) said that adequate pollination is a must for early yields and that lack of insect pollination is the most important single cause for low yield of beans. Blackwall also stated that where lack of pollination is a recurrent problem, it may be worthwhile to hire colonies of honey bees to supplement the local pollinator population. She recommended that beekeepers supply small, rapidly expanding colonies, which have a high need for pollen.

Free (*1966*) stated that because honey bees are clearly effective in pollinating scarlet runner beans, their use should increase yields where pollination is a limiting factor. However, he did not make a recommendation to growers on the use of honey bees as pollinators of this crop. The evidence indicates, however, that if the grower wants to obtain maximum yields and harvest the seeds as early as possible, he should have a high pollinator population in his field, particularly during early flowering.

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SESAME

Sesamum indicum L., family Pedaliaceae

Sesame, sometimes known as benne, is grown for its edible oil pressed from the seed and for the decorticated (hulled) edible seed (Martin and Leonard *1949**).

World production in 1968 was estimated at 640,000 tons of sesame oil. This would indicate that about 10 million acres were devoted worldwide to this crop. In 1955, about 15,000 acres were grown in the United States, mostly in Texas and New Mexico.[38] In the United States, sesame is grown in the Southwestern, Southern, and South Central States. Although there was essentially no production in 1971, there is considerable interest in reviving production. Tests have shown that under extremely favorable conditions as much as 2,000 pounds of seed per acre can be produced. Nonshattering cultivars were developed in 1953 (Kinman *1955*).

Plant

Sesame is an annual erect herb, 3 to 5 feet tall, which is grown in rows 18 to 42 inches apart with 6 to 10 plants per foot of row (USDA *1958*). The 3- to 5-inch-long leaves are opposite, oblong, and, in the older cultivars, smooth and flat. In the nonshattering cultivars the leaves are cupped and have small leaflike outgrowths on their underside. Some cultivars have many branches, whereas others are relatively unbranched. Thousands of cultivars are known, with lifespans ranging from 2 to 6 months. Sesame is killed by frost; however, seed harvest before frost is preferred. Because large-scale cultivation equipment can be used, growers can handle large acreages. A single plant is capable of producing several thousand seeds (Kinman and Martin *1954*).

Inflorescence

The tubular, pendulant, bell-shaped, two-lipped flower is pale rose to white and ¾ to 1 inch long. The two lobes of the upper lip are shorter than the three lobes of the lower (Bailey *1949**). One flower is produced at the axil of each leaf. The lower flowers usually begin blooming 2 to 3 months after seeding, and blooming continues for some time until the uppermost flowers are open.

Sesame is a source of nectar and some honey for beekeepers primarily because it flowers in midsummer when little else in the area is blooming. It is an excellent source of pollen for bees. It also attracts various other bees and other insects that feed on its pollen or nectar; however, honey bees are the primary visitors (Langham *1944*).

Pollination Requirements

Sesame is usually considered to be a self-pollinated crop (Kinman and Martin *1954*) although the amount of cross-pollination that occurs is considerable. Van Rheenen (*1968*) recorded 5.5 to 9.6 percent crossing but gave no indication as to what pollinators might be responsible. Langham (*1944*) obtained an average of 4.6 percent (0.50 to 9.58 percent) outcrossing, which he attributed to honey bees. Martinez and Quilantan (*1964*) observed 0.15 to 9.39 percent crossing, with higher crossing observed during winter when the bee population was higher. Langham (*1944*) covered plants to exclude insects and obtained relatively as much seed set as on plants exposed to bee visitation. However, Srivastava and Singh (*1968*) obtained yield increases of 43.66 percent over the best parent when they crossed Meghna with local cultivars and 38.0 percent when they crossed Meghna with wild plants. This indicated that hybrids might be produced that would outyield current cultivars. A crossing method involving bees might prove quite beneficial.

Pollinators

Honey bees are the primary visitors to sesame flowers. Langham (*1944*) stated that the bee alights on the protruding lip of the flower and squeezes inside. Later, it emerges coated with pollen and flies to another flower. However, no benefit from such crossing, although established in many other crops that have been considered self-pollinating, has been established for sesame. The high percentage of heterosis shown by Srivastava and Singh (*1968*) strongly indicates that insect pollination would be beneficial in the production of superior hybrid seed.

The effect of insect visitation on the individual flower has not been studied.

Pollination Recommendations and Practices

None.

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[38] KINMAN, M. L. SESAME PRODUCTION. U.S. Dept. Agr., Agr. Res. Serv., Tex. Agr. Expt. Sta. 1956. [Mimeographed.]

SISAL AND HENEQUEN [39]

Agave spp., family Agavaceae

Sisal and henequen are long hard fibers used primarily in cordage (ropes, cords, and twine). They are obtained from the 2- to 4-foot-long leaves of agave plants. Sisal, the most important fiber, is obtained from *A. sisalana* Perr. ex. Engelm. In 1965, it accounted for 779,000 tons or 85 percent of the world supply. Henequen is obtained from *A. fourcroydes* Lem., and it accounts for practically all of the remaining fibers produced. Sisal is produced in Tanzania, Brazil, Angola, Madagascar, and Haiti. In 1963, almost 1.5 million acres were devoted to sisal production in Africa and more than 300,000 acres in Brazil. Henequen, which is a much weaker fiber than sisal but which has a certain market, is produced primarily in Mexico.

Plant

The plant has stiff, heavy, persistent leaves, 2 to 4 feet long, 4 to 8 inches wide, and 1 to 4 inches thick that are basal or come from a short stem, 3 to 6 feet long. The flower stalk is a towering spike or panicle, 6 to 15 feet above the rosette of leaves. The plant grows slowly, attaining a height of only 6 inches 9 months after planting and 2 feet at the end of 2 years. It is about full grown at 4 years when its stem is about 8 inches in diameter and the harvesting of the lower leaves begins. An average of 185 leaves may be harvested before leaf growth ceases and the flower stalk or "pole," which resembles a giant asparagus sprout, shoots rapidly upward. From first appearance of the pole through flowering, fruiting, and death of the entire plant covers a span of about 6 months. About 100 plants per acre are maintained for maximum production of fiber.

Inflorescence

The 1½- to 2½-inch, pale-green, funnel-shaped flower is made up of six narrow, united lobes. Six long stamens come from the base of the corolla and surround the awl-shaped style with its three-lobed stigma. The ovary has three locules with two series of ovules in each, which develops into a green, fleshy capsule about 2 inches long, turning black at ripening. This capsule may have as many as 300 ovules but usually less than 100 seeds. The fertile seeds are triangular, black, and hard; the unfertilized ovules produce white, papery, nonviable seeds.

Flowering of the floret commences with the extrusion to 2 inches of the six anthers from the apex of the bud 36 to 48 hours before they release pollen and 3 to 4 days before the stigma becomes receptive. The anthers begin to dehisce early in the afternoon, and by next morning all pollen has been released. The style begins to elongate and becomes receptive, but by then the stamens have withered and hang limp. One to 2 days after fertilization, the style withers and ovarian development begins. All flowers on a branch of the panicle do not open at once; therefore, pollen from newly opened flowers can pollinate those that opened earlier. Flowering covers several weeks as it moves from the bottom to the top of the pole.

The flower produces large quantities of nectar and a rather heavy, yellow, strong-smelling pollen, both of which are highly attractive to bees. This pollen is usually completely removed from the anthers by bees before the stigma becomes receptive. The honey produced from agaves is generally of inferior quality with a strong unpleasant aroma, strong taste, and dark color.

Pollination Requirements

Propagation of the agaves is mainly by bulbils or suckers. The grower prefers this method because it enables him to maintain pure lines. However, where seed production is desired, cross-pollination is necessary. The pollen is released within a flower before the stigma is receptive; therefore, for fertilization to occur, pollen must be transferred to other flowers with receptive stigmas. Because of the large number of ovules in the ovary, numerous pollen grains must be deposited on the relatively small stigma. The heavy pollen is not a wind-carried type, nor would gravity be likely to account for the pollination of the numerous ovules of a flower.

Pollinators

Bees, and particularly honey bees, are the primary pollinators. For maximum seed production, the grower should consider building up the bee population in the area.

Pollination Recommendations and Practices

None.

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[39] Material in this section was largely taken from Lock (*1962*) and Wienk (*1969*).

SOYBEAN

Glycine max (L.) Merr., family Leguminosae

Soybeans comprise the most important oilseed crop grown in the United States. Approximately 41 million acres of soybeans were grown in 1969 with a farm value of $2.6 billion. The crop is widely grown in all areas

except New England and the West. The primary reason for growing the crop is for the beans, which are processed to obtain oil and a high protein meal.

Plant

The soybean is a bushy, upright, annual, summer legume, 1 to 4 feet tall, with dense, alternate, and usually trifoliate oval leaves 2 to 4 inches across. The plant is not frost resistant so it must be grown after spring frosts are past and have time for the seeds to mature before the first fall frost. Many selections or cultivars are bred for production under different day-length or other environmental conditions. They range in maturity from 75 to 200 days. There are hundreds of selections under test; however, only 17 cultivars make up 88 percent of the acreage in the 14 major producing States.[40]

The seeds are borne, one to five (usually two or three) to a pod (Weiss *1949*), the 3 to 15 pods are in a cluster on the short seed stalk in the rachis or base of the leaf. A productive plant may have as many as 100 seed clusters. The seeds are mechanically harvested after the plant sheds its leaves as it matures.

Inflorescence

There may be from 1 to 35 purple or white florets, three-eighths of an inch long, on each short raceme or flower cluster. A single plant may bear as many as 800 florets, but may set only 13 to 57 percent (van Shaik and Probst *1958*). The floret has the characteristics and shape of many other legume flowers—a large standard petal, two small wing petals, and a keel petal that encloses the staminal column (fig. 174). The calyx is relatively large in proportion to the flower or even to the calyx of other legumes. Each floret is capable of producing a bean pod. Southern grown cultivars stop growing when flowering begins. Flowering usually continues for 4 to 6 weeks. There may be one-half million florets per acre. There are no extrafloral nectaries (Jaycox *1970*).

Soybean flowers attract relatively few bees (Blickenstaff and Huggans *1962*); however, bees do visit the flowers for both pollen and nectar. The anthers dehisce before the flower opens so that the stigma is in contact with and receptive to the pollen on the anthers. Pollination and fertilization is usually accomplished before the flower opens. Beekeepers in some areas frequently report honey crops from soybeans (Hambleton *1936*, Jaycox *1970*, Pellett *1947**). Beekeepers in other areas report that bees never visit the flowers, or if they do no honey is obtained.

Pollination Requirements

The soybean is considered to be self-fertile and not benefited by insect pollination (Morse and Cartter *1937*, Rubis *1970*). Although there is no experimental evidence to support them, some soybean growers in Arkansas have indicated that bees increase production of beans, and they encourage the presence of apiaries near their fields. Tests with plants caged to exclude bees have shown no decrease in production over exposed plots (Woodhouse and Taylor *1913*, Milum *1940*, Piper and Morse *1910*). Culter (*1934*) obtained an estimated 5 percent cross-pollination in open plots surrounded by 36-inch cheesecloth fences with an apiary nearby. Gordienko (*1960*) used honey bees in cages with two cultivars of soybeans. He fed the bees a scented sirup to stimulate the floral visitation and obtained 29 percent hybrids on one cultivar and 44 percent on the other.

Various tests have been conducted to determine the amount of cross-pollination that occurred at different locations, but the agents responsible for the crossing obtained were usually not determined, possibly because the tests were conducted by agronomists who did not consider themselves qualified to record these observations (Caviness *1966*, *1970*; Caviness et al. *1970*; Garber and Odland *1926*; Woodworth *1922*).

Weber et al. (*1970*) stated that, for a higly self-fertilizing species such as soybeans, two requirements must be met for successful production of hybrid seed. First, there must be heterosis (or an increase in production, or some other beneficial effect, of the cross over the best parent), and there must be an economical, large-scale method of producing the hybrids. Brim and Young (*1971*) have reported that male sterility, although not cytoplasmic, has been found and that 99 percent of the seed set on the male-sterile plants was due to cross-pollination; however, the total seed set was extremely low.

Veatch (*1930*) showed that hybrid soybeans outyielded the average parent variety up to 95.9 percent and the higher parent variety up to 71.5 percent. Weiss et al. (*1947*) showed a range of 14.2 to 71.3 percent heterosis over the best parent in the greenhouse, and 5.9 to 38.6 percent increase over the best parent in the field. Weiss (*1949*) showed an increase of 19.6 to 117 percent increase of the hybrid over the best parent. Wentz and Stewart (*1924*) showed increases of 60 to 397 percent. Weber et al. (*1970*) showed an average for all tests of the hybrids over the best parents of 13.4 percent.

Mention might be made that the increased yields for hybrids are all based upon a relatively low number of widely spaced plants. Because of the problems in making a sufficient number of hand pollinations to satisfactorily evaluate F_1's in a normal-type planting, essentially no such studies have been conducted. The extremely large increases that have been reported are assumed to be partly a result of the extra space alloted to the plants.

Bradner (*1969*) stated that all of the breeding components have been described for the production of hybrid soybean seeds, except that a suitable pollen vector has not been found, although the honey bee "looks encouraging." Piper and Morse (*1923*) noted that soybean flowers were "much visited by bees." They also noted that three of their varieties, when in full flower at Jackson, Tenn., were very fragrant—the odor suggesting that of lilacs. Although they gave no indication that these varieties were more attractive to bees than other varieties, the information indicates that cultivars might

[40] UNITED STATES DEPARTMENT OF AGRICULTURE. Highlights of U.S. Crop Report as of November 1, 1971. U.S. Dept. Agr. Crop Prod. CrPr 2-2, 33 pp. 1971.

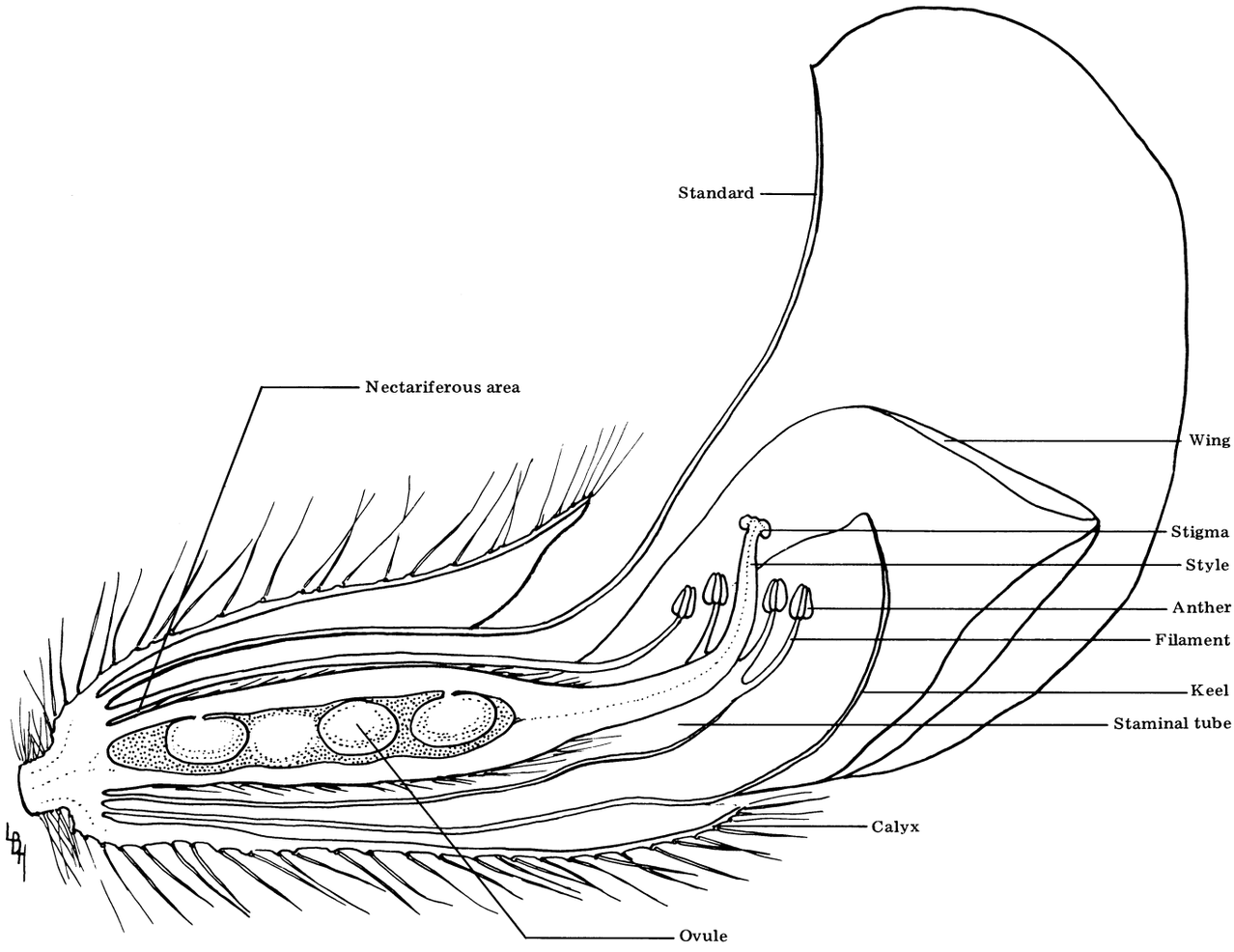

FIGURE 174.—Longitudinal section of soybean flower, × 25.

be selected with aroma or attractiveness that when incorporated in a hybrid seed program might efficiently attract pollinating insects. Because of the potential value of hybrid soybeans, the breeders might watch for selections that show attractiveness to bees.

Pollinators

Little attention has been paid to the prevalence of pollinating insects on soybeans. Jaycox (*1970*) reported only seven honey bees per 100 yards of row, but he gave no indication as to number of honey bee colonies and the acres of soybeans in the area. Blickenstaff and Huggans (*1962*) recorded only one honey bee, three leafcutter bees, and nine halictids in 25,346 individual insects collected on soybeans with a sweepnet, but this is a poor method for determining pollinator populations in dense foliage such as soybeans. Culter (*1934*) and Gordienko (*1960*) showed that honey bee populations can be built up on soybeans. Beard and Knowles (*1971*) showed that crossing at different locations in California varied: 10 percent at Five Points, 1 to 5 percent at Davis, and 0 to 7 percent at Shafter. No studies have been made on the value of concentrating the gregarious types of wild bees on soybeans, although such insects might prove to be more efficient than honey bees.

Woodworth (*1932*) indicated that thrips and honey bees might be responsible for some transfer of pollen; however, Caviness (*1970*) showed that thrips are ineffective as pollinators of soybeans, but that honey bees were responsible for 7.7 percent crossing.

Pollination Recommendations and Practices

There are no recommendations for the use of bees in pollination of soybeans. The subject is reviewed, however, because of the interest in hybrid soybeans and the possibility of using pollinating insects in hybrid soybean production.

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STRAWBERRY

Fragaria × *ananassa* Duch., family Rosaceae

The estimated acreage of U.S. strawberries in 1971 was 51,000, and the crop was valued at $116 million.

Oregon was the leading grower of strawberries, with 11,000 acres, followed by California (8,300 acres), Michigan (5,600), Washington (4,100 acres), and North Carolina (1,900 acres). Numerous other States produced more than 1,000 acres. California led with 151,500 tons, followed by Oregon (41,650 tons), Washington (13,350 tons), Michigan (12,300 tons), and Florida (7,600 tons). The numerous cultivars have changed rapidly over the last few years (Scott *1971*). Much of the material herein is drawn from the excellent reference by Darrow (*1966*).

Plant

The strawberry plant is a stemless, low creeping, and usually perennial herb that may live for many years, although it is sometimes grown as an annual in the South (Shoemaker *1955*). Some cultivars are evergreen and others tend to be deciduous, depending upon the area in which they are grown. The trifoliate leaves form a blanket cover of the ground from a few inches to 2 feet deep, which shelters the fruit. The creeping runners occasionally produce roots and inflorescences at the leaf bases.

The ripe fruit is 1 to 2 inches long and light red to dark red when ripe. It is an ovoid aggregate of achenes or one-seeded fruitlets around a receptacle that accumulates sugars and vitamins and ripens like a true, fleshy fruit. Each achene contains a single ovule and can therefore be considered an individual unit. Yet, if the stigma of the achene is not pollinated or if it is removed

soon after pollination, there is no growth on the receptacle. The weight of the strawberry is roughly proportional to the number of fertilized ovules (Nitsch *1950*).

Reproduction is almost exclusively with rooted runners, even though the seeds are viable.

Inflorescence

The strawberry flower cluster is a series of double-branching parts bearing a flower in the crotch of each branch. The flower in the first crotch is termed the primary flower, the two in the next two crotches are termed secondary flowers, the next four are tertiary flowers, the next eight are the quarternary, and the next 16, if they develop, are the quinary flowers. The primary flower opens first and usually produces the largest berry (fig. 175) (Shoemaker *1955*).

The individual flower is whitish (fig. 176), 1 to 1½ inches across, and usually composed of about 5 to 10 green sepals, five oval petals, numerous styles, and two to three dozen stamens arranged in three whorls. When the stamens contain viable pollen, they are a deep gold. Nectar is secreted by the receptacle and held at the base of the stamens next to the outer row of pistils.

The flowers of all current commercial cultivars are hermaphrodite. Clones that are only staminate or only pistillate may appear in the wild or in some seedling populations (fig. 177). The hermaphrodite flowers set fruit somewhat in proportion to the extent of pistillateness, that is, the higher the percentage of pistillate flowers, the more fruit the plant produces.

The stigmas are receptive before pollen of the same flower is available, which encourages cross-pollination. Sometimes, flowers that have pollen-laden anthers appear to set fruit far better when cross-pollinated than when fertilized with their own pollen. The pollen is mature before the anthers dehisce, but dehiscence does not occur until after the flower opens and the anthers dry a short while. This causes them to dehisce under tension so that the pollen is thrown onto some of the pistils. It can remain viable for several days, but some flowers are dried and shrunken on the second day after opening (Connor *1970*); therefore, it is no longer of value to the flower. No complete self-incompatibility exists in present-day cultivars.

PN-3843
FIGURE 175.—Cluster of 'Midway' strawberries in different stages of development.

PN-3844
FIGURE 176.—Strawberry blossoms, buds, and leaves.

The fruit of the first blossom to open is referred to as the primary berry and is usually the largest. The second flower to open is the secondary flower, and the fruit it produces is usually second in size. Fruits from later flowers are usually smallest. Darrow (*1966*) stated that Valleau (*1918*) found 382 seeds in primary berries, and 224, 151, and 92 seeds in the succeeding berries. Gardner (*1923*) recorded 518 pistils on one primary flower but only 83 pistils for the last flowers of the plant under his study. There can be less but never more achenes (fruitlets) than there are pistils.

Pollination Requirements

Flowers without stamens were common in earlier cultivars, and no fruit setting resulted unless pollen was brought from staminate flowers (Darrow *1927*, *1937*). Continued breeding and selecting has resulted in the hermaphrodite flowers in all commercial cultivars. However, hermaphrodite flowers may not be completely self-fertilizing. The stamens are so placed that when they crack open they readily scatter pollen onto many, but not necessarily all, of the pistils. Pollination of all of the pistils of a flower is necessary for maximum berry size. If all pistils are fertilized, a perfectly shaped berry should develop. If few are fertilized, an irregularly shaped berry or "nubbin," sometimes only one-fifth the size of well-fertilized berries, will develop.

Allen and Gaede (*1963*) studied fruitsetting of 'Shasta' strawberries in the greenhouse and showed that plants caged and undisturbed by man, insects, or breezes set no fruit; those uncaged and undisturbed set 20

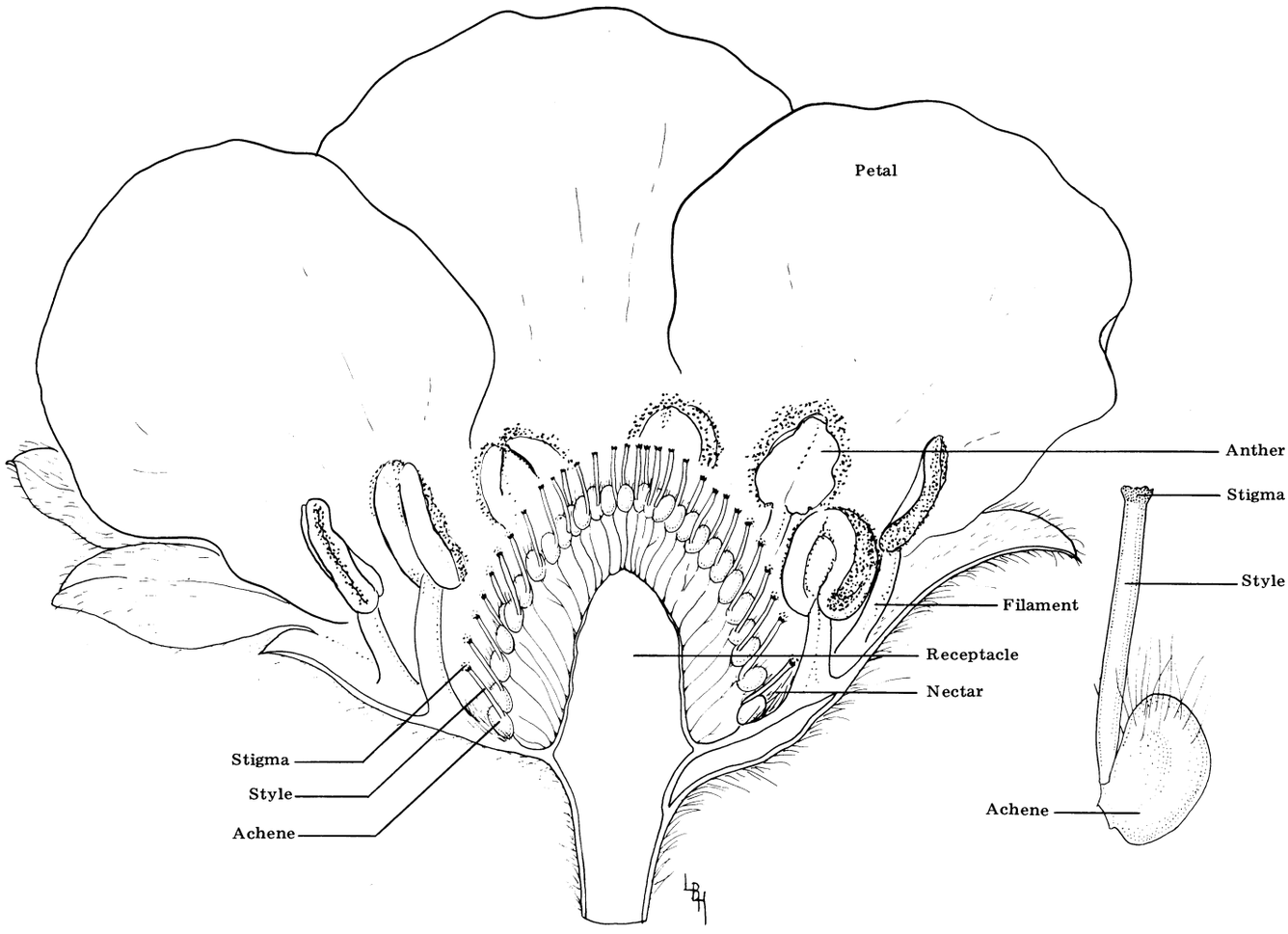

FIGURE 177.—Longitudinal section of 'Tioga' strawberry, × 7, with individual achene and style, × 35.

percent; those uncaged but receiving wind from a fan over them set 77 percent; whereas those that were caged, but brush pollinated daily, set 97 percent of the flowers. This finding indicated that the plants alone set few fruits, and wind has some effect, but insects may be more important than wind as pollinating agents. Couston (*1966*) also noted that malformation of berries was greater when adverse weather occurred at flowering time. He also obtained more number one berries from exposed plants than from plants caged to prevent insect visitation, indicating that insect pollination increased production.

Free (*1968a*) compared production of plots caged to exclude pollinating insects, plots caged with a colony of honey bees in each cage, and open plots. The cages without bees yielded the lowest percentage set, 55 percent as against 65.5 percent for the cage with bees. They also yielded the smallest berries, 6.7 g per berry in the cage without bees as against 8.3 and 8.4 g in the cages with bees and open plots, and the highest percentage of malformed berries, 48.6 percent in the no bee cages, 20.7 percent in the bee cage, and 15.4 percent in the open plots. Howitt et al. (*1965*) also associated strawberry fruit deformity with faulty pollination. Hughes (*1961*) noted that excluding pollinating insects resulted in decreased yield and malformed fruit. Kronenberg (*1959*) and Kronenberg et al. (*1959*) listed insufficient pollination by bees as one cause of poor fruit set.

Darrow (*1966*) stated that when the first flowers of perfect-flowered cultivars open and set well, but later flowers only partially set or do not set at all, natural sterility is the primary cause. However, he said that if the first flowers develop into nubbins, and yet later flowers produce good berries, the poor development is probably due to inadequate pollination.

Connor and Martin (*1973*) made the interesting observation that stamen height ranged from 2.5 mm in 'Surecrop' to 5.2 mm in 'Early Midway', and the flowers with the shorter stamens benefit most from insect pollination. Based upon their studies of 11 cultivars, they reported the following: "Self-pollination is responsible for development of 53 percent of the achenes; wind motion increased this development to 67 percent and insect pollination increased it to 91 percent."

Pollinators

Many types of insects visit strawberry flowers, including flies, beetles, thrips, butterflies, and various

bees; however, only the bees are of real consequence in transferring pollen effectively without injuring the flower parts. If wild bees are not plentiful so that the flower obtains the 16 to 25 bee visits recommended by Skrebtsova (*1957*), honey bees can be provided. Honey bees show preference for some cultivars over others, and they are not too strongly attracted to strawberries. However, this can be overcome with saturation pollination, or overstocking the area with colonies so the competing nectar and pollen are removed (fig. 178).

Although the strawberry blossom produces nectar and usually pollen, it is not overly attractive to honey bees. Also, different cultivars are visited by bees to different degrees, but none have been reported to be highly attractive. Free (*1968a*) stated that honey bee visits tend to be limited to good weather. Allen (*1937*) stated that when bees visited the strawberry blossoms, fruit production was increased, but the blossoms were not as popular with bees as one might wish.

In studying the activity of honey bees on strawberries, Free (*1968b*) found that although bees sometimes landed on the petals of a flower and approached the nectary from the side, they nearly always proceeded to walk over the stigmas. Some bees collected mostly nectar but also some pollen; however, some bees collected pollen deliberately. He stated, "Such bees either walked round the ring of anthers and scrabbled for pollen while doing so, or stood on the central stigmas and pivoted their heads and parts of their thoraxes over the ring of anthers. Some bees scrabbling for pollen also collected nectar." In either case, honey bees in sufficient numbers should be effective pollinators.

PN-3845

FIGURE 178.—Honey bee collecting pollen from strawberry blossom. In the process thorough pollination of the flower is assured.

Skrebtsova (*1957*) studied visitation of strawberry flowers by honey bees. She noted that the bees showed preference for some cultivars over others, but concluded that each flower should receive at least 16 to 20 visits. More visits resulted in heavier berries; 16 to 20 visits resulted in berries weighing 5.36 g, and 21 to 25 visits produced berries that averaged 8.13 g. Flowers pollinated at the most receptive time, the time of fullest development of the reproduction organs, produced berries 13.3 to 58.3 percent heavier than those pollinated before or after this time. Later, Skrebtsova (*1958*) recommended saturated pollination by bees to produce the maximum crop of highest quality berries.

Moore (*1964*) noted that strawberry flowers are receptive up to 7 days after opening. Darrow (*1966*) said 10 days in cool weather, but the number of seeds per berry was reduced in late-pollinated flowers. As previously stated, Connor (*1970*) reported that many flowers were dried and shrunken on the second day after opening. The best time for pollination seems to be during the first 1 to 4 days after the flower is open. Darrow (*1966*) noted that reaction to pollination is rapid, within 24 to 48 hours the petals fall and the pistils dry up. Connor (*1970*) did not distinguish between pollinated and other flowers.

Fletcher (*1917*) stated that 90 percent of the pollination of strawberries was performed by insects and that honey bees accounted for 90 percent of this activity. Lounsberry (*1930*) stated that when bee forage was marginal, the bees worked strawberry blossoms feverishly. In Russia, Shashkina (*1950*) concluded that wind was not a good pollen vector but that flies were the principal vectors in the Moscow area.

Mommers (*1961*) showed that honey bees increased production in the greenhouse. This was supported by Bonfante (*1970*). Muttoo (*1952*) stated that location of an apiary near a strawberry plot increased the average production of berries from 840 to 1,225 pounds per acre. Petkov (*1963*) stated that only 31 to 39 percent of flowers isolated from bees developed fruit compared to 55 to 60 percent of those freely visited by pollinating insects. Furthermore, the isolated flowers developed 60 to 65 percent culls compared to 14 to 17 percent culls from bee-visited flowers. The average weight of fruit from the isolated flowers was only a third of that from the bee-visited flowers.

Petkov (*1965*) stated that over a 4-year period of observation bees accounted for 50 to 78 percent of the flower visitors (in Bulgaria). Pammel (*1930, p. 922*) noted that the flowers at Ames, Iowa, were visited by honey bees and by species of *Halictus*.

Moore (*1969*) studied the effects of caging and bees on strawberries over a 4-year period. He concluded that caging, which reduced yields 41, 32, 59, and 71 percent, respectively, for the years 1965–68, was " . . . due to incomplete pollination as a result of excluding insects." While pollinating insects were shown to be unessential for fruit set, the maximum yields and fruit size are only realized under conditions of adequate and active insect pollinators. Anderson (*1969*) cited numerous references relating to strawberry pollination.

Pollination Recommendations and Practices

Free (*1968a*) discouraged the rental of bees "... unless the plantation is large." Darrow (*1966*) did not consider supplemental pollination, although he showed the need for insect visitation. Mommers (*1961*) recommended the use of bees on strawberries in greenhouses. Moore (*1969*) stated that "growers may someday have to provide colonies of honey bees for their plantations." Jaycox (*1970*) recommended one strong colony per 2 acres, with the bees in two or more groups on opposite sides of 10- to 50-acre fields. Unfortunately, as Connor (*1970*) pointed out, no specialist can wisely point to a strawberry field and state that the field is either well pollinated or needs additional pollination activity.

In general, strawberry growers do not take steps to provide additional pollination, nor even give much consideration to the local pollinator population in the field, although the evidence shows that visitation by pollinating insects is highly beneficial. The acreage devoted to strawberries on most farms is small compared to the foraging range of bees from an apiary, although some fields of 200 acres are in this crop. Thus, many acres of plants around a strawberry field can be more attractive to honey bees than the strawberry flowers. To overcome this competition would call for saturation pollination, or the placement of many colonies for each acre of strawberries, possibly 5 to 10 or even more. For a commercial grower who desires the maximum in perfect berries as well as in volume, saturation pollination should be profitable.

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STRAWBERRY CLOVER[41]

Trifolium fragiferum L., family Leguminosae

Strawberry clover is grown to a limited degree as a pasture plant in moist and alkaline soils in the west coast States and the northern Great Plains (Graham *1941**, Davies *1962*).

Plant

Strawberry clover is a perennial low-growing plant with creeping stems that root at the node to spread vegetatively as well as by seeds. The plant is difficult to distinguish from white clover when not in bloom. In maturity, the seeds are pressed closely to the ground making harvesting difficult. Tiver (*1954*) stated that strawberry clover in South Australia is a prolific seed producer, which yields up to 250 pounds of seed per acre.

Inflorescence

The flower heads are round, pink to white, and resemble a strawberry, hence the name of the plant. The blooms appear earlier than those of white clover. There may be 35 to 60 florets per head. Only one seed forms in a floret. As the seeds mature, the head takes on the appearance of a balloon. The flowers are extremely attractive to bees for both nectar and pollen.

Pollination Requirements

Johnson (*1951*) and Williams (*1931*) considered strawberry clover self-fertile. Hollowell (*1939*) also stated that the flowers are self-fertile, that crossing between flowers is not necessary, but that honey bees assist in the transfer of pollen to the stigmas. Davis and Young (*1966*) stated that most specimens from the Mediterranean area were completely self-sterile, but as the plant spread northward it was conditioned by its environment, probably lack of pollinating insects, to evolve into a self-fertile plant. Morley (*1963*) stated that the flowers are not self-pollinating and are largely self-incompatible. He stated, "It is difficult to understand how strawberry clover has been regarded as self-pollinating for so long. Seeds are expensive but shouldn't be if adequate honey bees are provided." He harvested only 0.25 seed per flower where bees were infrequent, but 0.70 per flower where bees were plentiful. Tiver (*1954*) considered honey bees important in increasing seed yields. Hollowell (*1960*) also noted that seed yields were increased if honey bee colonies were adjacent to the field. Todd (*1957**) listed strawberry clover in the group of plants "Seed production increased by Bees."

Peterson et al. (*1962*) stated that common strawberry clover is self-fertile, but bees help to move the pollen to the stigma. 'Salina' strawberry clover, however, is self-sterile and will not set seed without cross-pollination. In this case, bee activity is essential for seed production.

Wright (*1964*) made a study of the pollination requirements of strawberry clover using material from Australia and New Zealand. He studied 66 clones and learned that most of them were self-incompatible but that some set a relatively high percentage of seed autogamously; however, they set more seed if they were cross-pollinated. He also found that self-pollinated plants were less vigorous. He considered strawberry clover a cross-pollinated species and found a high correlation between set of seeds from hand and bee pollination.

Pollinators

Honey bees seem to be the primary pollinators.

[41] See "Clovers, General."

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Pollination Recommendations and Practices

Morley (*1963*) spoke of providing adequate honey bees for high seed yields. Hollowell (*1939*) stated that placing colonies of honey bees adjacent to flowering fields is necessary, but he did not indicate the number of hives per acre needed.

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SUBTERRANEAN CLOVER[42]

Trifolium subterraneum L., family Leguminosae

Plant

Subterranean clover is a low, pliant, running, reseeding, annual legume, with short seedstalks that carry clusters of three to four small creamy to pinkish flowers. It will grow on soil with fertility so low white clover will not thrive. As a winter annual in both Southern and Northern Hemispheres, subterranean clover blooms and sets seed in spring or early summer. The seed is dormant until fall, at which time it germinates. The plant name is derived from the fruiting characteristics. The seed head is made up of a cluster of forked hairs or bristles turned back around the seed pods. The ripening seed head turns downward, and the forked hairs help to bury many of the heads in the soil, somewhat like a peanut, but about half of the heads remain above ground (Lancaster *1949*, Smith *1948*).

Inflorescence

The flower is made up of three to seven, usually four, perfect, papilionate, usually white, florets. The ovary of each floret contains two ovules, but usually only one develops (Morley *1961*). Yates (*1957*) found that above-ground seeds were poorer in quality than those that developed below the ground surface. Howell (*1960*) stated that this clover can be distinguished from other annual species in Western United States by its non-involucrate head of fertile flowers that become abruptly deflexed on their very short pedicel after they open. At that time, numerous sterile flowers develop, enclosing the fertile ones in the burrlike cluster.

Pollination Requirements

Todd (*1957**) placed subterranean clover in the group of plants considered to be largely self-pollinated. A reference by Knuth (*1908*, p. 297*) that the flowers "are capable of self-fertilization, though perhaps they do not always do this," leaves some doubt that maximum seed production results from selfing. Morley (*1961*) considered the species self-fertilizing but with occasional hybridization by outcrossing. How insects can get to the flowers, which are likely to be covered by the plant's leaves, is not explained. More study on this plant should be made to determine if it is benefited by visitation from pollinating insects.

Pollinators

Morley (*1961*) stated that he had observed honey bees working the flowers, but only after fertilization would have taken place. However, he did not exclude them entirely as a cause of hybridization.

Pollination Recommendations and Practices

None.

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[42] See "Clovers, General."

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SUNFLOWER

Helianthus annuus L., family Compositae

There are two types of annual sunflower, oilseed and nonoil. Oilseed sunflower is a source of high-quality seed oil, which is used in cooking, salads, paints, and as an industrial lubricant. Seed from the nonoil type is used as a bird feed or roasted and marketed as a confectionery product. Until 1972, most of the sunflower acreage in the United States was of the nonoil type.

Minnesota and North Dakota are the major producing States. The crop is being tried in many other States to a limited extent. The oil from cultivars grown in Minnesota contains more of the desirable linoleic acid than the oil from the same cultivars grown in Central or Southern United States.

Other major sunflower producing countries are Russia (11 to 12 million acres), Argentina (3 million acres), and Romania (1½ million acres). There were 850,000 acres in the United States in 1972 (Robinson *1973*).

Plant

The sunflower is a widely adapted plant. It will grow in the arid Southwest, yet at some stages of growth it will tolerate light frosts. It is native to North America and is the only important annual crop to evolve and be domesticated within the confines of the United states. Little heed was given it, however, until it was transported to Europe and returned, via Canada, as an important oilseed crop. Not until 1947 did oilseed production develop in the United States, in Minnesota. Most of our cultivars originated in Russia, or they have been developed from Russian cultivars. However, Kinman and Earle (*1964*) showed that some of the best American cultivars outyielded the best Russian cultivars in tests with comparative linoleic acid values.

When handled as a row crop, most growers prefer row widths of 20 to 36 inches with 15,000 to 30,000 plants per acre. The exact plant population most desirable depends upon the type grown, rainfall, temperature, and soil fertility. Average production is about 1,100 pounds seed per acre (Anonymous *1969*), although much higher production has been reported by individuals (Killinger *1968*, Noetzel[43] , Trotter and Giran *1970*, Weibel et al. *1950*).

Inflorescence

The sunflower stalk has a main or primary flower head and may have one to several secondary heads (fig. 179). All commercial cultivars are composed of almost 100 percent single-headed plants. The main head may have from 1,000 to 4,000 individual florets, depending upon the cultivar and size of the head. A secondary head may have from 500 to 1,500 florets. The outer or ray florets with the showy yellow petals are sterile, having neither stamens nor pistil (fig. 180). The less conspicuous florets making up most of the head are hermaphrodite, but protandrous, and many are self-incompatible. They are normally open 2 or more days. The first day, the anthers release their pollen in the anther tube, which is partly exserted from the corolla. The pollen is collected freely by bees, along with the nectar at the flower base. The second day, the stigma pushes up through any pollen mass remaining, then its two lobes open outward, receptive to pollen but out of reach of its own pollen (Putt *1940*).

PN-3846

FIGURE 179.—Sunflower head, showing the brilliant yellow but sterile ray flowers around the outside, and the fertile florets in different stages of development in the center.

The opening of all the florets of a single head takes 5 to 10 days. If pollination occurs, the floret withers shortly; otherwise it may "wait" as long as 2 weeks for fertilization. Seed setting on such florets, however, is greatly reduced even with cross-pollination (Avetisyan *1965, pp. 209–248*). A typical head in bloom will have dried florets toward the outside, then a ring of florets with receptive stigmas, a ring of florets shedding pollen, and, finally, unopened florets toward the center. Radaeva (*1954*) stated that within 3 days after the first

[43] NOETZEL, D. M. 1968 INSECT POLLINATION RESULTS ON SUNFLOWERS. Pp. 108–112. Dept. Ent., N. Dak. State Univ., Fargo. 1968. [Mimeographed.]

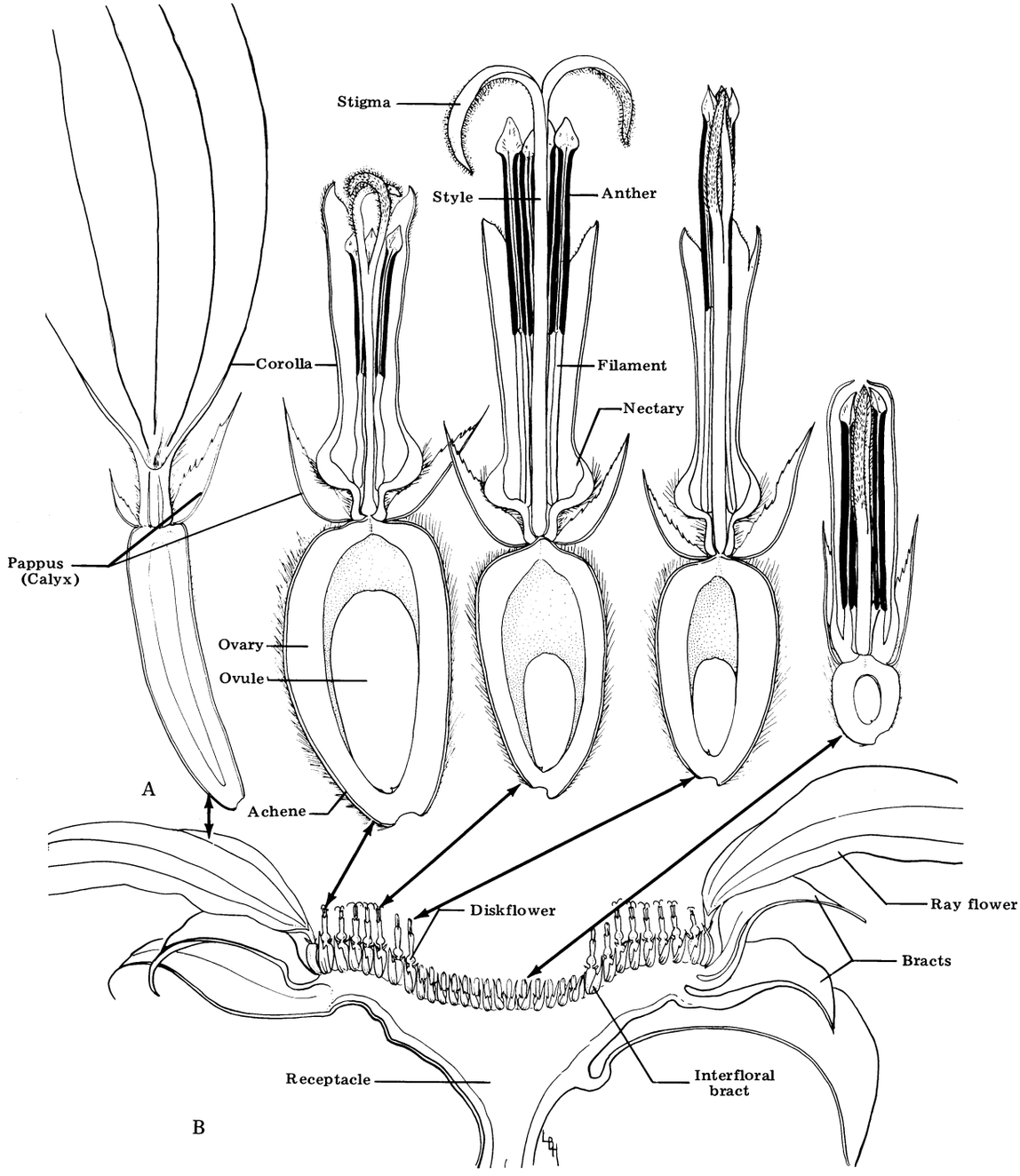

FIGURE 180.—Longitudinal section of sunflower head, ×½, with individual florets. *A*, Ray floret, ×5; *B*, disk florets in different stages of development, ×5.

flower head begins to open 83 percent of the remaining heads also begin to open.

Both the pollen and the nectar of sunflower are quite attractive to bees throughout the day (Bitkolov *1961*, Free *1964*). Nectar is secreted at the base of the floret, primarily during the pollen-producing stage of flowering but to some degree while the stigmas are receptive. Extrafloral nectaries in the bracts and on the upper leaves of the plant are sometimes visited by honey bees, particularly in the afternoon (Free *1964*).

Sunflowers are considered by beekeepers to be a fair source of pleasant-flavored, yellow-colored honey (Anonymous *1969*, Burmistrov *1965*). Furgala (*1954a*) reported that a colony on scales gained 104 pounds in 15 days while on sunflowers, which he considered an indication that the area was underpopulated for adequate sunflower pollination. Baculinschi (*1957*) calculated the nectar crop at about 20 lb/acre for the entire flowering period. This is roughly equal to nectar production of cantaloups, as calculated by McGregor and Todd (*1952**). Guynn and Jaycox (*1973*) reported a yield of 80 pounds of honey per colony when 15 colonies were placed at the center of a 45-acre field of sunflowers.

Pollination Requirements

If pollen from a floret is transferred to the receptive stigma of another flower on the same head and the flowers are self-compatible, seed will set. However, most cultivars are self-incompatible (Free and Simpson *1964*), in which case the pollen must come from another plant. When selfing (within the head) occurs, seed setting is usually low (Barrett *1954*, Cardon *1922*, Kalton *1951*), the seeds are undersized, and the oil content and germination are reduced. Selfed seed also sprout more slowly, and production from them is lower than from plants derived from crossed seed. Putt and Heiser (*1966*) described two types of genetic male sterility in sunflowers.

Putt (*1966*) observed strong hybrid vigor in sunflowers; 2,291 lb/acre with 33 percent oil in his crosses as compared to 1,156 lb/acre of seed with oil content of 30 percent in his inbreds. Some "hybrid" seed has been produced by use of either a self-incompatible line or one producing little viable pollen, which is pollinated by a line that is a copious producer of viable pollen (Robinson et al. *1961*). Genetic male sterility is also used to produce commercial F_1 hybrid seed, but full exploitation of the hybrid vigor possible in sunflower will come when cytoplasmic male sterile female parents can be crossed with male parents that will restore fertility to this hybrid (Kinman *1970*).

Sources of cytoplasmic male sterility (Leclercq *1970*) and fertility restoration (Kinman *1970*) have recently been discovered, and preliminary tests indicate that the yields of the F_1 hybrids produced by this method are comparable to yields of the best hybrids produced by other means.

When Pritsch (*1965*) compared seed set in cages with and without bees, his results were inconclusive. However, others have shown a strong beneficial effect from insect pollination. Sanduleac (*1960*) compared seed production from four pollination treatments: (1) Isolated under gauze; (2) isolated under gauze and hand pollinated four times; (3) open to insect pollination; and (4) open to insect pollination and hand pollinated four times. His production was always greatest on open plots, with no increase derived from the extra hand pollination. His pollinator population, however, was not indicated. Avetisyan (*1965*) said that for best seed production each floret should be visited 8 to 10 times. Habura (*1957*) also obtained a higher set of seed from cross-pollinated flowers than from selfed flowers. Pinthus (*1959*) stated that a higher percentage of selfed seed was produced under lower temperatures at flowering. He showed that although 50 to 60 percent of the seed of bagged flowers developed between October 15 and November 30, only 0.4 to 5.0 percent developed between June 10 and September 25, during the normal period of seed production. Luttso (*1956*) also compared set of seed on 10 heads exposed to three treatments. His results in grams of seed produced were: Caged without bees, 315 g; exposed to bees, 995 g; and exposed to bees in addition to supplemental pollination of the heads with a soft mitten, 1,000 g. He showed that the labor of 1 man-day per acre was about equal to the bee pollination services. Schelotto and Pereyras (*1971*) showed that sunflower seed yield in Argentina was increased five to six times, and the oil content of the seed was increased 25 percent in plots exposed to honey bee colonies as compared to plots isolated from insects during flowering.

Furgala (*1970*) reviewed the effects of insect pollination on seed production and urged that more research be conducted. The evidence is strong, however, that insect pollination is needed for commercial production of sunflower seed. Posey (*1969*) compiled 133 pages of literature citations on sunflowers from January 1960 to June 1967. Only 24 of these references concerned sunflower pollination, and only two of the 24 were published in the English language. This indicates the lack of interest in the pollination of this crop outside Russia.

Pollinators

Honey bees are the primary pollinating agents of sunflowers almost wherever they are grown (Cardon *1922*, Cirnu *1960*, Fomina *1961*, Glukhov *1955*, Overseas Food Corporation *1950*, Pritsch *1965*, Radaeva *1954*). If there is a shortage of honey bees in the sunflower fields, a small seed crop is harvested.

In some localities, bumble bees and sundry other wild bees visit sunflowers (Cockerell *1914*). Arnason (*1966*) indicated that in many instances these bees are adequate, but all other researchers have shown that the bulk of the pollination in commercial sunflower production is by honey bees. Radaeva (*1954*) showed that honey bees are much more effective than wild insects. The evidence indicates that if sufficient flower heads are available for bees to collect honey surplus to the needs of the colony, the ratio of bees per flower is inadequate for maximum seed production.

The exact number of bees needed for maximum pollination has not been determined. Measurements of bee activity have included bees per flower head, bees per unit of row, bees per acre, and colonies per acre. These have been correlated to some degree with seed production. For example, Noetzel[44] placed one colony per acre at the ends of different sunflower fields in North Dakota. He counted the bees per head and obtained seed production data at different distances from the apiary. He obtained an overall increase of 20 percent due to the bees alone, but beyond 400 feet from the apiaries he got no measurable increase in yield.

Noetzel's production ranged from 1,350 to 4,962 lb/acre within 50 feet of the apiary as compared to the range of from 734 to 2,249 lb/acre at 1,300 feet from the apiary. Robinson et al. (*1961*) harvested 1,231 to 1,653 lb/acre from their plots in Minnesota but gave no indication of the pollinator population in the plots. Bees were not provided to the plots, but apparently they were abundant in the vicinity. Furgala (*1954b*) reported that three to five colonies per acre significantly increased yield. Furgala (*1954a*) reported that a field produced 1,300 lb/acre near the apiary, 900 lb/acre at a distance of 400 feet, and 800 lb/acre at 1,000 feet,

[44] See footnote 43, p. 345.

whereas the field not supplied with bees produced about 700 lb/acre at all sites.

Alex (*1957*) obtained only 311 pounds per acre in cages without bees, 602 pounds from cages with honey bees present, and 931 pounds from open plots freely visited by bees, differences that were significant at the 5 percent level of confidence. All were relatively low yields, partly due to drought conditions. Blackman (*1951*) stated that a shortage of bees can be a limiting factor in maximum seed production. Glukhov (*1955*) showed the following correlation between honey bee visits and production of seed:

Number of honey bee visits per floret	*Kilograms of seed from a million florets*
1.0	53
1.4	76
3.4	133
6.0	210
10.0	210

This gives support to the recommendation of Avetisyan (*1965*) that each floret should receive 8 to 10 bee visits.

Kushnir (*1960*) obtained 1,696 g/8 m^2 plot at 400 m from the apiary, 1,373 g at 2,000 m, and 266 g from isolated plots. He had shown earlier, however, that weight of seed was not the entire story. For example, he (Kushnir *1957*) showed that 100 bee-pollinated seed weighed 9.27 g and had 86.9 percent germination, whereas 100 selfed seed weighed only 2.98 g with only 9.2 percent germination. In shape, the selfed heads were uneven. Later, he (Kushnir *1958*) found in another test that the kernels from 100 seeds from bee-pollinated flowers weighed 5.7 g, whereas kernels from 100 selfed seed weighed only 0.5 g.

Kurennoi (*1957*) likewise found that seed production 400 m from the apiary with 5.1 bees per flower was 1.81 tons /ha (1,465 lb/acre); at 2,000 m, production with 2.9 bees per flower was 1.77 tons/ha (1,384 lb/acre).

Kovalev and Ul'yanichev (*1961*) studied the effect of bee pollination on 12,000 ha of sunflower. They found that better pollination accounted for an overall 14.5 percent increase in yield of seed.

Cirnu (*1960*) stated that bee pollination increased production of seed 10 to 30 percent; Cirnu and Sanduleac (*1965*) reported that use of one colony per hectare on 5,582 ha increased seed production 21 to 27 percent, with bees brought in when 5 percent of the plants were in bloom.

Ponomareva (*1958*) conducted large-scale experiments with bees during 1950-56 on 66 sunflower farms in various Russian zones. When one colony per hectare was placed by the fields, the bees worked "sufficiently well at pollination and honey-gathering within a radius of 500 m of the apiary." Beyond that distance, seed production dropped rapidly. Overall, the fields that were supplied with bees produced 79 percent more seed than fields not supplied with bees. In 22 districts, where one-half colony per hectare was used, production was 890 kg/ha of seed; whereas, in 19 districts, where one colony per hectare was used, seed production was 1,270 kg/ha—an average increase of more than 42 percent. The number of colonies necessary for maximum production was not determined.

Lecomte (*1962*) counted 108 bees on 100 sunflower heads in the morning and 100 to 115 per 100 heads of cv. 'B-65-40' in the afternoon, and calculated the bee population in the field at 100,000 per hectare. This would indicate about one bee per head and 100,000 heads per hectare. If these heads contained 1,000 to 4,000 florets each and required 10 days to open, there would be an average of 10 to 40 million new florets per day.

Avetisyan (*1965*) calculated that only 2 million florets per hectare were available daily, and that each floret should be visited eight times; therefore, 16,000,000 bee visits per hectare per day are required. He further calculated that a foraging bee will visit 1,080 florets per day; therefore, 15,000 foragers could pollinate 1 ha. He reasoned that a colony with 6 kg of honey bees would supply enough foragers to adequately pollinate 2 ha of sunflower, providing the bees have nothing else to work on. This population is far below the 100,000 bees, or one bee per sunflower head, observed by Lecomte, and would seem to be an inadequate forager population for highest seed production.

Avetisyan (*1965*) based his recommendation on the assumption that there was nothing else for the bees to visit except sunflower, that each forager visits sunflower, and that the number of florets is the same each day. Actually, there are almost always competing plants, the number of florets is greater than the average during the peak of flowering, and many colonies do not contain 6 kg of bees. Allowances should be made for such differences when recommendations are issued. This need for allowances is supported by Benedek et al. (*1972*) who studied the relation of colony numbers, density of bees on the sunflowers, and seed production. They concluded that seed production is dependent upon density of honey bees on the flowers, but that many factors override the effect of colony concentration around the sunflower field and seed production.

To prevent the sharp decline in production with distance from the apiary, the Russians recommended "converging or saturation pollination" or the distribution of the apiaries in such a way that equal distribution of bees throughout the field is obtained. This is basically the method advocated by Todd and Crawford (*1962*) of distributing the bees every tenth of a mile in each direction in the field, a method utilized in most alfalfa fields today in Western United States.

Khalifman (*1959*) stated that heavy honey bee visits to sunflowers not only increased seed set but also limited the damage by the sunflower moth (*Homoeosoma nebulella* Denis & Schiffermuller), a delayed effect called hysteresis. Martin (*1968*) considered *H. electellum* (Hulst) the most serious pest of sunflower in South Carolina. Teetes and Randolph (*1970*) stated that the period of greatest sunflower moth oviposition was the third to sixth day after the sunflower head began to bloom. This is when the pollinating agents should also be at their peak; however, the use of insecticides highly toxic to honey bees is recommended for this same period. Both control of this harmful moth and the use

of insect pollinators are necessary for production of sunflower seed. Unless the programs are so arranged that both are successful, seed production is doomed to failure.

Pollination Recommendations and Practices

All research on sunflower pollination indicates that honey bees are the primary pollinating agents, and that colonies should be provided to the field (Barbier and Abid *1966*), and that they should be protected from harmful pesticides while they are in the field. The bees should be ready for the pollination task at the onset of flowering. The total flowering period is usually about 20 days, but 83 percent of the heads begin to open within 3 days after the first head opens. Evidence also indicates that the highest bee population and the highest production occur within a few hundred feet of the apiary. If adequate pollination throughout the field is provided, there should be no significant gradient of seed set in relation to apiary location.

The term "saturation pollination," meaning the patterned distribution of groups of colonies, sometimes used on other crops to provide adequate coverage throughout the entire field, is equally applicable and needed in sunflower production. Cirnu (*1960*) recommended two colonies per hectare, the bees to be moved in at 3 to 5 percent of bloom. Later, Cirnu and Sanduleac (*1965*) recommended one colony per hectare. Furgala (*1954b*) recommended one colony per acre, the colonies placed in rows 300 to 400 yards apart. Smith et al. (*1971*) recommended one-half colony per acre. The evidence is plain that, if the grower wants maximum seed production, he should not skimp on the use of bees.

The number of colonies per acre alone is not too meaningful. Distribution of colonies to give thorough coverage of all blooms is highly important, and strength and other conditions of the colony are equally important. The criterion the grower should use is the bee visits per floret or bees per head throughout his field. The presence of one bee per head throughout the day should provide adequate visitation, but additional research is needed to determine the exact bee population needed for maximum production of sunflower seed.

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SWEETCLOVER[45]

Melilotus spp., family Leguminosae

Two sweetclover species of importance are grown in the United States. They are sufficiently alike to be treated here as a single crop. The species, their common names, and cultivars are as follows:

Species	*Common name*	*Cultivar*
M. officinalis (L.) Lam.	Biennial yellow	'Aura', 'Goldtop', 'Madrid'.
M. alba Desr.	Biennial white	'Denta', 'Evergreen', 'Spanish', 'Willamette'.
M. alba annua[1] Coe	Annual white	'Emerald', 'Floranna', 'Hubam', 'Melana'.

[1] = subspecies.

Two other species, *M. indica* (L.) All. (yellow annual sour clover) and *M. suaveolens* Ledeb. (Daghastan sweetclover), are no longer important (Smith and Gorz *1965*).

The production of sweetclover seed has decreased from 254,000 acres in 1955 to 65,000 in 1970, primarily because of the damage to the seedling plants by the sweetclover weevil (*Sitona cylindricollis* Fahraens). The leading States in seed production acreage included Minnesota (18,000), South Dakota (14,000), Kansas (7,000), Nebraska (6,500), North Dakota (6,000), Texas (5,000), Illinois (4,500), and Ohio (4,000 acres). Yields ranged from 100 to 280 lb/acre.

Sweetclover will grow wherever the soil has sufficient lime and more than 17 inches of rain is suitably distributed over the season or water is supplied by irrigation. It may therefore be found in the irrigated valleys of the high intermountain States, along the Canadian border, in Canada, in the hot irrigated valleys of the Southwest, or along the coast of the Gulf Coast States.

Sweetclover is grown for pasture, hay, seed, soil improvement, and erosion control. Beekeepers have encouraged its growth because of its attractiveness to bees and its value as a honey-producing plant.

Plant

Sweetclover is an upright, drought-tolerant plant that may grow as tall as 10 feet but generally is 3 to 6 feet. It may have few or many fine branches, with shoots from buds near the crown and a branched, deep-penetrating, fleshy taproot. Its height, fragrant vanillalike odor, white or yellow flowering racemes, and trifoliate leaves are its identifying characteristics. In the South, the annual white cultivars are sometimes planted in the fall and turned under in the spring, or the seed is harvested in early summer. In the Northern States, they are planted in the spring, and the seed is harvested in the fall. The perennials are planted one year, then clipped or grazed, and allowed to set seed the following season.

Inflorescence

The sweetclover inflorescence is a 1- to 4-inch-long slender spike or loose raceme of white or yellow florets (fig. 181). Each floret is about one-eighth of an inch long, and as many as 100 florets may occur on a single spike. The short corolla permits various short-tongued bees to reach the nectar. The spike grows from a node of the branch in the axil of the leaf. Within the floret, the stamens and pistil are enclosed in the keel. The weight of a bee on the keel will cause the staminal

[45] See "Clovers, General."

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FIGURE 181.—Flowering stems of biennial white sweet clover.

column to project upward and touch the bee but return to the original position after the pressure is released. This permits repeated effective pollination visits by bees. When the bee visits the flower, both pollen and nectar are collected, but the visits are primarily for the copious nectar secreted at the base of the corolla. The flowers are highly attractive to various species of bees, particularly honey bees. Holdaway and Burson (*1960*) stated that if sweetclover is in bloom bees will visit it in preference to other crops and may travel as much as 3 miles to do so. The flowers on plants deficient in soil moisture yield little nectar (Pankiw *1940*).

Pollination Requirements

The different species of sweetclover vary in their need for insect pollinators and are discussed separately.

Biennial yellow sweetclover is largely dependent upon pollinating insects for maximum seed production. Brink (*1934*) obtained only 5.1 percent set of seeds where flowers were not pollinated, 16.4 percent set when flowers were selfed, but 47.1 percent set when they were crossed. Kirk (*1925*) obtained only 2.6 pods per raceme on plants enclosed to exclude pollinating insects, but 63.9 per raceme on open-pollinated plants. Alex et al. (*1952*) using 'Madrid' cv. obtained only 11 pounds per acre in cages without bees, but 288 lb/acre on open plots. The following year they obtained 130 lb/acre in cages without bees, 248 lb/acre in cages with bees, and 396 lb/acre on open plots with about one-half colony per acre. Sandal and Johnson (*1953*) concluded that the incompatible characteristic is genetic and not mechanical. Todd (*1957**) characterized *M. officinalis* as "normally cross-pollinated."

Biennial white sweetclover is greatly benefited by tripping and by cross-pollination between plants. Kirk (*1925*) obtained 34.9 pods per raceme on plants enclosed to prevent insect visitation but 66.4 pods per raceme on open-pollinated plants. Coe and Martin (*1920*) similarly obtained 29 and 66 percent set. Later Kirk and Stevenson (*1931*) stated that white sweetclover sets virtually no seeds when selfed. Shepperd (*1927*) also reported more than 100 percent increase in yield by honey bee pollination and that seed production was much higher within 120 rods of an apiary than beyond that distance. Pammel and King (*1930*, pp. 363–364*) stated that the flowers were self-fertile but required bees to trip them. Pieters and Hollowell (*1937*), however, stated that the individual plants vary from self-sterile to self-fertile.

Munro (*1950*) obtained 22 times as much seed from open plants as from caged ones. Kirk and Davidson (*1928*) stated that plants could self if the pistil and stamens were the same length, but that few seeds were produced if the pistil were longer than the stamens. Hartwig (*1942*) showed that plants from selfed seeds are less likely to produce seed than plants from cross-pollinated seed. Thus, a seed producer would be wise to plant seeds from fields that received maximum cross-pollination.

Alex et al. (*1952*) obtained only 33 lb/acre of seed from 'Evergreen' caged to exclude bees, 116 lb/acre from similar cages with honey bees present, and 146 lb/acre from adjacent open plots provided with about one colony of honey bees per acre. Holdaway et al. (*1957*) obtained 6 lb/acre without bees in contrast to 1,078 lb/acre with bee pollination. In another test, they obtained only 11 lb/acre from plots caged to exclude bees, but 288 lb/acre from open plots. This showed the need for bee pollination on biennial white clover indicated by Garver et al. (*1943*) and Todd (*1957**).

Annual white sweetclover falls in the same pollination category as biennial white. Weaver et al. (*1953*) obtained only 16 lb/acre from 'Hubam' cv. plots caged to exclude bees, 157 lb/acre from similar plots enclosing honey bees, and 130 lb/acre from open plots in a 200-acre area supplied with 55 colonies of bees. The plants were admittedly stunted from a severe drought. Weaver et al. (*1953*) concluded that 'Hubam' clover supplied with an adequate number of bees will yield 10 times as much seed as clover from which bees are excluded.

Yellow annual sourclover or *sour sweetclover* is seldom used in the United States. It is visited by bees and is commonly reported as a honey plant but is not nearly as important as the other sweetclovers. It is considered to be a largely self-pollinated plant (Lancaster *1949*, Smith *1927*, Todd *1957**) although little data support this assumption.

The effective time period for pollination of all sweetclover flowers has not been determined. Weaver et al. (*1953*) stated that blossoms wither quickly after they are pollinated, but those not pollinated remain open for days.

Pollinators

Although numerous pollinating insects visit the blossoms of sweetclover, none are nearly as important on this crop as honey bees (fig. 182). Few if any plants are more attractive to honey bees than sweetclover. For commercial pollination of this crop, honey bees are by far the most effective and practical agents.

Pollination Recommendations and Practices

Jaycox (*1971*), Munro (*1950*), and Wheeler (*1950*) suggested that one colony of honey bees per acre of sweetclover was adequate. Todd (*1957**) recommended one to two colonies per acre, Haws and Holdaway (*1957*) recommended two colonies per acre, although their data showed that seed yields were progressively increased to 10 colonies per acre. Pedersen et al. (*1961*) recommended two or more colonies per acre. Smith (*1960*) suggested two to three colonies per acre, the colonies within easy flight range of the field. The extremes were probably given in a statement (Anonymous *1944*), made without apparent verification, that one colony per acre was generally recommended, but 10 colonies per acre was nearer the number needed to make sure that all the blossoms were tripped at the proper time for maximum pollination. Most of these rates seem to be based on general observations or data taken on other crops rather than factual data on sweetclover pollination.

Few growers utilize the services of honey bees to the

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FIGURE 182.—Honey bee collecting nectar from sweet clover, a plant highly attractive to bees and a major source of honey.

fullest in a real effort to obtain maximum sweetclover seedset. Instead, they are inclined to leave to chance whatever pollination they are fortunate enough to receive from bees in the vicinity of their fields. The data indicate that the grower should obtain the greatest net profit if he used pollinating insects at the highest concentration necessary. This could probably mean from 1 to 10 colonies per acre, with the colonies in or adjacent to the field.

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SWEETVETCH

Hedysarum coronarium L., family Leguminosae

Sweetvetch, sulla, French honeysuckle, or Spanish sainfoin succeeds fairly well in a number of places where it has been tried experimentally in the United States (McKee and Pieters *1937*), but it is of no significance economically. The plants are sometimes confused with some species of *Astragalus*, but differ by having jointed pods, gland-dotted leaves, and squarish-tipped flowers. It is relished by all classes of livestock. In southern Europe, it is used as a hay and soil-improvement crop.

Plant

Sweetvetch is a perennial or biennial legume plant growing to 4 feet tall, with deep-red, fragrant flowers producing flat jointed pods of four or more ovules. It has pinnate leaves and deep roots (Graham *1941**) and yields an excellent honey.

Inflorescence

The ½- to ¾-inch-long flowers, which resemble those of scarlet runner beans, develop in crowded axillary racemes on long peduncles. Knuth (*1908*, pp. 317–318*) stated that when a bee visits the flower the stigma and 10 anthers protrude from the keel and press against the ventral surface of the bee.

Pollination Requirements

The stigma projects beyond the anthers, so it is first to emerge when pressure of the bee is applied to the flower, thus cross-pollination is assured and self-pollination is rendered difficult.

Sacchi (*1950*) found that plants caged to exclude bees set practically no seed, but plants exposed to bees set good crops in proportion to the bee population in the area and visitors to the flowers. Honey bees were the primary visitors. His data indicate that this crop is dependent upon insect pollinators for adequate seed set.

Pollinators

No tests have been conducted on the relative value of different pollinators to sweetvetch; however, honey bees work the plant sufficiently to obtain a honey crop. This indicates that they probably would be effective pollinators.

Pollination Recommendations and Practices

None.

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TEA

Camellia sinensis (L.) *O. kuntze*, family Theaceae

Tea is an evergreen shrub widely cultivated throughout the tropics and subtropics especially in hilly or mountainous regions for its tender leaves that are dried and used for a mildly stimulating beverage. Asia produces more than a billion pounds annually; Africa, more than 200 million pounds; and South America, more than 26 million pounds. We import about 140 million pounds from Africa, 100 million pounds from Asia, and 3 million pounds from South America (Purseglove *1968**). Harler (*1969*) stated that about 970 pounds per acre were produced in northeastern India.

Tea growing was tried in South Carolina over a century ago on about 300 acres, and, even though it grew well, its production was not economical so it was discontinued (Mitchell *1907*).

Plant

Tea prospers in areas with a moderate temperature, high humidity, and moderate to high rainfall. It is killed by frost. Under cultivation, it is usually kept pruned to a spreading shrub 2 to 5 feet in height, with about 2,000 plants per acre. A plant may live 40 to 100 years, its shoots (the bud and two tender leaves) can be plucked each 7 to 14 days, 4 pounds of which yield 1 pound of dried or "made" tea. Mature plants annually yield about 1,000 pounds of made tea per acre.

The fruit is a thick-walled, brownish-green, three-lobed, and usually three-celled capsule, ¾ to 1 inch in diameter. Upon maturity, 9 to 12 months after flowering, it splits from the apex to release the 1- to 1½-cm-long seeds.

Tea is planted from seed, the estimated acreage planted annually ranging from 20,000 to 50,000 acres. Planting is at the rate of about 40 pounds of seed per acre. When seed is produced commercially, only 70 to 100 trees per acre are maintained instead of the 2,000 used for production of leaves. Production of 1,000 pounds seed per acre is considered a conservative estimate. This means that annually from 800 to 2,000 acres must be devoted to production of seed.

Inflorescence

The fragrant flowers, 2.5 to 4.0 cm in length, are axillary, solitary, or in clusters of two to four flowers. They have five to seven white or pink-tinged petals, numerous ½-inch-long stamens, with three to five stigmatic lobes of the style about level with the anthers. According to Free (*1970**), the flower opens in the afternoon and remains open for 2 days.

Pollination Requirements

The flowers are pollinated by insects. Tea is virtually self-sterile and almost entirely cross-pollinated (Purseglove *1968**, Wight and Barua *1939*, Wu *1967*). Kutubidze (*1958*) reported that supplementary pollination produced more, larger, and heavier capsules, better viability, and a higher grade of seed. Simura and Oosone (*1956*), in studying the embryology of the tea plant, noted that, as in many other plants, self-pollen grows much more slowly in the style than foreign pollen. Tomo et al. (*1956*) also concluded that tea was highly self-incompatible, largely due to inhibition of pollen tube growth at the tip of the ovary. Kutubidze (*1958*) noticed that supplementary pollination of hybrid and commercial strains by mixed pollen of other plants of the same strain increased set of fruit and size of capsule. Bakhtadze (*1932*) reported that isolated plants had an 85- to 95-percent reduction in seed set. Self-pollination did not help to increase set, and, furthermore, only 34-percent germination resulted from selfed seed, whereas crossed seed had 75-percent germination. A greater percentage of the crossed seeds developed into plants that reached maturity, and these plants were more vigorous than the selfed plants. Harler (*1964*) stated that only about 2 percent of the tea flowers on a tree produced seed, although by artificial pollination this can be raised to 14 percent. He concluded that, to get even 2 percent, at least nine random trees are needed for cross-pollination. Pollinating agents were not mentioned.

Bakhtadze (*1932*) stated that bees are the chief pollinating agents of tea, but that there were not enough bees present in his area to effect complete pollination of all the flowers. He made no mention of bringing in pollinators to the crop. Kutubidze (*1964*) recommended that steps be taken to obtain additional cross-pollination for increasing yield and quality of tea.

Pollination Recommendations and Practices

None, although the evidence is sufficiently strong to recommend the building up of pollinators in tea seed fields.

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TEPHROSIA

Tephrosia vogelii Hook. f., family Leguminosae

Tephrosia is a potential source of rotenone, an important nonresidual insecticide, and also a material useful in killing undesirable fish (Blommaert *1950*). It is maintained as a semicultivated plant in dooryards in some primitive areas where it is used for poisoning fish. Seeds are saved and planted, and the plants are tended, yet the plant also occurs in the wild state. It has not been grown commercially, although recent tests (Barnes et al. *1967*, Gaskins et al. *1972*) indicate that production might be economically feasible if the culture and handling of the crop could be similar to that of some hay crops. Other species of *Tephrosia* native to the United States have also been tested and show some promise as sources of rotenone (Sievers et al. *1938*).

Plant

Tephrosia is a short-lived, slow-growing, herbaceous, frost-susceptible perennial. Barnes et al. (*1967*) suggested that for commercial production of rotenone, which is derived largely from the leaves, the plants

should be grown at the rate of 30,000 to 37,000 per hectare. Barnes and Freyre (*1969*) reported that when plants were spaced 1.0 to 8.9 m apart, the seed yield per plant ranged from 1.1 to 8.9 g, with the highest-yielding line producing at the rate of only 70 kg seed/ha.

Many individual plants produce good seed yields, whereas others are poor, indicating that considerable improvement through breeding for seed production is possible. Based on variations among accessions in seed set and other agronomic traits, Martin and Cabanillas (*1970*) suggested that cross-breeding procedures might result in improved seed production.

Gaskins et al. (*1972*) stated that seed production is impeded by the flowering requirements of the species, by a naturally occurring system of sterility, and by frequent shortages of pollinating insects.

Inflorescence

The flower is typically papilionaceous (fig. 183), about an inch across, and purple with white markings or white. The flowers are borne on compact racemes that bloom over a 3- to 6-week period. There may be 20 to 30 flowers per raceme with up to 200 flowers per plant (Gaskins et al. *1972*). Pods usually contain 8 to 16 seeds. The flowers have a faint but definite pleasant aroma and bees visit them freely for both nectar and pollen.

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FIGURE 183.—Flowering stems of a tephrosia plant.

Flowering occurs on decreasing day-lengths. If the plant is grown in the United States, it is likely to be killed by frost before flowers appear, therefore the plant requires a tropical home for seed production. The flower may last about 2 days during cool or rainy weather but only 30 hours during dry weather (Martin and Cabanillas *1970*).

Pollination Requirements

The plant is considered to be self-pollinated. The stigma appears to be receptive to pollination at anthesis. Often it is in contact with dehisced anthers, particularly if the stamens are long. Furthermore, data indicate that self-pollination generally occurs, because recessive white flowered selections grown next to dominant purple-flowered ones never produce purple-flowered offspring. Also, flowers bagged before anthesis frequently produce some pods with seed; however, when viewed from an agronomic standpoint the seed set is poor, and large differences in seed production occur in different locations. Martin and Cabanillas (*1970*) showed that pollination is a factor by comparing plants in the open, plants caged with bees, and plants caged without bees. The results showed that from 10.8 to 22.8 percent of the pods set in open plots, 17.4 percent set in the cage with bees, but only 0.8 to 3.7 percent of the pods set in cages without bees. There were also fewer seeds per pod in the cage without bees.

Knowing that visiting bees, largely honey bees or carpenter bees, caused scratches on the stigmas, possibly making them more receptive to pollination, some stigmas were intentionally damaged with a needle before pollination. Others were pollinated as gently as possible. the results were significant: a 50 percent increase in pod set and more than 100 percent increase in seed set were obtained from flowers with damaged stigmas.

Pollinators

Martin and Cabanillas (*1970*) concluded that "bees appear to have a role in pollinating tephrosia." Honey bees were the most frequent visitors. Some were nectar-seeking bees that visited only "younger" flowers and usually did not touch the stigma. Pollen-seeking bees, on the other hand reportedly visited chiefly older flowers. They forced open the upper suture or short leg of the keel to remove pollen, but the effect of the bee behavior on the flower was not visibly discernible but did not "appear to lead to pollination." How the authors arrived at this conclusion is not clear. They concluded that carpenter bees (*Xylocopa brazilianorum* L.) were the principal pollinators. Gaskins et al. (*1972*) concluded that insects facilitate self-pollination but contribute little to cross-pollination. They considered the honey bee too small to trip the flowers, yet they reported that most flowers had scratches on the stigma but were not tripped. A high percentage of these untripped flowers were found to be self-pollinated. Thus, they concluded, bees facilitate self-pollination by changing the relative position of keel, stigma, and pollen, without tripping, preparing the stigma for pollination by breaking up the stigmatic surface.

Pollination Recommendations and Practices

Martin and Cabanillas (*1970*) recommended that plantings be made close to weedy areas and in abandoned fields where dead trees or legume plantings occur. (They also recommended that research be conducted on methods of increasing natural populations of carpenter bees.) Their discussion of the pollination of this crop is so reminiscent of the early history of alfalfa pollination that one is led to wonder if flooding the field of tephrosia with honey bees might not have the same beneficial effect it has had on alfalfa seed production.

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TOMATO

Lycopersicon esculentum Mill., family Solanaceae

The tomato crop was produced on an estimated 395,500 acres in 1971 and valued at $444 million, making it second only to another vegetable of the same family, the potato (*Solanum tuberosum* L.), which was produced on 1,380,000 acres and valued at $626 million. Tomatoes are grown in almost every State, out of doors in season and in glass and translucent plastic houses for off-season markets. Recent innovations in mechanical harvesting and the breeding of cultivars that have improved shipping capabilities have caused considerable changes in the industry. Cold storage of fruit and its production under glass and translucent plastic, along with the ease of shipping tomatoes long distances now permit the public to have this vegetable on the food table throughout the year.

The plant is grown for its fruit, a fleshy berry, which is consumed fresh, canned, or used to produce juice, sauces, pastes, or powder. The seed yields 24 percent oil, which is used in salad oil, margarines, and soap (Purseglove *1968**). The number of seeds in a fruit may vary from 73 to 346 (Hafen and Stevenson *1956*).

Plant

The tomato, as it is grown in the United States, is a many-branched annual plant, 2 to 6 feet, at first erect but later becoming prostrate, with alternate many-branched leaves, 6 to 12 inches long, and clusters of 2 to 12 or more flowers. The plant is covered with short coarse hairs and has a glandular secretion with a characteristic unpleasant odor, particularly when bruised. It is cultivated in rows, 3 to 6 feet apart in the field, but usually tied up on strings when grown in greenhouses. Under commercial harvesting methods, cultivars are desired that set a maximum amount of fruit in a relatively short time, and the fruit retains its keeping qualities for several days both on the vine and after it is harvested.

Inflorescence

The inflorescence may arise terminally, opposite or between the leaves. The individual flower is about three-quarters of an inch in diameter with a 5- to 10-part green calyx, that clings to the fruit until it matures. There are usually six golden yellow petals that recurve as they expand. There are usually six stamens, which are united with their yellow anthers (fig. 184) to form a tube or cone about one-half inch long, that surrounds the pistil, and, with the recurved petals, gives the pendant flower a shooting star or rocket appearance. Depending upon cultivars and environmental conditions, the style may range from slightly shorter than the tip of the anthers to as much as 2 mm beyond the tip, terminating with a capitate, simple, narrow or somewhat bulbous stigma (Muller *1940*). The flower is hermaphrodite, hypogynous, and regular.

The style elongates about the time the anthers begin to split at the terminal end and release their pollen into the stylar tube. The stigma is receptive to its own or other pollen 1 or 2 days before anther dehiscence (Fink *1898*), which favors cross-pollination. The stigma remains receptive for 4 to 8 days (Jones and Rosa *1928**). The construction of the anthers, delicately united with the filament, permits them to vibrate at the slightest touch and send a rain of pollen down the cone outlet and around the stigma.

Nectar secretion from tomato plants is apparently of little, if any, value in attracting bees. Schneck (*1928*) referred to "the absence of nectar" in the tomato flower. Neiswander (*1954a, 1956*) stated that the blossom "contains little or no nectar." Fink (*1898*)

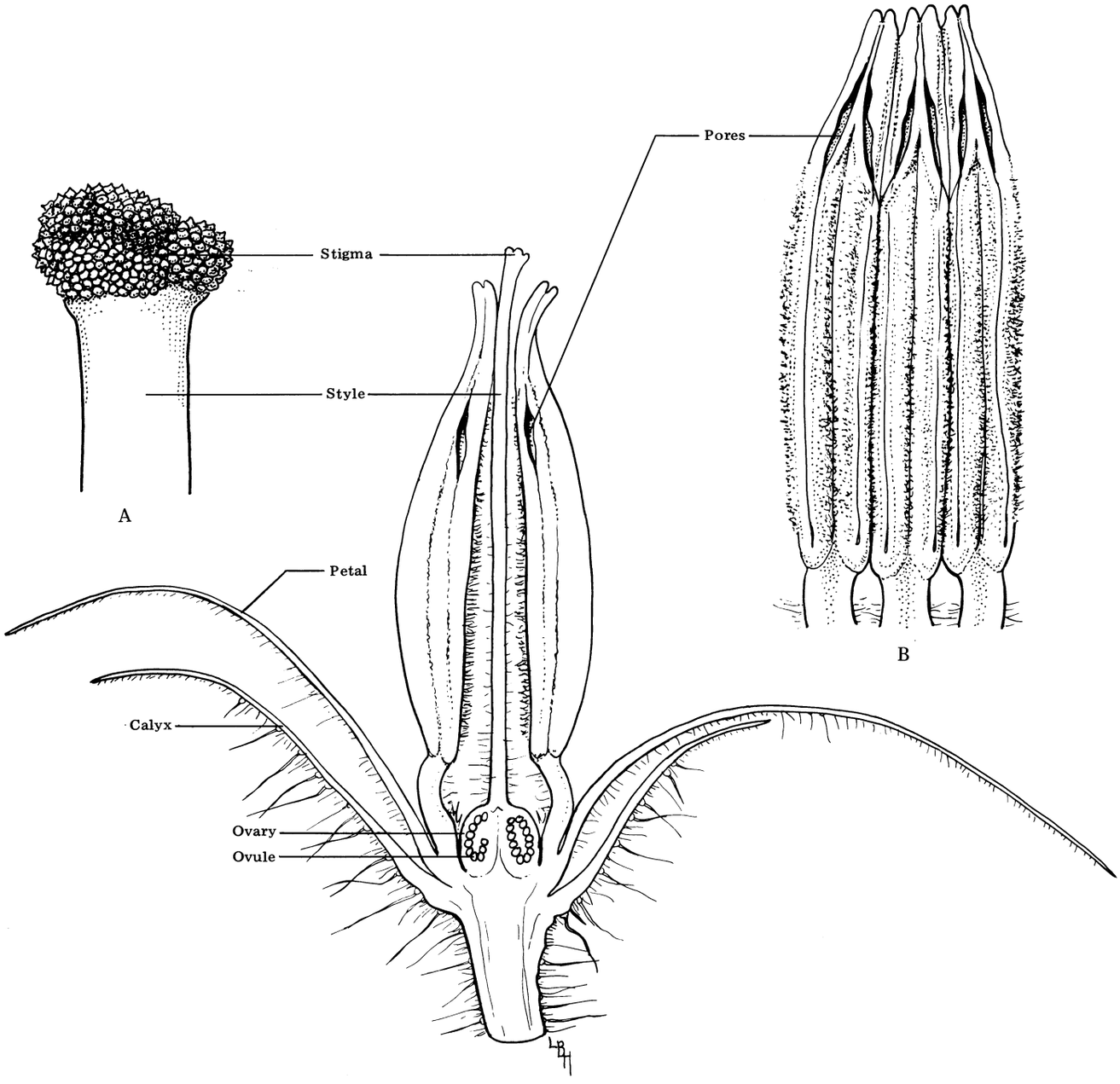

FIGURE 184.—Longitudinal section of tomato flower, ×9. *A*, Tip of pistil; *B*, three anthers, greatly enlarged.

reported that bumble bees "gathered chiefly pollen" from tomato flowers. Thus, if nectar is produced, a question that should be settled, it is of little significance in the relation of insect pollination of tomatoes. The pollen is more attractive to wild bees than honey bees.

Pollination Requirements

Various tests in greenhouses have proven that the tomato flower is not self-pollinating. However, if the inflorescence is shaken, the pollen will fall from the anthers onto the stigma and fertilization will result. One pollen grain is needed for each seed, so many grains are needed on each stigma. Incomplete pollination results in misshapen fruit. Cool or cloudy weather retards pollen shedding (Stoner *1971*). Growers of tomatoes in greenhouses use various types of vibrators or other devices each few days to shake the flower clusters (Beattie *1939*; Bouquet *1919*, *1924*; Cottrell-Dormer *1945*; Fletcher and Gregg *1907*; Hoffman *1958*; Kerr and Kribs *1945*; Lesley and Lesley *1939*; Moore *1968*; Neiswander *1954a*, *b*, *1956*; Ross *1963*; Verkerk *1957*; White *1918*; Wittwer and Honma *1969*). Moore (*1968*) obtained only 4.3 pounds of fruit from control plants in a plastic greenhouse; 6.6 pounds, from hormone treated plants; 8.8 pounds, from vibrator treated plants; and 9.8 pounds, from plants treated with both hormones and vibration. For maximum effectiveness, vibration must be repeated every 2 or 3 days.

Although Bailey and Lodeman (*1895*) concluded that

bees in the greenhouse were of no value as pollinators of tomatoes, Neiswander (*1954a, b, 1956*) found that visits of honey bees increased fruit production even though the flowers had also received the shaking treatments. Marr and Hillyer (*1968*) showed that self-pollinated plants (in greenhouses) yielded less and had more misshapen fruit than crossed plants.

Jones (*1916*) observed 1.98 percent cross-pollination of tomatoes in New Jersey and estimated that an equal undetected amount of crossing occurred. This figure has been frequently used over the years, without regard to the insect pollinator population or variety under test. He stated that he "saw no insects," although others have associated cross-pollination with insects almost exclusively.

Tomato flowers in the open are usually considered to be sufficiently vibrated by wind currents to cause the pollen to fall onto the stigma and affect maximum set (Lesley and Lesley *1939*). Wind is not a factor in transferring pollen from plant to plant (Currence and Jenkins *1942*); however, if the weather remains calm or if the blossom is so situated on the plant that it is not vibrated by the wind its pollination would conceivably be prevented. Under such conditions, visitation by pollinating insects would be beneficial. Cross-pollination in the field is common although the percentage is usually low (Azzam *1960*; Lesley *1924*; Purseglove *1968**; Richardson and Alvarez *1957a*; Rick *1947, 1949, 1950*; Schneck *1928*; Smith *1935*; Soost and Rick *1957*).

A factor favoring self-pollination of the tomato is the relatively long time that the stigma is receptive to pollen, from 1 to 2 days before anther dehiscence to 4 to 8 days after dehiscence (Smith *1935*). Another factor is the length of the stigma. If the style is short and the stigma is surrounded by dehiscing anthers, selfing after vibration is most likely. If the style is long or if it grows through the anther tube before pollen is shed, its likelihood of being cross-pollinated is increased. Jones and Rosa (*1928**) stated: "In some varieties, however, and probably in some flowers of all varieties, the style elongates before the anthers dehisce, thus exposing the stigma to foreign pollen." Regardless of how the pollen is applied, the more pollen (within limits) the larger the fruit (Fink *1898*), and the more symmetrical it is (Hoffman *1958*).

Pollinators

In greenhouses, the various types of mechanical vibrators are satisfactory pollinators. In the field, the wind vibrates the plants. Neither of these methods contributes to the pollination of male-sterile plants. Only insects can serve in this capacity (fig. 185). They also contribute to pollination of those plants or cultivars with styles that extend beyond the stigma. Currence (*1944*) showed that use of hybrids could increase yields by 20 percent, and he reported finding a male-sterile plant that set good crops from artificial pollination. Barrows and Lucas (*1942*) estimated the value of hybrid seed at $8 per ounce. This might be decreased if the grower could incorporate a seedling marker to aid in weeding out nonhybrids (Hafen and Stevenson *1956*).

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FIGURE 185.—A bumble bee collects pollen from a tomato flower in an unusual way. The bee clings underneath the flower and vibrates its body rapidly, causing the pollen to fall from the anther tubes onto the underside of the bee's body.

Others (Hojby *1958*, Kerr *1955*, Oba et al. *1945*, Roever *1948*, and Wellington *1912*) have shown the value of hybrid tomato production. Shifriss (*1945*) reported the production of hybrid tomato seeds, produced by the relatively inexpensive labor of college girls. Kerr (*1955*) associated greater numbers of seeds with larger and more rapid fruit development.

Where hand pollination is impractical, insects can be used. Richardson and Alvarez (*1957a, b*) considered the Halictid bee (*Augochloropsis ignita* Smith) the most effective pollinator in their area. Bullard and Stevenson (*1953*) considered neither houseflies, blowflies, nor honey bees of value under cheesecloth cages over six plants. Azzam (*1960*) observed few bumble bees on tomato flowers in Puerto Rico but several hundred *Exomalopsis glubosa* F. bees.

It is generally known, however, that a few honey bees in such a cage do not act normally. Fletcher and Gregg (*1907*) hinted that honey bees might be used to distribute tomato pollen. Lesley and Lesley (*1939*) indicated that "bumble bees and other insects also assist." Neiswander (*1954a, b, 1956*) showed that honey bees can be of value as pollinators of tomatoes. Fink (*1898*) considered bumble bees to be effective pollinators. Rick (*1950*) suggested the use of "wild solitary bees" for cross-pollination of male-sterile tomatoes. Rick (*1947*) mentioned the value of insect pollinators of tomatoes and their protection from insecticides. Rick (*1949*) stated that at Riverside, Calif., *Anthophora urbana* Cresson was most common, but various species

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of solitary bees and a few species of bumble bees contributed to pollination of tomatoes. Schneck (*1928*) stated that bumble bees are fond of tomato flowers but that honey bees do not work them "probably because of the peculiar structure of the flower and the absence of nectar." The problem seems to be that wild pollinators in most areas are too scarce to have an impact on pollination of tomatoes from the production standpoint.

Occasionally, honey bees visit tomato flowers, as was demonstrated in the greenhouse. Apparently, if they are sufficiently concentrated in a tomato-growing area, the competition could "force" them to visit tomato blossoms for pollen. Unless cultivars are found that produce nectar, there can be no insect pollination of male-sterile varieties for hybrid production.

If such cultivars are found, honey bees might be practical, or useful species of wild bees might be brought from Peru, the native homeland of the tomato, to provide adequate pollination. A new look should therefore be taken at current cultivars in which there has been incorporated new germ plasm to determine if nectar is being produced or if the flower has been changed in any other way that might affect pollinating insects.

Pollination Recommendations and Practices

Because of current agricultural practices as well as the relative unattractiveness of tomato flowers to honey bees, many U.S. tomato fields are largely devoid of pollinating insects. Neiswander (*1954a, 1956*) concluded that honey bees should not replace vibrators in the greenhouse even though they increased production on an average of 1.1 pounds per plant on plants vibrated mechanically.

There are no recommendations for supplying pollinating insects to commercial fields, although the evidence indicates that if a heavy population of insect visitors could be established the effects would be beneficial.

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TREFOIL

Lotus spp., family Leguminosae

Three species of birdsfoot trefoil are of agronomic importance in the United States. They are broadleaf trefoil (*L. corniculatus* L.), narrowleaf trefoil (*L. tenuis* Waldst. & Kit. ex Willd.), and big trefoil (*L. uliginosus* Schk.) (Seaney and Henson *1970*). Some experts disagree in the classification of the various species and cultivars of the genus *Lotus* (Gist *1960*, Howell *1948*, Levy *1918*, MacDonald *1944*, McKee and Schoth *1941*, Seaney and Henson *1970*, Wheeler and Hill *1957**).

In the United States, birdsfoot trefoil is grown for hay and permanent pasture, primarily in the New England States and western Oregon, and to a limited extent in several other Central and Northern States. Practically all big trefoil seed is produced in Oregon. According to Seaney and Henson (*1970*), over 2 million acres of trefoil were grown in 1967, and potentially the crop can produce 600 to 1,000 pounds seed per acre.

Plant

Trefoil is a perennial plant that has an extensive root system with a strong taproot. It is therefore more drought-resistant than many other legumes. If conditions are unfavorable, the plant may grow only a few inches tall, but if favorable it may produce 100 or more stems and reach a height of 3 feet. It is the only legume with five leaflets, which consist of a terminal and two opposite lateral ones at the apex and two opposite leaflets at the base of the leaf petiole (fig. 186) (Hughes *1951*).

The plant shape varies greatly between cultivars (Peterson et al. *1953*). Some plants tend to grow upright (hay types), and some tend to be low or prostrate growing (pasture types).

Ten or more seed are produced in a cylindrical pod an

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FIGURE 186.—Broadleaf birdsfoot trefoil showing flowers, pods, and leaves.

inch or more long. Several seed pods are attached to the stem at a single point, and toward maturity they spread apart on a lateral plane giving the appearance of a bird's foot. The pods dehisce or pop open on maturity and the seeds are scattered. A nondehiscent type of plant would greatly increase the volume of seed harvested.

Inflorescence

Trefoil flowers are borne in an umbel or cluster at the end of a short flowering stem, somewhat like sweet peas. Big trefoil usually has 8 to 12 flowers in a cluster or umbel, and it has vigorous underground stems or spreading rhizomes. Broadleaf and narrowleaf trefoils have only five (rarely six to seven) flowers in the umbel, and they do not have spreading rhizomes. The flowers of narrowleaf trefoil are smaller than those of broadleaf. They are bright yellow to orange, about one-half inch broad, and shaped much like the garden pea but much smaller. Knuth (*1908*, pp. 300–304*) stated that the nectar is secreted in the usual place, at the base of the staminal column, and is sought after by numerous insects. He stated that the 10 anthers dehisce before the flower opens, then they shrivel. Then five of the filaments become club shaped and elongate to form a pistonlike action that pushes the dehisced pollen forward into the keel tip.

When the insect exerts pressure on the petals, the thickened filaments push a quantity of pollen out the keel opening. As the pressure increases, the stigma also protrudes and becomes exposed so that either self- or cross-pollination may take place. The former, however, is largely ineffective. When the pressure is removed, the parts return to their original position. The pollen is extruded in a ribbonlike somewhat pasty mass, and when contact is made it adheres to the underside of the bee. As further pressure causes the stigma to emerge, it also contacts the same area of the body of the insect, which may be coated with pollen obtained from other blossoms, and cross-pollination can result (Watson *1963*). Release of pollen may result from as many as 10 bee visits. Flowers not visited by bees remain open 8 to 10 days, but visitation by bees (and probably fertilization of the stigma) reduce this period to less than 4 days.

Trefoil is highly attractive to bees for its nectar and pollen. When foraging on trefoil is extensive, colonies frequently build up rapidly and then swarm (Anonymous *1959*).

Vansell[46] reported that honey bees were extremely active on trefoil blossoms, collecting both nectar and pollen, although "little nectar could be seen in the 2 large pit-like nectaries." He noted six bees per square yard mainly collecting trefoil pollen. Pellett (*1944*) considered broadleaf birdsfoot trefoil in Iowa more attractive to bees than sweetclover. Trefoil produces a superb honey, although on a national scale the amount produced annually is not great.

Pollination Requirements

The rather thorough study of the pollination of the trefoils by numerous workers (Bader and Anderson *1962*, MacDonald *1944*, Miller and Amos *1965*, Miri and Bubar *1966*, Morse[47] *1958*, Silow *1931*) leaves little doubt that these plants require insect pollination for commercial production of seed. The flower is so constructed that pollen is released before the flower opens (Seaney and Henson *1970*), and self-pollination appears feasible. MacDonald (*1944*) showed that single plants of *L. corniculatus* enclosed with "sterile" bees produced 100-percent fertilized florets, which proved that the plant was self-fertile. However, plants from which bees were excluded produced no fertilized ovules, which proved that the florets were incapable of fertilizing themselves without the aid of an outside agency. Other workers concluded that trefoils are only partially self-fertile. In any event, they are not self-fertilizing. MacDonald (*1944*) also showed that about twice as many flowers were fertilized with pollen from other plants of the same species as with pollen of the same plant. Even if individual trefoil plants are self-fertile, they benefit from cross-pollination between plants within the species.

Pollinators

Bees are the only insects that pollinate the trefoils to an appreciable degree (Bader and Anderson *1962*, MacDonald *1944*, Morse[48], Peterson et al. *1953*, Vansell[49]). Honey bees and bumble bees account for the big majority of the bee visitors, and of these the honey bee is predominant (Morse[50]). Although Bohart (*1960**) recorded higher populations of wild bees than honey bees on plots of trefoil in Utah, Bader and Anderson (*1962*) concluded that pollen-collecting honey bees were better pollinators of *L. corniculatus* than were nectar collectors in that the former set 7.00 seeds per

[46] VANSELL, G. H. [BIRDSFOOT TREFOIL.] U.S. Dept. Agr., Pacific States Bee Culture Field Lab., Davis, Calif. First Quart. Rpt., p. 8. 1952.

[47] MORSE, R. A. THE POLLINATION OF BIRDSFOOT TREFOIL. 119 pp. 1955. [Unpublished diss. submitted to Cornell Univ., partial fulfillment for Ph.D. degree, Cornell Univ., New York.]

[48] See footnote 47.

[49] See footnote 46.

[50] See footnote 47.

pod, whereas the latter set only 4.92 per pod. (A pod can have 10 or more seeds.) Miller and Amos (*1965*) concluded that about two-thirds of all trefoil flowers set as many seeds from one honey bee visit as if five or six visits had been permitted. Morse (*1958*)[51] stated that slightly less than one honey bee per square yard of flowering trefoil was a sufficient pollinator population in New York. Vansell[52] observed six bees per square yard in California, but the significance of this bee population in terms of seed production is unknown.

Miller (*1969*) noted that clones differ in cross-compatibility to the extent that some crosses set very few seeds. If this condition exists under field conditions, and it could quite logically do so, such a cross-visit would require an additional bee visit from a more acceptable clone if seed is to be set. To that extent, heavy visitation might be desirable.

Because of the tendency of the seeds to set over a period of several weeks and to shatter when they become ripe, the harvesting of large crops of seed is difficult. McKee and Schoth (*1941*) stated that 100 pounds of clean seed per acre was usual. MacDonald (*1944*) reported the production of 22 growers averaged only 46 pounds. Howell (*1948*) reported an average of 127 lb/acre in Oregon. Tremblay (*1962*) reported 99 and 139 lb/acre in Vermont for 1958 and 1959. (Incidentally, he reported that the cost of bees for trefoil pollination ranged from $0.04 to $3.56 (average, $1.16) per acre.) Anderson (*1955*) found that least shattering and maximum seed was obtained if harvest occurred when the maximum number of pods were light green to light brown. Peacock and Wilsie (*1957*) showed that shattering was reduced by 17 percent in one cycle of plant selection, and they believed that nonshattering plants might be developed.

Pollination Recommendations and Practices

Morse (*1958*) was of the opinion that in central New York—where apiaries of 25 to 50 colonies were about 2 miles apart (one colony per 50 to 100 acres)—sufficient bees were in the area and moving colonies into the area for pollination of trefoil would be of little or no value. He was probably giving more consideration to honey production than pollination of trefoil, or he gave considerable credit to local wild bees. Wheeler and Hill (*1957**) stated that insect pollination appeared to be essential for seed production of big trefoil, but if the supply of local bees was not adequate additional honey bees should be added. Eckert (*1959**) recommended one strong colony per acre of trefoil. He stated that colonies of bees interchanged between trefoil and alfalfa reportedly gave excellent service. Smith (*1960*) recommended two to three colonies of honey bees per acre of trefoil, the colonies placed in or close to the field.

The number of bee visitors per unit area of the crop should be considered when determining the adequacy of the population. Morse[53] considered one bee per square yard adequate, although Vansell[54] observed as many as six bees per square yard. The grower wants to set the maximum seed crop in as short a period as possible. It would appear then that he should strive for the bee population that would accomplish this. If that population is not present, additional colonies should be brought in until it is reached. This may require more than the one colony indicated by Morse or the two to three colonies recommended by Smith (*1960*).

[51] See footnote 47, p. 362.
[52] See footnote 46, p. 362.
[53] See footnote 47, p. 362.
[54] See footnote 46, p. 362.

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TUNG

Aleurites fordii Hemsl., family Euphorbiaceae

The tung tree has also been known as tung-nut, tung-oil, or china wood-oil tree (Fairchild *1913*). The word tung is Chinese for "heart," the general shape of the leaf (Potter and Crane *1957*). In 1964, there were about 7.5 million tung trees in the Southern States: Mississippi, 4.4 million; Florida, 1.7 million; Lousiana, 1.3 million; and Alabama, 0.1 million; with a few thousand in Georgia. Production of nuts amounted to 123,300 tons with a value of $7.6 million. Production amounted to only 11,700 tons valued at less than $1 million in 1970, when production estimates in USDA Agricultural Statistics were discontinued.

Tung oil, which is pressed from the nuts of this tree, is used by the protective coating industry in varnishes, enamels, and electrical insulators.

Plant

Tung is a soft wooded, smooth-barked deciduous tree that may grow to 30 feet. First blooms appear from late February to April before the leaves appear. In bloom, the tree (fig. 187) is highly attractive because of its mass of pink blossoms similar to flowers of catalpa (*Catalpa* spp.). These are followed by the dense foliage of 3- to 5-inch heart-shaped dark-green leaves. Current orchard recommendations include 100 to 140 trees per acre (Potter and Crane *1957*) with suggested spacings ranging from 12 by 30 feet to 15 by 40 feet. Growers allow the trees to start branching 4 to 6 feet above the ground. Tree shape is oval and symmetrical.

Inflorescence

The colorful and attractive blossoms (fig. 188), which are borne on the ends of the growing shoots of the previous season, vary in type. They may be all staminate, all pistillate, or predominantly one or the other (Dickey and Reuther *1940*, McCann *1942*). The percentage of pistillate flowers may depend on the vigor of the tree, with more such flowers produced on trees making more vigorous growth (Abbott *1929*). The reddish-white flowers occur in panicled cymes or clusters with usually about 60 staminate and one pistillate flower each, with rarely a perfect flower (Newell *1924*).

PN-3852

FIGURE 187.—Eleven-year-old tung orchard in full bloom.

Each flower may be an inch or more in length, and the tree is covered with the canopy of blossoms. The pistillate flowers have a three- to five-celled ovary that, when pollinated, produces a top-shaped fruit 2 to 3 inches in diameter, usually bearing five seeds. The blossoms secrete some nectar, and the staminate flowers produce a copious amount of pollen (Pering *1937*). Bees visit the blossoms freely.

Pollination Requirements

Angelo et al. (*1942*) showed that plants caged to exclude bees set no fruit and that wind or shaking the tree was of no value in fruitsetting, but when a tree was caged with a colony of honey bees a good set was obtained. Others (Hambleton *1950*, Pering *1937*) also credit honey bees with setting the crop. The tree is not self-sterile. It merely needs the agency to transfer the sticky pollen from the anthers of the staminate flowers

PN-3853

FIGURE 188.—Closeup of a flowering tung branch.

to the stigma of the pistillate flower. Brown and Fisher (*1941*) showed that pollination can occur over several days of the life of the blossom. Webster (*1943*) concluded that when staminate and pistillate flowers are on separate trees, one staminate tree for 20 pistillate trees was sufficient for satisfactory pollination, provided that some staminate flowers open by the time the pistillate flowers are receptive.

Pollinators

The pollination of tung trees is dependent upon the honey bee. Other insects visit the blossoms but rarely in sufficient abundance to be of significance. Under orchard conditions, practically every ovule of every pistillate flower is capable of developing a seed. This means that at least one viable pollen grain must land on each of the four or more lobes of the stigma of each flower at the right time to permit fertilization of the ovules. The bee population necessary to accomplish this has not been determined.

Pollination Recommendations and Practices

No recommendations have been made on the use of bees in the pollination of tung, even though there is no doubt about their need in the production of this crop. The need for transfer of pollen grains from the staminate to all of the lobes of the pistillate flower may not require repeated visits of honey bees, but the grower should not overlook this need. To assure maximum set of nuts, he should arrange for an appropriate number of strong healthy colonies of honey bees so that every pistillate flower is well pollinated. Because of the small acreage now being grown in the United States, the demand for insect pollination is not great.

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TURNIP AND RUTABAGA

Brassica rapa L., and *B. napobrassica* Mill., family Cruciferae

Turnip (*B. rapa*) and rutabaga (*B. napobrassica*) are sufficiently alike from the botanical and pollination standpoints to be combined. Turnips are about 10 times as important as rutabagas. About as much turnip as radish seed is produced annually, 1,500 to 3,000 acres. Seed production is primarily in the Pacific Northwest (Hawthorn and Pollard *1954**).

Plant

The plants of the two species are grossly similar

except that the turnip has prickly leaves, whereas those of the rutabaga are glabrous (smooth). Turnip leaves arise from a smaller neck than that of rutabaga leaves, and the turnip blossoms have brighter more yellow flowers than those of the rutabaga.

The plants are biennial, each producing a fleshy, edible, globular root, 2 to 6 inches thick. The first year the growth above ground consists of a rosette of leaves about a foot across. A main flowering stem, 2½ to 4 feet long, and its branches develop the second year. The rutabaga root is somewhat larger than the turnip root. Rutabagas grow more slowly than turnips (Jones and Rosa *1928**). The plants cross readily.

Inflorescence

The flowers of turnips and rutabagas are identical in structure to those of other Cruciferae (see "Cole Crops"). The main flowering stem is also similar, but the ⅜-inch flowers of rutabaga are less golden than turnips, rape, or mustard. The flowering period lasts 22 to 30 days. A single bloom will last 2 or 3 days if pollinated, but if caged so that bees are excluded, it may stay open as long as 12 days (Nikitina *1950*). Both turnips and rutabagas provide a good source of nectar for bees.

Pollination Requirements

Pollination is a requisite to good seed production in both turnips and rutabagas but more so in turnips. Nikitina (*1950*) reported that turnips isolated from bees produced only one-third as much seed as open-pollinated plants. Also, the seeds from the bee-pollinated plants had better germination and produced more vigorous plants. Jones and Rosa (*1928**) stated that cross-pollination was more essential in turnips than rutabagas, and more essential in white-fleshed than yellow-fleshed turnips. Hawthorn and Pollard (*1954**) stated that to insure a good seed set, the pollination of all the flowers is necessary.

Pollinators

Nikitina (*1950*) stated that in Russia 60 percent of the floral visitors to turnips and rutabagas were honey bees. He reported yields of 450 to 560 kg seed per ha, where there were 67 colonies and 10 acres of the crop. Farms with fewer colonies produced less. Hawthorn and Pollard (*1954**) stated that honey bees are the chief pollinators.

Pollination Recommendations and Practices

Hawthorn and Pollard (*1954**) stated that with large plantings the grower should make sure that colonies of bees are adjacent to the field. They did not say how many colonies were needed. However, to obtain the pollination of all the flowers, which they stated was necessary for a good seed set, one or more colonies per acre would doubtless be required, the number depending, as in other crops, upon plant competition, colony fitness, and crop condition.

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VANILLA

Vanilla spp., family Orchidaceae

Three species of *Vanilla* are of commercial importance: *V. planifolia* Andrews [*V. fragrans* (Salisb.) Ames], *V. pompona* Schiede, and *V. tahitensis* J. W. Moore. The first is by far the most important (Childers et al. *1959*). Vanilla is cultivated for its pods which, under processing, yield vanilla extract. In 1950, world production was 3 million pounds of extract, of which Madagascar produced more than half and Mexico about a fourth. The United States is the primary consumer of vanilla extract (Childers et al. *1959*).

Plant

Vanilla is a tropical, evergreen, leafy, and somewhat fleshy vine (fig. 189) that may climb to the top of trees, 50 to 75 feet, if unchecked. It has thick, oblong, 6- to 9-inch, dark-green leaves and forms roots opposite the leaves by which it clings to the tree. It is propagated vegetatively, pruned at the tip, and trained onto a trellis. The plants are usually set 6 feet apart in the row, the rows about 9 feet apart (Kanman and Pillai *1966*). The fruit is a beanlike pod, 4 to 6 inches long by about one-half inch thick (fig. 190). The better pods are 5 inches or more in length. A single pod contains thousands of seeds almost microscopic in size (⅓ to ¼ mm).

A healthy vine should produce about 100 pods per year, which mature 8 to 9 months after flowering. If too many flowers are pollinated and too many pods set, the vine may be overloaded and will die.

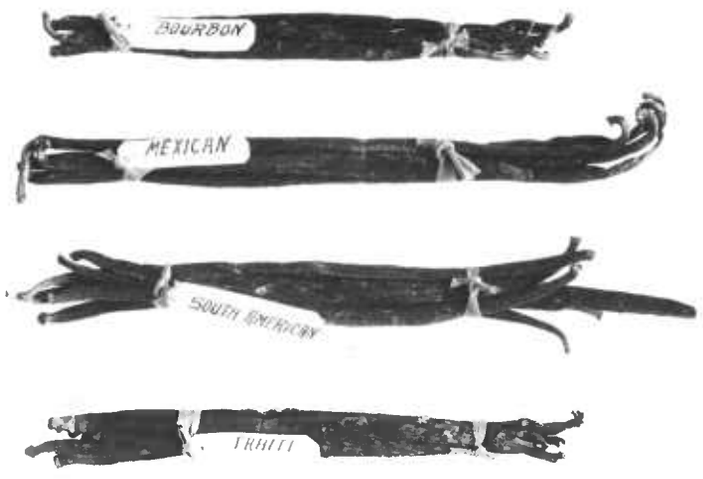
Just before the plant flowers, the grower usually prunes 4 to 6 inches from the vine tip; this stops linear growth and seems to benefit flowering (Childers et al. *1959*).

Irvine and Delfel (*1961*) dispelled the former belief that plants will not flower unless they are climbing, by showing that inflorescences were produced satisfactorily on horizontal and even descending stems. Of 10 plants studied, one ascending stem had 82 inflorescences, one 60 feet tall and still climbing had only 18, and one descending vine had 29. This proved that maintenance of plants on trellises did not necessarily cause a decrease in yield.

Inflorescence

The small lilylike, greenish-yellow vanilla flowers, 1½ by 2½ inches long (Woebse *1963*), develop in

PN-3854
FIGURE 189.—Section of vine of vanilla (*Vanilla planifolia*) growing on tree trunk.



PN-3855
FIGURE 190.—Dried vanilla beans from 4 different cultivars.

axillary racemes (fig. 191). There may be as many as 100 flowers in a raceme but usually there are about 20. Usually, only one flower in a raceme opens in a day, with the entire flowering period of the raceme lasting an average of 24 days. Flowering for an average plant in Puerto Rico begins in January, reaches a peak in March, and ends in June. In the Philippines, flowering extends from March to June, with the largest percentage of the flowers appearing in April (David *1953*).

The individual flower has three sepals and three petals, one of the petals being enlarged and modified to form the trumpetlike lip, and a central column comprised of the united stamen and pistil. The anther is at the apex of the column and hangs over the stigma, but a flap or rostellum separates them.

The flower opens in the morning and closes in the afternoon, never to re-open. If it is not pollinated, it will

PN-3856
FIGURE 191.—Flowers of *Vanilla pompona*.

shed the next day. The optimum time for pollination is in midmorning (Childers et al. *1959*).

The pollen clings together in a mass and is feebly attractive to certain bees and hummingbirds (Cobley *1956**, DeVarigny *1894*). The nectar source is seldom mentioned, although hummingbirds visit flowers primarily, if not exclusively, for nectar. Many species of the family Orchidaceae are noted for their nectar secretion (Darwin *1877**). Correll (*1953*) stated that the flowers are visited for the "honey" secreted at the base of the lip.

Pollination Requirements

The vanilla flower is self-fertile, but incapable of self-pollination without the aid of an outside agency to either transfer the pollen from the anther to the stigma or to lift the flap or rostellum then press the anther against the stigma. The only time this can be accomplished is during the morning of the one day the flower is open. Unless pollination occurs, the flower drops from the vine the next day. Correll (*1953*) stated that insect pollinated flowers, being cross-pollinated, produce viable seed, but flowers that are hand pollinated, being self-pollinated, produce only sterile seeds.

Pollinators

The reference occurs repeatedly in the literature that in its native Mexico the flowers of vanilla are pollinated by small bees of the genus *Melipona* and also by

hummingbirds (Ridley *1912**). Childers and Cibes (*1948*) noted that this report has not been carefully checked and later Childers et al. (*1959*) said that there is no experimental proof that they are actually effective pollinators. Mention is made by Childers et al. (*1959 p. 477*), that "The first effort made toward solving the (pollination) problem was to introduce bees of the genus *Melipona* from Mexico, but they did not thrive. After this failure a mechanical means of pollination was tried." Then Albius, in 1841, discovered the practical method (Childers et al. *1959*) of using a small splinter of wood or a grass stem to lift the rostellum or flap out of the way so that the overhanging anther can be pressed against the stigma to effect self-pollination.

Now, practically all vanilla is produced by hand pollination, which accounts for 40 percent of the total labor cost in vanilla production (Gregory et al. *1967*).

No further study seems to have been made on the utilization of *Melipona*, or other insects, or hummingbirds. No attempt has been made to concentrate pollinating insects for this purpose. It would appear logical that if nectar is secreted, as indicated by Correll (*1953*), honey bee colonies could be amassed in the area when desired, and the workers could be "forced" to visit the flowers. The relative cost of a high concentration of honey bee colonies as compared to the cost of human labor, would make such exploitation of honey bees highly worthwhile investigating. The reference by DeVarigny (*1894*) that Cuban bees, whether indigenous or naturalized European bees, were pollinating vanilla in Cuba indicates that bees could be used satisfactorily.

Pollination Recommendations and Practices

There are no recommendations for the use of bees, bats, birds, or other agencies. The evidence indicates, however, that saturation pollination by honey bees or certain other bees offers possibilities because vanilla in Mexico was probably pollinated by bees at one time to some extent.

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VEGETABLE SPONGE

Luffa cylindrica (L.) Roem., family Cucurbitaceae

The vegetable sponge is also known as sponge gourd, dishrag gourd, dishcloth gourd, loofah gourd, and smooth loofah (Purseglove *1968**, Whitaker and Davis *1962**). It is grown for food in India, where the young tender fruits of the nonbitter types are eaten fresh like cucumbers, cooked as a vegetable, or used in soups. The seeds yield a colorless, odorless, tasteless oil that can be used in cooking. Its primary use, however, is for the fibrous material inside the mature fruit, which is used in commercial filters and for insulation in pot-holders, bathmats, and related uses (Porterfield *1955*).

Except during the war years of 1941–45, Japan has maintained an unbroken monopoly on the production of vegetable sponge filters for industrial purposes (Whitaker and Davis *1962**, Howes *1931*). Before World War II, 60 percent of the vegetable sponge imported into the United States was used in filters of marine steam and diesel engines (Purseglove *1968**). Production in other areas of the world has not been too successful (Wester and Boswell *1943*).

Plant

The plant is a vigorous trailing or climbing annual that has a distinctive fetid odor when bruised. The leaves are 3 to 12 inches across, kidney shaped, smooth, and softly pubescent. It is commonly trained on a trellis and pruned to the main stem. The fruit is oblong to cylindrical, 1 to 2 feet in length, and full of strong fibrous cells and numerous seeds. The rind is hard but thin and can be softened when soaked in water about 5 days, when it and the seeds can then be removed leaving only the fiber.

The seeds are planted in hills 3 to 4 feet apart, the plants thinned to one; then it is trimmed and thinned to permit development of only 20 to 25 fruits. About 24,000 fruits per acre may be produced. Some cultivars produce the best vegetables and some produce the best sponge (Purseglove *1968**).

Inflorescence

The flowers are produced in the leaf axil with 4 to 20 staminate flowers and one pistillate flower in the same axil. The yellow showy flowers are 2 to 5 inches across, with five free petals, five free stamens, and three stigmas. The flower opens in the early morning and is

open only 1 day. The pistillate flower has a long, tubular ovary. Singh (*1958*) reported that *L. cylindrica* was only monoecious but that other species of *Luffa* had four types of inflorescences: monoecious, andromonoecious, gynoecious, and hermaphroditic.

Pollination Requirements

Vegetable sponge flowers require the transfer of pollen from the staminate to the pistillate flowers during the 1 day a flower is open.

Pollinators

The vegetable sponge is not wind pollinated. It is pollinated by insects (Purseglove *1968**), principally bees.

The number of seeds in a mature fruit would indicate that numerous bee visits may be beneficial.

Pollination Recommendations and Practices

No recommendations on the need for or supplying of pollinators have been made; however, if the crop were grown on a large scale, the need of supplemental pollination to ensure adequate pollen transfer would doubtless be necessary.

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VERNONIA

Vernonia anthelmintica (L.) Willd., family Compositae

The seeds of vernonia are of current interest because they are the source of an oil containing vernolic acid (Higgins *1968*, Krewson et al. *1962*). Yield and related results have recently been obtained (Berry et al. *1970*, Lessman and Berry *1967*, Massey *1969*). However, not too much attention was given to the pollination requirements.

Later, through the use of flower color as a genetic marker, Berry and Lessman (*1969*) noted cross-pollination in open plots. Berry et al. (*1970*) reported 13 percent outcrossing and noted an abundance of bees. They considered the plant to be essentially self-pollinated.

If this crop is to come into commercial production, more careful and extended studies of its pollination requirement should be made.

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VETCH

Vicia spp., family Leguminosae

The various species and cultivars of the genus *Vicia* are grown for forage production, soil improvement, erosion control, and food for wildlife. The beans of some species are used as human food (Herman *1960*, McKee *1948*, McKee and Schoth *1934*, Schoth and Hyslop *1925*). Wheeler and Hill (*1957**) listed 10 species, Gunn (*1971*) listed 11 species, and Heywood and Ball (*1968*) listed seven species, as being the more important ones; however, the pollination requirements of some of these species are unknown. The species on which there is pollination information include the following:

Scientific name	*Common name*
V. angustifolia L.	Narrowleaf vetch
V. benghalensis L.	Purple vetch

Scientific name	*Common name*
V. dasycarpa Ten.	Woollypod vetch, or smooth vetch
V. pannonica Crantz	Hungarian vetch
V. sativa L.	Common vetch, or spring vetch
V. villosa Roth	Hairy vetch, woolly vetch, or winter vetch

Another important species (*V. faba* L.) is discussed under "Broad Beans and Field Beans."

The areas of production are primarily in the Pacific Northwest, Midwest, South, and Southwest. About a quarter of a million acres are devoted to vetch growing. The economic value is difficult to determine, but it doubtless runs into many millions of dollars.

Plant

The vetches are generally partly-viny to weak-stemmed with leaves that usually terminate in tendrils and stems that are 2 to 5 feet or more in length, depending on the species and the condition under which they are grown. They are among the best of the legumes in their ability to be productive in low fertility or acid soils. They are often seeded with grain, the stalks of which support the vetch vines. The common vetches are annuals, except for hairy vetch, which may be either annual or biennial. All of the common agricultural species are viny.

Inflorescence

The vetch inflorescence is usually a raceme that bears few to many solitary light-blue to dark-purple or lavender flowers. The flower, like that of most legumes, has the sexual column enclosed in the keel petal. If the column remains closed, only self-pollination can result (if the style and pollen are compatible). If the column is freed, or tripped, and the stigma comes in contact with pollen from other flowers, cross-pollination can occur. Some species benefit by tripping even if cross-pollination does not occur. Repeated visitation to the flower by pollinating insects also increases productiveness in some species. The flower must be tripped if bees are to collect pollen from it.

Nectar is usually secreted inside the corolla, sometimes on the outside of the base of the corolla. In many species, including at least *V. sativa*, *angustifolia*, and *pannonica*, nectar is also secreted in a nectary located on the leaf stipule (Knuth *1908*, p. 320*; Herman *1960*). Normally, when a bee visits the vetch flower for pollen or floral nectar, it settles on the wing petals, then forces its proboscis or "tongue" down the corolla. The pressure depresses the keel petal and forces the hairy style and pollen-laden anthers out. The pollen is thus shed onto the stigma, and some of it rubs off onto the bee, which then carries it to other flowers, resulting in cross-pollination. However, Weaver (*1956b*) stated that bees sometimes collect nectar from the side of the corolla without depressing the keel petal. Common and hairy vetches are an important source of excellent quality honey, and the production is usually sufficient for the storage of surplus quantities for the beekeeper. Hairy vetch is erratic, however, in its nectar production and attractiveness to pollinating insects (Alex et al. *1950*). Common vetch produces a thick stipular nectar, which is more attractive to the bees than the floral nectar (Scullen *1956**).

Hungarian vetch has the reputation of supplying nectar in larger quantities for a longer period than any other cultivated plant (Schoth *1923*).

Pollination Requirements

Not too much is known about the pollination requirements of the different species and cultivars of *Vicia*. McKee and Pieters (*1937*) stated that "so far as is known the vetches are close-pollinated, and seldom if ever does crossing take place." However, there is no longer doubt that seed production of some species is greatly increased with bees. Alex et al. (*1950*), Bieberdorf (*1952, 1954*), Coe (*1949*), Mlyniec (*1962*), Mlyniec and Wojtowski (*1962*), Pritsch (*1966*), von Schelhorn (*1942*), Scullen (*1956**), Thomas (*1950*), Weaver (*1954, 1956a, b, 1957*), and Wojtowski and Mlyniec (*1964*) have shown that production of hairy vetch (*V. villosa*) is greatly increased by bee visitation. Svetsugo and Kobayashi (*1952*) stated that fertilization of *V. villosa* is impossible when the plant is isolated from insects. Whether some of these workers considered the smooth-stemmed *V. dasycarpa* as a subspecies of *V. villosa* is not clear, but apparently the pollination requirements of the two are the same. Von Schelhorn (*1946*) concluded that Carniolian honey bees were superior to other bees in his area as pollinators of hairy vetch. Todd (*1957**) listed both hairy and purple vetch in the group of plants that produced more seed as a result of insect pollination. He also stated that the brush arrangement of the vetch tripping mechanism, required repeated insect visits for thorough pollination. He listed common Hungarian and narrowleaf vetches as largely selfed plants. Scullen (*1956**) stated that bees seldom visit Hungarian or the Willamette strain of common vetch, and that any pollination is probably done by bumble bees or other native bees. Scullen made no mention of the value of insect pollination or whether floral visitation might be increased with heavier bee populations than was used by beekeepers for honey production.

McKee and Schoth (*1925*) stated that common vetch is self-pollinated, however, Schoth (USDA *1942*) later submitted the following list of vetches as benefited by insect pollination: *V. villosa*, *V. benghalensis*, *V. pannonica*, and *V. sativa*. In the revised (USDA *1946*) edition, only *V. villosa* and *V. pannonica* were listed as benefited by bees.

Knuth (*1908*, p. 325*) stated that *V. sativa* anthers dehisce in the bud so that automatic self-pollination is inevitable. However, he noted that the flowers were visited by pollinating insects. Further, on the same page, he stated that the flower mechanism of *V. angustifolia* agrees with that of *V. sativa*, which would indicate that this species is capable of producing self-pollinated seeds. These flowers were visited by honey bees and other pollinating insects.

In summary, therefore, the data indicate that hairy vetch (*V. villosa*) is greatly benefited by insect polli-

nation, and that this probably applies equally to woollypod (smooth) vetch (*V. dasycarpa*). Purple, common, Hungarian, and narrowleaf vetches may be benefited by insect visitation either in increased seed production during the current year or the ability to produce at the maximum potential in future years, although the literature is scant in this area.

The pollination requirement of all of the species of vetch grown in the United States is badly in need of clarification. Like many other of our agricultural crops and cultivars, the problem offers an excellent opportunity for plant scientists to conduct experiments likely to yield data of considerable economic importance to our agriculture.

Pollinators

Honey bees are the primary pollinators of hairy and smooth vetch (fig. 192). This has been established quite positively by von Schelhorn (*1946*), Weaver (*1956a, b, 1957, 1965*), and others. There is little information on the floral visitors of other species. Scullen (*1956**) stated that hairy vetch was worked freely by bumble bees and that they assisted in its pollination. He also stated that any pollination of Hungarian vetch was probably done by bumble bees or other native bees, but they seldom visit the flowers of the 'Willamette' cv. of common vetch. Where large-scale production of vetch seed is practiced in the United States, honey bees are used as a commercial practice. Alex et al. (*1950*) observed that fields with no colonies of bees within 2 miles produced 410 pounds seed per acre and fields with 0.1 to 1.0 colonies per acre within a mile produced 713 lb/acre; whereas fields with 1.5 to 3.0 colonies per acre within one-half mile produced 1,277 lb/acre. From these and other observations, they concluded that the bee saturation point had not been determined for hairy vetch.

PN-3857

FIGURE 192.—Honey bee collecting nectar from vetch flowers.

Pollination Recommendations and Practices

There are few recommendations on the pollination of vetch. Alex et al. (*1951*) conservatively concluded that more than one colony of honey bees per acre increases hairy vetch seed production. Weaver (*1954*) stated that several colonies per acre were necessary for maximum pollination of hairy vetch but that the use of more than one colony per acre "might not be economical." Later, Weaver (*1956a*) estimated that one strong colony could provide adequate pollination for 3 to 5 acres.

The data indicate that, because repeated visits to individual flowers are desired and because the vetches are not always overly attractive to bees, a relatively heavy bee population on the crop is desired. Thus, the several colonies per acre previously mentioned seems to be a more realistic recommendation than the one colony per several acres.

Of particular interest were the results of Drayner (*1956*), which showed that on continued inbreeding the ability to set selfed seed was progressively lost, but on hybridization self-fertility was restored. This is an area of benefit from pollination that has been largely overlooked and illustrates the value of bee pollination to such crops as vetches, which are considered to be self-fertile and even self-fertilizing. The results showed that the use of pollinating insects would be profitable and should be recommended for such self-fertile crops as the vetches.

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WATERMELON (AND STOCKMELON, PIE MELON, OR CITRON MELON)

Citrullus lanatus (Thunb.) Mansf., family Cucurbitaceae

The watermelon is our largest edible fruit. When ripe, the sweet juicy pulp is eaten fresh, and the rind is sometimes preserved (Dupree et al. *1953*). The pulp of the relatively rare stockmelon, pie melon, or citron melon is used in pies. This melon, indistinguishable externally from the watermelon, can only be opened with great difficulty. It is inedible in the raw state.

Watermelons usually range in size from about 10 to 50 pounds, depending upon the cultivar and area where it is grown. Isolated growers in southwest Arkansas and northeast Texas specialize in jumbo sizes that weigh in excess of 100 pounds (Kennerly *1960*); one was produced near Hope, Ark., that weighed 195 pounds.

Watermelons are grown in almost every State, but roughly two-thirds of the 276,900 acres grown in 1969 were in four States: Texas (70,000), Florida (53,500), Georgia (37,500), and South Carolina (24,000 acres). The value of the 1969 crop was $54 million. Production per acre ranged from 3.35 tons in Texas to 7.8 tons in California.

In recent years, triploid or "seedless" and hybrid watermelons have been produced in limited quantities

(Kihara *1951*, Mohr et al. *1956*, Watts *1962*). They have not attained prominence, compared to regular open-pollinated watermelons.

Plant

The watermelon plant is a slender, sprawling, slightly hairy, monoecious annual. The stems or runners may extend 1½ to 5 yards. The deeply lobed leaves are 1 to 6 inches wide and 2 to 10 inches long, on 1- to 5-inch stems. The fruit varies according to the cultivar; the shape from oblong to round; the rind, from light green to dark green or mottled light and dark green; the flesh, from red to yellow, rarely to light green or white; the seeds, from white to yellow, brown, black or reddish black; and the shipping quality, from a tender easily broken or bruised skin to a firm and tough rind (Whitaker and Davis *1962**). Spivey (*1960*) listed three types of melons—regular, icebox, and seedless. Juice from the red part of a watermelon contains 8 to 10 percent solids, of which 20 to 50 percent is sucrose. An edible sirup can be made from the juice (Webster and Romshe *1951*).

The fruit and the vine are susceptible to frost. The plant is started from seed in rows about 6 feet apart, the plants 1 to 6 feet apart in the row. From one to four marketable melons are harvested per plant.

Because of the care necessary and the time consumed in harvesting the perishable ripe melons, vast acreages are seldom grown by individuals. Fields of 20 to 50 acres are most prevalent although fields of 200 to 300 acres are not rare.

Inflorescence

All cultivars of watermelons and citron melons bear staminate and pistillate flowers, except for a few that bear hermaphrodite flowers instead of pistillate ones (Rosa *1925*, Goff *1937*). The pale yellow to greenish flowers, about 1 inch in diameter, are much less conspicuous than those of several other genera of the family Cucurbitaceae. The flowers are borne singly in the axils, the pistillate or hermaphroditic one occurring in every seventh axil, the staminate ones occupying the intervening axils. The petals of the flower are united in a tiny tube, just as in the cucumber, and are deeply five-lobed, with three stamens around a short blunt style and a three-lobed stigma tightly crowded into the corolla tube. Nectar is secreted in the base of the corolla. All staminate and most of the pistillate flowers shed, and there does not seem to be a definite cycle to fruit setting. The fruit sets more or less irregularly throughout the season, or at least as long as the plants are growing vigorously.

The flowers open 1 to 2 hours after sunrise. The pistillate flower and the staminate flower just below it open the same day. The anthers have dehisced when the corolla expands, but the pollen remains on the anthers in sticky masses. The stigma is receptive throughout the day although most pollination takes place in the forenoon. In the afternoon, the flower closes never to reopen, whether pollination has or has not taken place (Jones and Rosa *1928**).

The flowers are attractive to bees for both the nectar and the pollen. The number of blossoms per square yard is never great compared to the blossoms of clover, alfalfa, and most fruit.

Pollination Requirements

Watermelon pollen is not windblown (Porter *1931*). The flowers are almost exclusively insect pollinated. There is no self-sterility so far as the plant is concerned. Pollination is equally effective if the pollen is brought from the adjacent staminate flower on the same branch or from another plant. At least 1,000 grains must be evenly deposited on the three lobes of the stigma if a uniform melon is to result (Adlerz *1966*). The watermelon style has no stylar canal, but most pollen grains grow directly downward from their point of deposit. Mann (*1943*) found that 21 to 22 percent of the pollen tubes show some lateral movement, but if an insufficient amount of pollen is deposited on one lobe of the stigma, an asymmetrical melon results. It may be lopsided or it may be smaller on one end than the other. Watermelons are severely graded according to symmetry.

Adlerz (*1966*) studied the relationship between time of day and set of flowers visited by six or more bees or pollinated by hand. He (and Parris *1949*) found that the highest percentage of fruit set resulted from deposition of pollen on the stigma between 9 and 10 a.m. Porter (*1933*) and Poole and Porter (*1933*) concluded that fertilization after hand pollination was most likely between 7 and 11 a.m. The morning activity of the bees is of greatest concern in watermelon pollination. Goff (*1937*) reported that bees, in Florida melon fields, reached their greatest abundance around 8:30 to 9 a.m.

Adlerz (*1966*) also studied the relationship between fruit set and length of the ovary at time of pollination. He found that the longer the ovary the better the chance that a fruit would set. Only 22 percent of 103 ovaries 20 mm or less in length set fruit, whereas 67 percent of those over 28 mm set fruit. Cunningham (*1939*) concluded that both the physiological condition of the plant and the number of fruit already set on it seem to determine the number of pistillate flowers that set later. Hibbard (*1939*) showed the value of thinning by stating that most growers fail to harvest one melon per plant. Also, the presence of a cull will inhibit setting of normal fruit for several weeks. It therefore appears that number of bee visitors (eight or more), time of bee visits (6 to 10 a.m.), length of ovary at time of pollination (28 mm or longer), plant vigor, and number of melons already set on the vine, all contribute to the greatest percentage of fruit set.

Pollinators

The recognition of the need for insect pollination of watermelons is not new. Newell (*1903*) quoted the following statement made by P. J. Berckmans in August 1877, "Our watermelon growers would find their occupation gone if honey bees and other (pollinating) insects were out of existence."

Porter (*1933*) concluded that watermelon pollination is almost entirely by insects. Goff (*1937*, *1947*) collected different species of bees, *Apis mellifera* L., *Halictus*

spp. *Augochlorella gratiosa* Smith, *Agapostemon splendens* Lepeletier, and *Augochloropsis caerulea* Ashmead (listed in the order of their abundance) and concluded that the honey bee was by far the most abundant. Rosa (*1925*) and Jones and Rosa (*1928**) concluded that pollination was chiefly by bees. Purseglove (*1968**) stated that the watermelon is pollinated by insects, particularly honey bees. Brewer (*1974*) also concluded that honey bees were adequate, but he believed that increasing the bee population did not improve melon weight or seed yield. Adlerz (1966) showed that honey bees are highly effective as pollinators if they are sufficiently abundant in the field. Smith (*1933*) concluded that the lack of sufficient honey bees to pollinate early watermelon blooms in the Big Bend area of Oklahoma cost the growers in that district thousands of dollars annually.

Honey bee visits to melon flowers are primarily in the morning from 1 to 2 hours after sunrise when the flower first opens. Visitation continues until about midafternoon, depending on temperature and other weather conditions. The peak period of activity is usually midmorning. The bees visit the flowers for both nectar and pollen, but because of the scarcity of blooms they never store surplus amounts of either. Adlerz (*1966*) recorded the average time that honey bees spend on melon flowers: 5.7 seconds per female flower in 1959, and 8.0 seconds per female and 5.7 per male flower in 1960. He considered duration of the visit relatively unimportant as the bee seemed to move about but little after it began to collect the food from the flower. This type of visitation indicates that the honey bee is obtaining a substantial amount of food from one blossom. For most efficient pollination, the bee should be forced to "shop around" among numerous flowers to obtain its load of food.

The effect of number of visits to the flower is of great importance to production of the mature melon. Adlerz (*1966*) learned that fruit set and yield after eight or more bee visits to the flower was superior to four or fewer visits. Only two of 64 flowers receiving one bee visit and one of 72 receiving two bee visits developed fruit and these fruits were small, badly shaped, and unmarketable. No melons set on flowers caged to exclude bees. Fruit set after eight bee visits was significantly better than after two or four visits. He considered eight visits to be the minimum for adequate pollination. Because bees do not uniformly visit all flowers, many flowers will receive more than eight visits if all are to receive this number.

Adlerz (*1966*) concluded that distribution of pollen over the stigmatic surface depended more upon multiple visits than upon length of visits or movement of the bee on the flower. Mann (*1943*) showed that if adequate amounts of pollen are not deposited on every stigma lobe, the melon will be misshapen—the most common reason for rejecting melons from the number one or highest priced category.

Pollination Recommendations and Practices

Peto (*1951*) reported that one to five hives of honey bees were used per acre on cucumbers, cantaloupes, and watermelons grown for seed in relatively small fields. Wadlow (*1970*) used one colony per five acres of watermelons, the colonies placed in small groups in the field. Breece (*1962*) recommended one colony per acre, the bees on at least two sides of a 40-acre field. Adlerz (*1966*) made his studies in fields with one colony per acre and concluded that he had more visitors than necessary to provide eight visits per flower. Eckert (*1959**) stated that one colony for each 2 acres may be enough. The Arizona Agricultural Experiment Station and Cooperative Extension Service (*1970*) recommended a bee population that will provide one bee for each 100 flowers in all parts of the field. This recommendation seems to be the best considering the influence of various environmental factors on bee activity.

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WELSH, JAPANESE, OR SPRING ONION

Allium fistulosum L., family Amaryllidaceae

The Welsh, Japanese, or spring onion (see "Onion") is rarely grown in the United States, although it is of some importance in England and continental Europe. Its leaves are used in seasoning foods (Anonymous *1955*).

Plant

The cylindrical hollow leaves are larger than those of the onion and have enlarged midareas, but the flowering stalk is short, 12 to 20 inches long, and thick. The bulbous base is little thicker than the stem (Bailey *1949**). Propagation is by seeds or division of the plant. It is a perennial that forms seed stems the second year and each year thereafter. Seed yields usually range from 700 to 1,000 lb/acre (Hawthorn and Pollard *1954**).

Inflorescence

Similar to onion, except that the flowers begin opening at the apex.

Pollination Requirements

Similar to onion.

Pollinators

Probably similar to those attracted to onions.

Pollination Recommendations and Practices

None.

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WHITE CLOVER[55]

Trifolium repens L., family Leguminosae

White clover consists of three general types—large, primarily 'Ladino'; intermediate; and small.

About 16,000 acres were devoted to production of 'Ladino' clover seed in California in 1969. Production of seed of the intermediate and small types came from about 10,000 acres, 4,000 acres of which were in Louisiana, and the remainder in Idaho and Oregon. 'Ladino' seed production was 305 lb/acre; intermediate and small types, 105 lb/acre in Louisiana; and 300 lb/acre in the Idaho-Oregon area (Henderson et al. *1969*). California and Oregon are the leading States in production of 'Ladino' clover seed; Idaho leads in production of the other types.

Plant

White clover is a low-growing, shallow-rooted legume that spreads by creeping stems that root at the nodes (fig. 193). By the end of the second year, the runners of a single plant have formed a dense mat 2 to 3 ft^2 with a height of 3 to 24 inches depending upon types and

[55] See "Clovers, General."

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FIGURE 193.—Individual 'Ladino' clover plant in bloom.

cultivars (Eby *1941*). White clover is a short-lived perennial in the Northern States, but in the South it is often used as a winter annual (Wheeler *1950*). The crop may be seeded with grasses, but sometimes a pure stand is maintained. It is usually grazed by livestock until the grower is ready for a seed crop to be produced.

Inflorescence

The globose, white flower head consists of 50 to 250 (average of 100) florets. Each floret may produce seven but averages about 2.5 seeds (Dunavan *1952*, *1953*, Dessureaux *1950*, Green *1957*, Vansell *1951*). When a high number of ovules is present, high seed setting results if pollination is adequate (Dessureaux *1951*). About 10 florets open daily on a head.

Within the floret, nectar is secreted on the inner side of the base of the staminal tube. The calyx is only 3 mm long so the nectar is easily reached by most nectar-collecting bees. The wing petals are fused with the keel on either side so that both move simultaneously when the keel petal is depressed by a bee visit. This pressure is sufficient to expose the staminal tube, and it touches the underside of the bee. After the bee departs, the staminal tube returns to its original position. When the bee goes to the next flower, the pollen is transferred to its stigma and crossing results. The stigma extends beyond the anthers so selfing is not possible (Knuth *1908*, pp. 284–298*).

The intermediate and small types of white clover constitute probably the most important honey producing crop in the United States, and provide also a good source of pollen for the bees. Vansell (*1951*) and others have indicated that 'Ladino' clover is a poor nectar source and that most of the bee visitors to 'Ladino' flowers were collecting pollen. Oertel (*1961*) reported that on 'Louisiana' white clover some bees were collecting nectar, some were collecting pollen, and others collecting both. Johnson and Wear (*1967*) stated that boron caused an increase in the number of seeds of white clover per head. Possible reasons suggested for this increase included increased bee activity and increased number of flowers. Smith and Johnson (*1969*) observed no increased bee visitation to treated plants in bloom but concluded that boron is necessary for nectar production, which indirectly influences pollination and subsequent seed production.

Pollination Requirements

Since Darwin's (*1889**) original experiment, various workers have shown that white clover is largely to completely self-incompatible. Hollowell (*1936*) pointed out that this means that pollen must be transported from plant to plant rather than between florets on a plant; thus, the yield of seed depends on the number of flowers and the cross-pollination between plants. Dunavan (*1952*, *1953*) obtained less than three seeds per head in cages where bees were excluded, but 90 seeds with bees present. Williams (*1931*) obtained 5.8 seeds per head from selfed plants. Palmer-Jones et al. (*1962*) got no seed set in cages that excluded bees. Weaver (*1957a*) harvested 12 lb/acre in cages with bees excluded and 82 lb/acre with bees present. Vansell (*1951*) likewise obtained no seeds from bagged 'Ladino' clover heads, but open heads visited by bees produced an average of 247.6 seeds each. Most of the pods contained 2 or 3 seeds. Martin (*1930*), Erith (*1924*), and Williams (*1931*) noted that self-pollination rarely takes place. Atwood (*1941a*, *1942*) found that self-compatibility varied with plants. Atwood (*1941b*) associated this variation with cytological interference zones on the stigma and in the style.

Vansell (*1951*) stated that no 'Ladino' florets opened before 9:30 a.m. and few before 11 a.m. The length of time that florets are capable of being pollinated after they open has not been determined, although Wheeler and Hill (*1957**) stated that the floret should be tripped the day it opens.

Florets that are not visited by bees will stay open and fresh looking for a week or longer, but when they are pollinated they wilt within a few hours (Weaver *1957a*, *b*). The grower can determine the degree of white clover pollination by examining the flower head. When pollination is progressing satisfactorily, the head will have wilted florets at the base, buds toward the apex, and no more than a dozen fresh open florets in between.

Pollinators

The honey bee is the most important pollinator of white clover. The plant is highly attractive to bees ('Ladino' much less so than the intermediate or small types), and bees are likely to be found visiting the flowers to some extent wherever the plants are grown (Atwood *1943*).

Bohart (*1960**) stated that wild bees are apparently a negligible factor in white clover pollination under commercial conditions; nevertheless, *Osmia*, *Halictus*, *Tetralonia* [*Synhalonia*], and *Bombus* are especially fond of white clover blossoms. He stated: "It is probable that there is no shortage of wild pollinators in small seed fields adjacent to good territory for wild bees." Pedersen et al. (*1961*) stated that bumble bees and many other wild bees were useful.

Honey bees can be moved to white clover fields when desired in whatever numbers desired for pollination (fig. 194). This permits greater dependability than is permitted with wild bees.

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FIGURE 194.—One of several rows of honey bee colonies distributed uniformly across a 'Ladino' clover seed field.

Pollination Recommendations and Practices

Harrison et al. (*1945*) recommended that white clover seed fields should not be more than 2 miles from a beeyard and preferably less than 1 mile. Lancaster (*1949*) recommended one colony per acre of clover within 1.5 miles. Green (*1956, 1957*) indicated that one colony per 15 to 20 acres was sufficient. Forster (*1966*) stated that clover within about a mile of a concentration of one colony per 8 acres received ample visits. Weaver (*1957a*) concluded that under ideal conditions one strong colony should be able to visit all the blossoms open on any day on slightly more than 3 acres of the best stand of clover. Hollowell (personal commun., 1971) stated that these recommendations were far too low. Hollowell (*1936*) recommended colonies of honey bees in the immediate vicinity of clover-seed producing fields, but later (*1942*) recommended that colonies be adjacent to the fields.

Oertel (*1943*) first recommended one or two colonies per acre, then later (*1954*) recommended not less than one strong colony per acre, but still later (*1961*) he considered one colony per 3 acres if there was no plant competition for the bees. Paddock (*1946*) concluded that for every 10 acres, five to ten colonies should be provided. Owen (*1953*), Lyle (*1944*), and Eckert (*1959**), recommended one colony per acre. They defined a strong colony as one having not less than seven combs of brood and enough bees to cover at least 15 frames in a two-story hive. Wheeler and Hill (*1957**), Osterli and Miller (*1951*), and Miller et al. (*1952*) recommended one to one and a half colonies per acre. Pedersen et al. (*1961*) recommended one or two strong colonies per acre. Scullen (*1956**) stated that one colony per acre will supply about one bee per square yard but that two bees per square yard were needed, and, if there were more than 127 blooms per square yard, even more bees were needed. Smith (*1953*) recommended two to three colonies per acre. Smith et al. (*1971*) recommended one colony per acre. Bohart (*1960**) concluded, "The question of the number of colonies per acre (or bees per square yard) for maximum white clover seed production has not been resolved, in spite of the fact that nectar and pollen collectors are apparently about equal in pollinating efficiency, and competition of other plants is not as severe as with many crops."

The best criteria for adequate pollination is either the appearance of the crop or the activity of the bees on it. Weaver's (*1957b*) statement that flower heads with a band of withered florets around the base, a band of buds at the top, with a narrow band of open florets in between, affords a satisfactory guide, as does the need expressed by Scullen (*1956**) for two or more bees per square yard of flowers. The number of colonies required to provide this population could conceivably vary with every field. The flower evaluation method can be made at any time of day. Bee counts must be made when weather conditions permit bees to fly.

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WHITE-FLOWERED GOURD, CUCUZZI, OR CALABASH GOURD

Lagenaria siceraria (Mol.) Standl., family Cucurbitaceae

The white-flowered or calabash gourd is known as a "camp follower" as well as a cultivated plant. No figures are available on the volume or value of its production, which doubtless is not great. The fruit is produced for its use as an ornamental, a musical instrument, a float to support fish nets, and in primitive areas as a cooking utensil. The young tender leaves and the dry seed are sometimes used as food (Whitaker and Davis *1962**, Pathak and Singh *1950*).

The plant is usually cultivated individually or as only a few plants in an area near dwellings, except on seed supply farms where the seeds are produced for sale. The vine is held up by strong supports so that the fruit may be suspended above ground. In India, each plant yields 10 to 15 fruits weighing 1 to 3 pounds each. The seed kernels contain about 45 percent oil (Purseglove *1968**).

Plant

The white-flowered gourd plant is a half-hardy, vigorous, annual, strongly running or climbing vine to 30 feet in length with kidney-shaped, softly pubescent leaves 6 to 12 inches across. The fruits vary in length from 3 inches to 6 feet, from a few ounces to several pounds, and from oval to cylindrical, pyriform, and club- or egg-shaped. At maturity, the skin is hard and smooth, and green, greenish white, tan, striped, or mottled. The variation in size and shape of the fruit distinguishes plants, but this alone does not provide cultivar status. There are various cultivars (Purseglove *1968**), known in the trade as 'Flat', 'Bottle', 'Dipper', 'Spoon', 'Pipe', 'Powder', 'Kettle', and 'Birdsnest'.

Inflorescence

The flowers of the white-flowered gourd are mono-

ecious and produce singly in the leaf axis (fig. 195). They are funnel- or bell-shaped with a long corolla tube, and they have a musklike odor, typical of many nocturnal, bat-visited flowers. The staminate flowers are borne on a very long peduncle that rises above the foliage. The pistillate flowers have a short peduncle and a hairy ovary. The blossom persists much longer than that of *Cucurbita*.

The flowers open during the night and remain open until the next afternoon. The nectar is not easily accessible. Pollination probably takes place at or shortly after dawn if pollinators are available.

Pollination Requirements

The flowers, being monoecious, cannot be self-pollinated. The pollen must be transferred from the staminate to the pistillate flower by an outside agent. Shah and Patel (*1966*) obtained a higher percentage of fruit set with hand pollination than was obtained in the open, indicating an insufficiency of pollinating agents in the area.

Pollinators

Concerning the pollination of white-flowered gourd, Pammel and King (*1930* p. 862*) stated, "Since the flowers are monoecious it is absolutely necessary that the pollen be conveyed by insects, and probably in most cases cross-fertilization results, because the pollen may come from another plant." Knuth (*1908* p. 454*) and Purseglove (*1968**) gave primary credit to bees. Knuth also noted that the flowers appear to be visited by crepuscular (twilight or dawn) insects. He stated that the flowers are adapted to hummingbirds and smaller bees, although a species of bumble bee was observed visiting the flowers. Considering the flower odor and the fact that it is open during the night, nectar-collecting bats probably also contribute to its pollination.

Pollination Recommendations and Practices

No recommendations on the use of insect pollinators on white-flowered gourds have been made, but the indications are plain that if a sizeable volume of fruit of this plant were desired the concentration of bees nearby would be worthwhile.

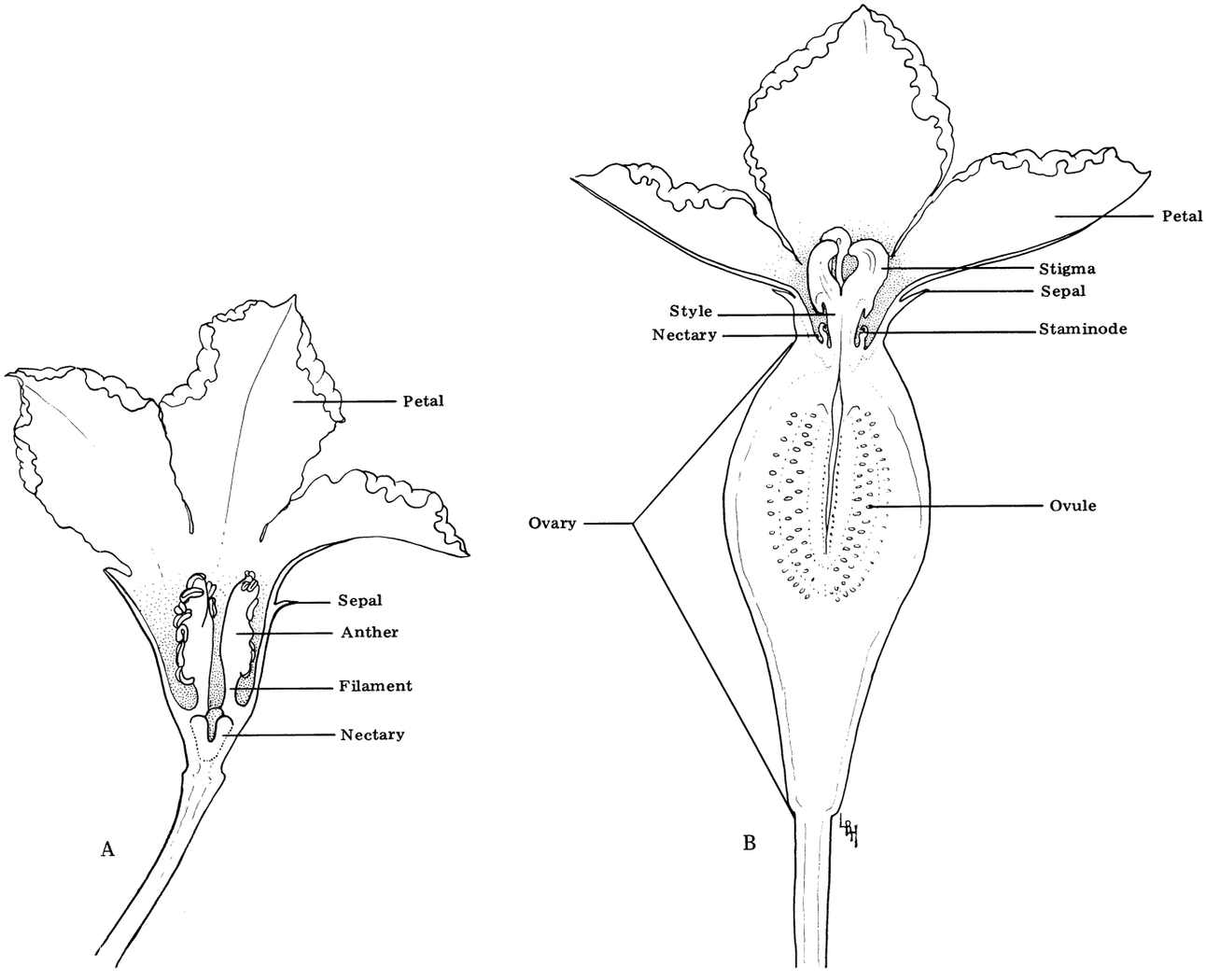

FIGURE 195.—Longitudinal section of flowers of white-flowered gourd, ×2. *A*, Male; *B*, female.

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WHITE GOURD, CHINESE PRESERVING MELON, OR CASSABANA

Benincasa hispida (Thunb.) Cogn., family Cucurbitaceae

This plant provides a staple Chinese food common in San Francisco markets and to some extent in southern Florida. The fruit may be eaten raw, similar to cucumbers, or cooked. It is bland and filling, but is not high in calories, being more of a food extender.

Plant

The white gourd is a long running vine with brown hairy stems and broad leaves, 6 to 10 inches across. It produces a nearly spherical to oblong, 10- to 16-inch fruit, somewhat like a watermelon (Bailey *1949**). The rind is not durable, but the fruit may keep 12 months.

Inflorescence

The plant is monoecious, the flowers being 3 to 4 inches across, yellow, and showy. The staminate flowers have long peduncles, the pistillate ones are short stalked or almost sessile; the three stigmas lead to many ovules. Flowers constantly form which permits constant refruiting.

Pollinators

Apparently, this plant is insect pollinated, but the pollinating agents are unknown.

Pollination Recommendations and Practices

None.

WHITE SAPOTE

Casimiroa edulis Llan. & Lex., family Rutaceae

Hoffman (*1970*) reported that although white sapote is a tropical plant it is becoming popular in the mild areas of California and Florida. Mowry et al. (*1967**) stated that it was growing in scattered locations in these two States. Mortenson and Bullard (*1968**) pointed out that this plant is not a true "sapote", which is in the family Sapotaceae, but a relative of the citrus. According to Mowry et al. (*1967**), it is more common than any other plant known as sapote. (Also see, "Mamey Sapote," p. 253.)

Plant

White sapote is a medium to large, erect to spreading, evergreen tree, with leaves 3 by 6 inches in size. It produces ovoid fruit up to 3 inches in diameter, with a greenish skin that becomes yellow at maturity. The creamy or yellowish juicy fruit, rich in vitamin C, has a distinctive sweet aroma. Each fruit has one to five large ovoid seeds imbedded in the flesh. The fruit is eaten out of hand or as a fruit dessert with cream and sugar (Mortensen and Bullard *1968**).

Inflorescence

The small (5 mm), whitish-green flowers are produced in great numbers along the branchlets, but few ever produce mature fruit (fig. 196). Abundant nectar is produced from these flowers in southern Mexico, primarily in January and February (Ryerson *1925*, Wulfrath and Speck *no date*).

The individual flower has five pale-green, strongly reflexed petals with five short, stout, slightly reflexed stamens. Each stamen arises between two petals. The position of the petals and anthers leaves the globose green ovary exposed. The stigma is sessile, resting directly on the ovary, and leads directly to five ovules, which normally form the one to five seeds in the fruit. Nectar is secreted on the base of the petals next to the ovary.

Pollination Requirements

Mature fruits are sometimes irregular in shape from lack of seed development in one or more carpels, and heavy shed of immature fruit has been reported (Kennard and Winters *1960**). Although the flowers are hermaphrodite, Mustard (*1954*) showed that there is partial to total pollen sterility within the flower. He concluded that this factor was responsible for failure to set a good crop of fruit. Mortensen and Bullard (*1968**) stated that in Florida the 'Dade' cv. must be cross-pollinated because it does not have "normal" pollen. Mustard (*1954*) reported that partial pollen sterility may be a factor in failure to obtain good sets of fruit.

Pollinators

The honey bees in visiting the flowers for nectar

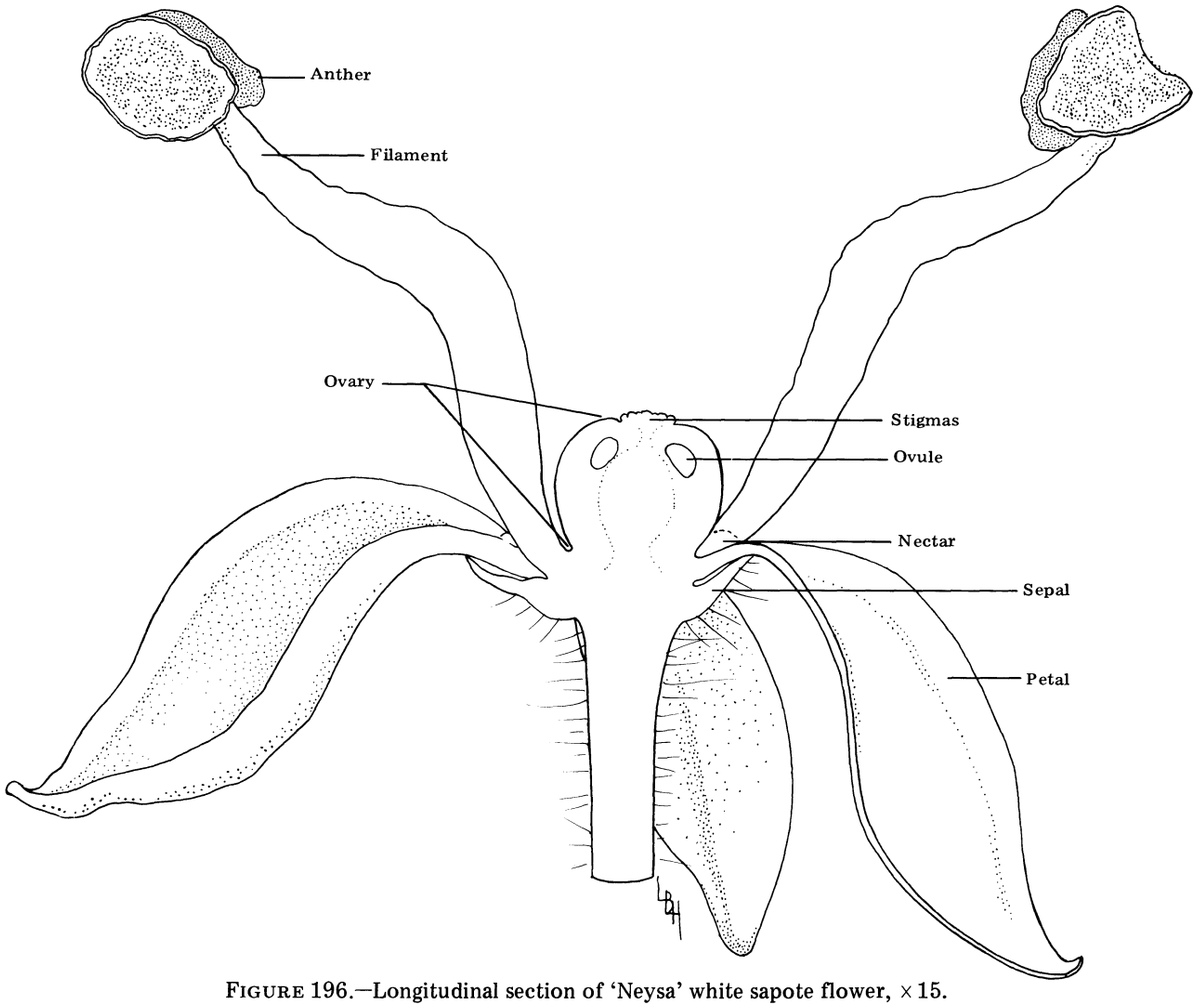

FIGURE 196.—Longitudinal section of 'Neysa' white sapote flower, × 15.

doubtless serve as pollinators of the plants, particularly if they are sufficiently concentrated in the area of the trees.

Pollination Recommendations and Practices

None.

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ZIGZAG CLOVER[56]

Trifolium medium L., family Leguminosae

Zigzag clover is of little or no economic importance in the United States. Wheeler and Hill (*1957**) stated that if seed were available it might become one of our good pasture legumes for our moist cool climates. It grows primarily as an escape plant in infertile soil or waste places in northeastern United States.

Plant

Zigzag clover is a stout perennial up to 18 inches tall with stems that grow in zigzag fashion, hence the name.

[56] See "Clovers, General."

It spreads by seeds and by rhizomes on underground stems.

Inflorescence

The flower head and flower mechanism are similar to red clover, but the flowers are of a brighter, deep red-purple. Nectar secretion is about the same as in red clover (Robertson and Armstrong *1964*). The heads average about 37 florets and set 14 to 21 seeds per head if properly pollinated. The floret has two ovules but produces only one seed.

Pollination Requirements

Robertson and Armstrong (*1964*) believed that the long corolla tube precluded pollination by honey bees, but that bumble bees were most important, with seed setting directly proportional to the frequency of bumble bee visits. Townsend (*1967*) made detailed studies in Colorado on the self- and cross-incompatibility of this crop. He bagged heads to exclude pollinators and found that of 42 noninbred bagged plants tested all were highly self-incompatible, 36 did not set a single seed under selfing, and the seed set for the remaining six ranged from only 0.25 to 1.25 seeds per head versus 14 to 21 in open-pollinated heads. He believed that the poor seed production of zigzag clover may be due to preference of pollinators for other plants. Keim (*1957*) compared production of plants caged with honey bees with open plots near honey bee colonies and concluded that differences in seed set of various clones were due to genetic differences and to bee preference.

Pollinators

Knuth (*1908*, p. 293*) reported that honey bees as well as *Andrena*, *Bombus*, *Colletes*, *Halictus*, *Megachile*, and *Psithyrus* bees, visited the flowers. Robertson and Armstrong (*1964*) recorded 97 percent bumble bee, 2 percent honey bee, and 1 percent other bee visitors. Keim (*1957*) considered honey bees quite important.

Pollination Recommendations and Practices

None.

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APPENDIX

CONVERSION TABLES OF WEIGHTS, MEASURES, AND TEMPERATURES [1]

Length

Myriameter	10,000 meters	6.2137 miles.	Meter	1 meter	39.37 inches.
Kilometer	1,000 meters	0.62137 mile.	Decimeter	0.1 meter	3.937 inches.
Hectometer	100 meters	328 feet 1 inch.	Centimeter	0.01 meter	0.3937 inch.
Dekameter	10 meters	393.7 inches.	Millimeter	0.001 meter	0.0394 inch.

Area

Hectare	10,000 square meters	2.471 acres.
Are	100 square meters	119.6 square yards.
Centiare	1 square meter	1,550 square inches.

Weight

Name	Number of grams	Volume corresponding to weight	Avoirdupois weight
Metric ton, millier or tonneau	1,000,000	1 cubic meter	2,204.6 pounds.
Quintal	100,000	1 hectoliter	220.46 pounds.
Myriagram	10,000	1 dekaliter	22.046 pounds.
Kilogram or kilo	1,000	1 liter	2.2046 pounds.
Hectogram	100	1 deciliter	3.5274 ounces.
Dekagram	10	10 cubic centimeters	0.3527 ounce.
Gram	1	1 cubic centimeter	15.432 grains.
Decigram	.1	0.1 cubic centimeter	1.5432 grains.
Centigram	.01	10 cubic millimeters	0.1543 grain.
Milligram	.001	1 cubic millimeter	0.0514 grain.

Capacity

Name	Number of liters	Metric cubic measure	United States measure	British measure
Kiloliter or stere	1,000	1 cubic meter	1.308 cubic yards	1.308 cubic yards.
Hectoliter	100	0.1 cubic meter	2.838 bushels; 26.417 gallons.	2.75 bushels; 22.00 gallons.
Dekaliter	10	10 cubic decimeters	1.135 pecks; 2.6417 gallons.	8.80 quarts; 2.200 gallons.
Liter	1	1 cubic decimeter	0.908 dry quart; 1.0567 liquid quarts.	0.880 quart.
Deciliter	.1	0.1 cubic decimeter.	6.1023 cubic inches; 0.845 gill.	0.704 gill.
Centiliter	.01	10 cubic centimeters.	0.6102 cubic inch; 0.338 fluid ounce.	0.352 fluid ounce.
Milliliter	.001	1 cubic centimeter	0.061 cubic inch; 0.271 fluid dram.	0.284 fluid dram.

Common Measures and Their Metric Equivalents

Common measure	Equivalent	Common measure	Equivalent
Inch	2.54 centimeters.	Dry quart, United States	1.101 liters.
Foot	0.3048 meter.	Quart, imperial	1.136 liters.
Yard	0.9144 meter.		

[1] Source: U.S. GOVERNMENT PRINTING OFFICE. STYLE MANUAL. 548 pp. Washington, D.C. 1973.

Common Measures and Their Metric Equivalents — Continued

Common measure	Equivalent	Common measure	Equivalent
Rod	5.029 meters.	Gallon, United States	3.785 liters.
Mile	1.6093 kilometers.	Gallon, imperial	4.546 liters.
Square inch	6.452 square centimeters.	Peck, United States	8.810 liters.
Square foot	0.0929 square meter.	Peck, imperial	9.092 liters.
Square yard	0.836 square meter.	Bushel, United States	35.24 liters.
Square rod	25.29 square meters.	Bushel, imperial	36.37 liters.
Acre	0.4047 hectare.	Ounce, avoirdupois	28.35 grams.
Square mile	259 hectares.	Pound, avoirdupois	0.4536 kilogram.
Cubic inch	16.39 cubic centimeters.	Ton, long	1.0160 metric tons.
Cubic foot	0.0283 cubic meter.	Ton, short	0.9072 metric ton.
Cubic yard	0.7646 cubic meter.	Grain	0.0618 gram.
Cord	3.625 steres.	Ounce, troy	31.103 grams.
Liquid quart, United States	0.9463 liter.	Pound, troy	0.3732 kilogram.

Temperature

0° Celsius (= Centigrade) = 32° Fahrenheit
Fahrenheit (F) to Celsius (C) $C = \frac{5}{9}(F - 32)$
Celsius to Fahrenheit $F = (\frac{9}{5}C) + 32$

SCIENTIFIC AND COMMON NAMES OF PLANTS MENTIONED IN TEXT, ARRANGED ALPHABETICALLY BY FAMILY, GENUS, AND SPECIES

Scientific name	*Common name*
ACTINIDIACEAE	
Actinidia chinensis Planch.	Chinese gooseberry.
AGAVACEAE	
Agave fourcroydes Lem.	Henequen.
A. parryi Engelm.	Parry agave.
A. sisilana Perr. ex Engelm.	Sisal.
Yucca spp.	Yucca.
AMARYLLIDACEAE	
Allium ascalonicum L.	Shallot.
A. cepa L.	Onion.
A. fistulosum L.	Welsh, Japanese, or spring onion.
A. porrum L.	Leek.
A. sativum L.	Garlic.
A. schoenoprasum L.	Chives.
ANACARDIACEAE	
Anacardium occidentale L.	Cashew.
Mangifera indica L.	Mango.
ANNONACEAE	
Annona cherimola Mill.	Cherimoya.
A. diversifolia Saff.	Llana.
A. montana Macf.	Mountain soursop.
A. muricata L.	Soursop or guanabana.
A. reticulata L.	Custard apple or Bullock's heart.
A. squamosa L.	Sugarapple or sweetsop.
Asimina triloba (L.) Dunal	Papaw.
Cymbopetalum odoratissimum Rodr.	([1])
APOCYNACEAE	
Vinca rosea L.	Periwinkle.
AQUIFOLIACEAE	
Ilex aquifolium L.	English holly.
I. opaca Ait.	American holly.
ARACEAE	
Philodendron pinnatifidum (Jacq.) Kunth	Philodendron.
Zantedeschia spp.	Calla.
ASCLEPIADACEAE	
Asclepias fruticosa L.	Milkweed.
BIGNONIACEAE	
Catalpa spp.	Catalpa.
BOMBACACEAE	
Bombacopsis spp.	([1])
BORAGINACEAE	
Myosotis sylvatica Hoffm.	Forget-me-not.
CACTACEAE	
Carnegiea gigantea (Engelm.) Britt. and Rose	Saguaro.
Echinocactus wislizenii Engelm.	Barrel cactus.
Lemaireocereus thurberi (Engelm.) Britt. and Rose	Organpipe cactus.
CAMPANULACEAE	
Campanula carpatica Jacq.	Tussock bellflower.
CARICACEAE	
Carica papaya L.	Papaya.
CARYOPHYLLACEAE	
Dianthus caryophyllus L.	Carnation.
CHENOPODIACEAE	
Beta vulgaris L.	Beet.
COMMELINACEAE	
Tradescantia spp.	Spiderwort.
COMPOSITAE	
Carthamus tinctorius L.	Safflower.
Chrysanthemum cinerariifolium (Trevir.) Vis.	Pyrethrum.
Cichorium endivia L.	Endive.
C. intybus L.	Chicory.
Cynara cardunculus L.	Cardoon.
C. scolymus L.	Artichoke.
Guizotia abyssinica (L.f.) Cass.	Niger.
Helianthus annuus L.	Sunflower.
Lactuca sativa L.	Lettuce.
Tagetes spp.	Marigold.
Taraxacum officinale Weber	Dandelion.

SCIENTIFIC AND COMMON NAMES OF PLANTS MENTIONED IN TEXT, ARRANGED ALPHABETICALLY BY FAMILY, GENUS, AND SPECIES — CONTINUED

Scientific name	*Common name*
COMPOSITAE — Continued	
Vernonia anthelmintica (L.) Willd.	Vernonia.
CRUCIFERAE	
Brassica spp.	
B. alba (L.) Rabenh.	Mustard.
B. campestris L.	Rape.
B. carinata A. Br.	Abyssinian mustard.
B. chinensis L.	Pak choi or Chinese cabbage.
B. fimbriata DC.	Curled kitchen kale.
B. hirta Moench	Mustard.
B. juncea Coss.	Mustard.
B. napobrassica Mill.	Rutabaga.
B. napus L.	Rape.
B. narinosa Bailey	Broadbeaked mustard.
B. nigra (L.) Koch	Black mustard.
B. oleracea L.	Cole crops.
B. o. var. *acephala* DC. sub. var. *laciniata* L.	Curly kale.
B. o. var. *a.* sub. var. *medullosa* Thell.	Marrow-stem kale.
B. o. var. *a.* sub. var. *millecapitata* (Lev.) Thell.	Thousand-head kale.
B. o. var. *a.* sub. var. *palmifolia* DC.	Tree kale.
B. o. var. *a.* sub. var. *plana* Peterm.	Smooth-leaf kale.
B. o. var. *botrytis* L. sub. var. *cauliflora* DC.	Cauliflower.
B. o. var. *b.* sub. var. *cymosa* Lam.	Sprouting (Italian) broccoli.
Brassica o. var. *capitata* L. f. *alba* DC. f. *rubra* (L.) Thell.	White cabbage, red cabbage.
B. o. var. *gemmifera* DC.	Brussels sprout.
B. o. var. *gongylodes* L.	Kohlrabi.
B. o. var. *sabauda* L.	Savoy cabbage.
B. parachinensis Bailey	Mock pak choi.
B. pekinensis (Lour.) Rupr.	Pe-tsai.
B. perviridis Bailey	Tendergreen or spinach mustard.
B. rapa L.	Turnip.
B. ruvo Bailey	Ruvo kale.
B. septiceps Bailey	Seven-top or Italian kale.
Iberis umbellata L.	Candytuft.
Matthiola spp.	Stock.
Raphanus sativus L.	Radish.
CUCURBITACEAE	
Benincasa hispida (Thunb.) Cogn.	White gourd, Chinese preserving melon, or cassabana.
Citrullus lanatus (Thunb.) Mansf.	Watermelon.
Cucumis anguria L.	Gherkin.
C. melo L.	Muskmelon.
C. sativus L.	Cucumber.
Cucurbita maxima Duch.	Pumpkin or squash.
C. mixta Pang.	Pumpkin or squash.
C. moschata Duch. ex Poir.	Pumpkin or squash.
C. pepo L.	Pumpkin or squash.
Lagenaria siceraria (Mol.) Standl.	White flowered or calabash gourd.
Luffa cylindrica (L.) Roem.	Vegetable sponge.
Mormordica charantia L.	Balsam-pear, bitter cucumber, or peria.
Sechium edule (Jacq.) Swartz	Chayote.
CYPERACEAE	
Dichromena ciliata Vahl	Sedge.
EBENACEAE	
Diospyros kaki L. f.	Kaki or oriental persimmon.
D. texana Scheele	Persimmon.
D. virginiana L.	Persimmon.
ELAEAGNACEAE	
Shepherdia argentea Nutt.	Buffaloberry.
ERICACEAE	
Arctostaphylos spp.	Manzanita.
Gaylussacia baccata (Wang.) K. Koch	Black huckleberry.
G. brachycera (Michx.) Gray	Box huckleberry.
G. dumosa (Andr.) T. and G.	Dwarf huckleberry.
Kalmia angustifolia L.	Sheep laurel.
K. latifolia L.	Mountain laurel.
Rhododendron canadense (L.) Torr.	Rhodora.
Vaccinium alto-montanum Ashe	([1])
V. angustifolium Ait.	Lowbush blueberry.
V. ashei Reade	Rabbiteye blueberry.
V. australe Small	([1])
V. corymbosum L.	Highbush blueberry.
V. macrocarpon Ait.	Cranberry.
V. membranaceum Dougl.	([1])
V. myrtilloides Michx.	Sour-top bilberry.
V. ovatum Pursh	Huckleberry.
EUPHORBIACEAE	
Aleurites fordii Hemsl.	Tung.
Phyllanthus emblica L.	Mirobalan.
FAGACEAE	
Castanea crenata Sieb. and Zucc.	Japanese chestnut.
C. dentata (Marsh.) Borkh.	American chestnut.
C. mollissima Blume	Chinese chestnut.
C. sativa Mill.	Spanish chestnut.
FUMARIACEAE	
Dicentra cucullaria (L.) Bernh.	Dutchman's breeches.
GENTIANACEAE	
Gentiana spp.	Gentian.
GRAMINEAE	
Sorghum vulgare L. [= *S. bicolor* (L.) Moench]	Milo maize.
HIPPOCASTANACEAE	
Aesculus californica (Spach) Nutt.	California buckeye.
HYDROCHARITACEAE	
Vallisneria americana Michx.	Eel-grass.
IRIDACEAE	
Freesia spp.	Freesia.
LABIATAE	
Lavandula latifolia Medic.	Lavender.
L. stoechas L.	Lavender.
L. vera DC.	Lavender.
Mentha spp.	Mint.
Origanum vulgare L.	Wild marjoram.
LAURACEAE	
Persea americana Mill.	Avocado.
LEGUMINOSAE	
Alysicarpus spp.	Alyce clover.
Anthyllis vulneraria L.	Kidney vetch.
Arachis hypogaea L.	Peanut.
Astragalus spp.	([1])
A. cicer L.	Cicer milkvetch.

SCIENTIFIC AND COMMON NAMES OF PLANTS MENTIONED IN TEXT, ARRANGED ALPHABETICALLY BY FAMILY, GENUS, AND SPECIES — CONTINUED

Scientific name	*Common name*
LEGUMINOSAE — Continued	
A. sinensis	Milkvetch.
Cajanus cajan (L.) Millsp.	Pigeonpea.
Cercis spp.	Redbud.
Colutea arborescens L.	Bladder senna.
Coronilla varia L.	Crownvetch.
Crotalaria intermedia Kotschy	Crotalaria.
C. juncea L.	Crotalaria.
Crotalaria lanceolata E. Mey.	Crotalaria.
C. mucronata Desv. [*C. striata* DC.]	Crotalaria.
C. spectabilis Roth	Crotalaria.
Cytisus scoparius (L.) Link	Scotch broom.
Glycine max (L.) Merr.	Soybean.
Hedysarum coronarium L.	Sweetvetch.
Lespedeza bicolor Turcz.	Lespedeza.
L. cuneata (Dum.) G. Don	Lespedeza.
L. cyrtobotray Miq.	Lespedeza.
L. intermedia (Wats.) Britt.	Lespedeza.
L. japonica Bailey	Lespedeza.
L. sericea (Thunb.) Miq.	Lespedeza.
L. stipulacea Maxim.	Lespedeza.
L. striata (Thunb.) H. and A.	Lespedeza.
L. virginica (L.) Britt.	Lespedeza.
Lotus corniculatus L.	Broadleaf birdsfoot trefoil.
L. pedunculatus Cav.	Big birdsfoot trefoil.
L. tenuis Waldst. and Kit. ex Willd.	Narrowleaf birdsfoot trefoil.
L. uliginosus Schk.	Wetland deervetch.
Lupinus angustifolius L.	([1])
L. nanus Dougl.	Sky lupine.
Medicago arabica Huds.	Spotted burclover.
M. hispida Gaertn.	Toothed burclover.
M. lupulina L.	Black medic or yellow trefoil.
M. sativa L.	Alfalfa.
Melilotus alba Desr.	Biennial white sweetclover.
M. a. var. *annua* Coe	Annual white sweetclover.
M. indica (L.) All.	Yellow annual sourclover.
M. officinalis (L.) Lam.	Biennial yellow sweetclover.
M. suaveolens Ledeb.	Daghastan sweetclover.
Onobrychis viciifolia Scop.	Sainfoin.
Phaseolus aureus Roxb.	Mung bean.
P. coccineus L.	Scarlet runner bean.
P. lunatus L.	Lima bean.
P. vulgaris L.	Bean.
Pueraria thunbergiana (S. and Z.) Benth. [= *P. lobata* (Wild.) Ohwi]	Kudzu.
Tephrosia vogelii Hook. f.	Tephrosia.
Trifolium alexandrinum L.	Berseem or Egyptian clover.
T. ambiguum Bieb.	Kura (Pellett) clover.
T. campestre Schreb.	Large hop clover.
T. dubium Sibth.	Small hop clover.
T. fragiferum L.	Strawberry clover.
T. glomeratum L.	Cluster clover.
T. hirtum All.	Rose clover.
T. hybridum L.	Alsike clover.
T. incarnatum L.	Crimson clover.
T. isthmocarpum Brot.	([1])
T. lappaceum L.	Lappa clover.
T. medium L.	Zigzag clover.
T. michelianum Savi	([1])
T. nigrescens Viv.	Ball clover.
T. pallidum Waldst. and Kit.	([1])
T. pratense L.	Red clover.
LEGUMINOSAE — Continued	
T. repens L.	White clover.
T. resupinatum L.	Persian clover.
T. striatum L.	Striate clover.
T. subterraneum L.	Subterranean clover.
T. uniflorum L.	Solitary clover.
T. vesiculosum Savi	Arrowleaf clover.
T. xerocephalum Fenzl.	([1])
Vicia angustifolia L.	Narrow-leaf vetch.
V. benghalensis L.	Purple vetch.
V. dasycarpa Ten.	Woolly-pod or smooth vetch.
V. faba L.	Broad or field bean.
V. pannonica Crantz	Hungarian vetch.
V. sativa L.	Common or spring vetch.
V. villosa Roth	Hairy, woolly, or winter vetch.
Vigna sinensis (L.) Savi ex Hassk.	Cowpea.
LEMNACEAE	
Lemna spp.	Duckweed.
LILIACEAE	
Asparagus officinalis L.	Asparagus.
Rohdea japonica Roth	([1])
Urginea maritima (L.) Baker	Squill.
LINACEAE	
Linum usitatissimum L.	Flax.
LOBELIACEAE	
Lobelia ramosa[2]	Lobelia.
LORANTHACEAE	
Phoradendron spp.	Mistletoe.
LYTHRACEAE	
Lythrum salicaria L.	Spiked or purple loosestrife.
MALPIGHIACEAE	
Malpighia glabra L.	Acerola, Barbados, or West Indian cherry.
MALVACEAE	
Althea rosea (L.) Cav.	Hollyhock.
Gossypium arboreum L.	Asiatic cotton.
G. barbadense L.	American Pima or Pima cotton.
G. herbaceum L.	Asiatic cotton.
G. hirsutum L.	Upland cotton.
G. tomentosum Nutt. ex Seem.	Hawaiian cotton.
Hibiscus cannabinus L.	Kenaf.
H. esculentus L.	Okra.
MARTYNIACEAE	
Proboscidea spp.	Unicorn plant.
MORACEAE	
Ficus carica L.	Fig.
MUSACEAE	
Musa ensete Gmel.	Abyssinian banana.
MYRISTICACEAE	
Myristica fragrans Houtt.	Nutmeg.
MYRTACEAE	
Feijoa sellowiana Berg	Feijoa.
Pimenta dioica (L.) Merr.	Pimento or allspice.
Psidium guajava L.	Guava.
Syzygium aromaticum Merr. and L. M. Perry	Clove.
NAIADACEAE	
Zostera marina L.	Eel-grass.
NYCTAGINACEAE	
Mirabilis jalapa L.	Four-o'clock.
OLEACEAE	
Olea europaea L.	Olive.

SCIENTIFIC AND COMMON NAMES OF PLANTS MENTIONED IN TEXT, ARRANGED ALPHABETICALLY BY FAMILY, GENUS, AND SPECIES — CONTINUED

Scientific name	*Common name*
ORCHIDACEAE	
Angraecum sesquipedale Thou.	([1])
Coryanthes spp.	([1])
Cycnoches chlorochilon	Orchid.
Habenaria obtusata Richards	Orchid.
Vanilla fragrans (Salisb.) Ames	Vanilla.
V. planifolia Andrews	Vanilla.
V. pompona Schiede	Vanilla.
V. tahitensis J. W. Moore	Vanilla.
OXALIDACEAE	
Averrhoa carambola L.	Carambola.
PALEMONIACEAE	
Several genera, not named in text.	Phlox.
PALMACEAE	
Cocos nucifera L.	Coconut.
Elaeis guineensis Jacq.	Oil or African oil plam.
Phoenix dactylifera L.	Date.
PAPAVERACEAE	
Eschscholzia californica Cham.	California poppy.
PASSIFLORACEAE	
Passiflora edulis Sims	
f. *edulis*	Purple passionfruit.
f. *flavicarpa* Deg.	Yellow passionfruit.
P. quadrangularis L.	Giant granadilla
PEDALIACEAE	
Sesamum indicum L.	Sesame.
PIPERACEAE	
Piper nigrum L.	Pepper, black and white.
POLYGONACEAE	
Fagopyrum esculentum Moench	Buckwheat.
F. sagittatum Gilib.	Buckwheat.
F. tartaricum (L.) Gaertn.	Tartary buckwheat.
PORTULACACEAE	
Claytonia virginica L.	Spring beauty.
PRIMULACEAE	
Cyclamen persicum Mill.	Cyclamen.
Primula vulgaris Hill	English primrose.
PROTEACEAE	
Dryandra spp.	([1])
Macadamia integrifolia Maiden and Betche	Macadamia.
M. tetraphylla L. A. S. Johnson	Macadamia.
Protea mellifera Thunb.	([1])
PUNICACEAE	
Punica granatum L.	Pomegranate.
RAFFLESIACEAE	
Pilostyles thurberi Gray	([1])
Rafflesia arnoldii R. Br.	([1])
RESEDACEAE	
Reseda lutea L.	Mignonette.
R. odorata L.	Mignonette.
RHAMNACEAE	
Ziziphus jujuba Mill.	Jujube.
ROSACEAE	
Amelanchier alnifolia Nutt. ex Roem.	Juneberry.
Chaenomoles sinensis (Thouin) Koehne	Quince.
Cydonia oblonga Mill.	Quince.
Eriobotrya japonica (Thunb.) Lindl.	Loquat.
Fragaria × *ananassa* Duch.	Strawberry.
Malus sylvestris Mill.	Apple.
ROSACEAE — Continued	
M. s. × *M. baccata* (L.) Borkh.	Crabapple.
Prunus amygdalus Batsch	Almond.
P. armenica L.	Apricot.
P. avium L.	Cherry.
P. besseyi Bailey	Sand cherry.
P. cerasifera Ehrh.	Plum.
P. cerasus L.	Pie, sour, or tart cherry.
P. domestica L.	European plum.
P. gondouinni (Poit. and Turp.) Rehd.	Duke cherry.
P. insititia L.	Damson plum.
P. mahaleb L.	Mahaleb cherry.
P. pensylvanica L.	Pin cherry or pinchberry.
P. persica (L.) Batsch	Peach.
P. salicina Lindl.	Japanese plum.
P. simonii Corr.	Simon plum.
Pyrus communis L.	Common, French, or European pear.
P. pyrifolia (Burm. f.) Nakai	Chinese sand pear.
Rosa spp.	Rose.
R. rugosa Thunb.	Rose hips (source of).
Rubus spp.	Brambles.
R. idaeus L.	Red raspberry.
R. occidentalis L.	Black raspberry.
R. strigosus Michx.	Red raspberry.
R. strigosus × *R. occidentalis*	Purple raspberry.
R. ursinus Cham. and Schlecht.	Pacific Coast blackberry.
R. u. subsp. *loganobaccus* *Bailey*	*Loganberry.*
RUBIACEAE	
Coffea arabica L.	Arabica coffee.
C. canephora Pierre ex Froehner	Robusta coffee.
C. dewevrei Wildem. and Dur.	Coffee.
C. excelsa Cheval.	Coffee.
C. liberica Bull ex Hiern	Liberica coffee.
C. robusta Linden	Coffee.
Posoqueria fragrans Roxb.	([1])
RUTACEAE	
Casimiroa edulis Llan. and Lex.	White sapote.
Citrus aurantifolia (Christm.) Swingle	Lime.
C. aurantium L.	Sour orange.
C. grandis (L.) Osbeck	Pummelo or shaddock.
C. hassaku Hort. ex Y. Tanaka	Hassaku orange.
C. limettoides Tan.	Sweet lime.
C. limon (L.) Burm. f.	Lemon.
C. limon × *C. medica*	Meyer lemon.
C. medica L.	Citron.
C. paradisi Macf.	Grapefruit.
C. reticulata Blanco	Mandarin and tangerine.
C. r. var. *austera* Swingle × *Fortunella* spp.	Calamondin.
C. sinensis (L.) *Osbeck*	Sweet orange.
C. s. × *Poncirus trifoliata*	Citrange.
C. unshiu Marc.	Satsuma orange.
Fortunella margarita (Lour.) Swingle	Kumquat.
Poncirus trifoliata (L.) Raf.	Trifoliate orange.
SAPINDACEAE	
Litchi chinensis Sonn.	Litchi or lychee.
SAPOTACEAE	
Calocarpum sapota (Jacq.) Merr.	Mamey sapote.

SCIENTIFIC AND COMMON NAMES OF PLANTS MENTIONED IN TEXT, ARRANGED ALPHABETICALLY BY FAMILY, GENUS, AND SPECIES — CONTINUED

Scientific name	*Common name*
SAPOTACEAE — Continued	
C. viride Pittier	Green sapote.
SAXIFRAGACEAE	
Ribes americanum Mill.	Currant.
R. aureum Pursh	Missouri currant.
R. glutinosum Benth.	Gooseberry.
R. grossularia L.	Gooseberry.
R. hirtellum Michx.	Gooseberry.
R. nevadense Kellogg	Gooseberry.
R. nigrum L.	Currant.
R. odoratum Wendl.	Currant.
R. roezlii Regel	Gooseberry.
R. rubrum L.	Currant.
R. sativum (Reichenb.) Syme	Currant.
R. viscosissimum Pursh	Gooseberry.
SCROPHULARIACEAE	
Antirrhinum majus L.	Snapdragon.
Digitalis purpurea L.	Foxglove.
Linaria vulgaris Hill	Butter-and-eggs.
Penstemon gracilis Nutt.	Penstemon.
SELAGINELLACEAE	
Lycopodium spp.	Clubmoss.
SOLANACEAE	
Capsicum annuum L.	Pepper.
C. frutescens L.	Pepper.
Cestrus nocturnum L.	Night-blooming jessamine.
Lycopersicon esculentum Mill.	Tomato.
Petunia nyctaginiflora Juss.	Petunia.
P. violacea Lindl.	Petunia.
Solanum melongena L.	Eggplant.
S. tuberosum L.	Potato.
STERCULIACEAE	
Cola acuminata (Beauv.) Schott and Endl.	Kolanut.
C. nitida (Vent.) Schott and Endl.	Kolanut.
Theobroma cacao L.	Cacao.
THEACEAE	
Thea sinensis L.	Tea.
TYPHACEAE	
Typha latifolia L.	Cattail.
UMBELLIFERAE	
Anethum graveolens L.	Dill.
Anthriscus cerefolium (L.) Hoffm.	Chervil.
Apium graveolens L. var. *dulce* (Mill.) DC.	Celery.
A. g. L. var. *rapaceum* (Mill.) DC.	Celeriac.
Carum carvi L.	Caraway.
Coriandrum sativum L.	Coriander.
Daucus carota L.	Carrot.
Foeniculum vulgare Mill.	Fennel.
Pastinaca sativa L.	Parsnip.
Petroselium crispum (Mill.) Nym.	Parsley.
Pimpinella anisum L.	Anise.
VIOLACEAE	
Viola tricolor L.	Pansy.
VITACEAE	
Vitis aestivalis Michx.	Grape.
V. labrusca L.	Grape.
V. labruscana Bailey	Grape.
V. lincecumii Buckl.	Grape.
V. munsoniana J. H. Simson ex Planch.	Grape.
V. rotundifolia Michx.	Grape.
V. vinifera L.	Grape.
V. vulpina L.	Grape.
ZINGIBERACEAE	
Elettaria cardomomum (L.) Maton	Cardamom.
ZYGOPHYLLACEAE	
Tribulus terrestris L.	Puncture vine.

[1] No common name.

[2] Authorship of plant name in doubt. It may be *Lobelia tenior* R. Br. or *L. fulgens* Willd.

GLOSSARY OF BOTANICAL TERMS

Achene . . . Dry indehiscent, one-seeded pericarp.

Adventitious buds . . . Buds produced out of their regular order.

Aggregate fruit . . . Fruit, like strawberry, in which pistils were distinct in flower, but carpels are crowded together in a mass on a common receptacle.

Amphidiploid . . . Having complete diploid chromosome set from each parent strain as a result of chromosome doubling in first hybrid generation.

Androecium . . . Collective staminate system of flower.

Androgynous . . . Having both pistillate and staminate flowers in same cluster.

Andromonoecious . . . Having both hermaphrodite and staminate flowers.

Anemophilous . . . Wind loving, or plants whose pollen is carried by wind.

Annual . . . Plant that completes its growth and fruiting, then dies within a year.

Anther . . . Part of the stamen that normally produces pollen.

Anthesis . . . Time of opening of flower.

Apomyxis . . . Development without fertilization.

Aril . . . Network or covering of seed, usually covered by outer layer.

Asexual . . . Without sex (vegetative in terms of reproduction).

Axil . . . Upper angle between leaf and stem.

Axillary . . . Occurring in axil.

Berry . . . Fleshy fruit with skinlike covering, having one to many seeds (but no stone), developed from single pistil.

Biennial . . . 2-year period, plant that completes its growth and fruiting then dies within 2 years.

Bilabiate . . . Two-lipped.

Bisexual . . . Having both male (stamens) and female (pistil) parts.

Bolt . . . To develop seed stalk prematurely.

Bract . . . Usually small leaf or scalelike structure near base of flower.

Bulb . . . Usually underground bud covered with fleshy leaflike scales.

Bulbil . . . Usually deciduous, aboveground small bulb arising from mother bulb.

Calyx . . . Sepals or outer whorl of perianth.

Capitate . . . Bunched into compact cluster.

Caprification . . . Pollination of figs with certain tiny wasps.

Capsule . . . Dry, dehiscent seed pod from flower with compound pistil.

Carina . . . Keel or united lower petals of papilionaceous flower.

Carpel . . . Unit or division of compound pistil.

Catkin . . . Spike or pendulous type of inflorescence made up of flowers of only one sex.

Centripetal . . . Development of florets of flower head from without toward center.

Chasmogamous . . . Pollination occurs while flower is open.

Cleistogamous . . . Flowers that are self-fertilized without opening.

Clone . . . One or more individuals obtained from single parent by vegetative reproduction.

Close-fertilization . . . Fertilization by its own pollen.

Compatible . . . Capable of crossing between plants.

Complete flower . . . Flower that has all normal parts.

Corm . . . Fleshy, bulblike, solid, underground stem.

Corolla . . . Petals or inner whorl of perianth.

Corona . . . Crown.

Corymb . . . Flat-topped cluster of flowers, outer flowers of which open first.

Crenulate . . . Finely toothed.

Crepuscular . . . Active at twilight or at dawn.

Cross . . . Union of two cultivars of same species.

Cross-compatible . . . Capable of being fertilized with pollen of different variety.

Cross-fertilize . . . To fertilize ovary of one flower with pollen from another flower.

Cross-pollinate . . . Transfer pollen of one flower onto stigma of another.

Cruciferous . . . Cross-bearing, petals of flower form a cross.

Cultivar . . . Group of cultivated plants distinguished by any significant character which, when reproduced sexually or asexually, retain their distinguishing characteristics.

Curd . . . Thick, fleshy, spherical flower stalk of cauliflower.

Cyme . . . Broad, flat, compact cluster of flowers that open centrifugally or in center first.

Cytoplasm . . . Material of cell surrounding nucleus.

Deciduous . . . Sheds leaves in fall.

Dehisce . . . Opening of seed pod or anther and releasing contents.

Dichogamy . . . (Apart, marriage) sexual organs effective at different times.

Dioecious . . . Stamens or male parts and pistils or female parts are on different plants.

Diploid . . . Having twice as many chromosomes as in haploid condition.

Disk . . . Flat base of flower on which outer parts are supported, fleshy expansion of receptacle.

Drupe . . . A succulent or fleshy fruit having one seed enclosed in stony endocarp.

Drupelet . . . One drupe in fruit made up of aggregate of drupes, as in the strawberry.

Ecology . . . Reciprocal relations between organisms and their environment.

Embryo . . . Rudimentary organism.

Endocarp . . . Inner layer of pericarp.

Entomophilous . . . Insect loving, or insect pollinated.

Epigynous . . . Upon ovary.

Essential organs . . . Sexual organs of flower.

Evergreen . . . Usually green throughout year.

Exocarp . . . Outermost layer of fruit wall.

Exserted . . . Protruding beyond margin of envelope or corolla.

Extrafloral . . . Outside flower.

F_1 . . . First filial offspring or generation.

Farina . . . Meal or starchy matter, archaic name for pollen.

Female flower . . . One with stigma.

Fertile . . . Capable of bearing fruit.

Fertilization . . . Union of germ of pollen grain with egg of ovule.

Filament . . . Hairlike element of stamen supporting anther.

Flora . . . Flowers.

Floral nectary . . . Nectary within flower.

Floret . . . One small flower.

Flower . . . Reproductive growth of plant.

Fruit . . . Mature ovary with all its parts and adherents.

Fruitful . . . Plant or cultivar that produces fruit abundantly.

Gamete . . . Sexual cell.

Gene . . . Material substance in chromosome of cell that determines or conditions one or more hereditary characters.

Germination . . . Development of plant from seed.

Glabrous . . . Smooth.

Gynoecious . . . Producing only or predominantly pistillate flowers.

Gynoecium . . . Female parts of flower.

Herb . . . Not woody, dying to ground at end of season but perennial underground.

Hermaphrodite . . . Bisexual (stamens and pistil in same flower).

Heterogamous . . . Two or more kinds of flowers on same plant.

Heterosis . . . Increased vigor, growth, or reproduction usually resulting from cross of two unlike organisms.

Homogamous . . . All flowers of same kind.

Hybrid . . . Cross between two or more parents more or less unlike.

Hybrid vigor . . . See Heterosis.

Hydrophyllous . . . Water loving.

Hypogamous . . . Inserted under pistil, on receptacle.

Indehiscent . . . Not splitting open by its valves.

Indeterminate . . . Continues to grow after flowing starts.

Indigeneous . . . Native to area.

Infertile . . . Sterile.

Inflorescence . . . Flower or arrangement of flowers on stem.

Integument . . . Coat of ovule or seed.

Interspecific . . . Between species.

Intersterile . . . Failure to set fruit when flowers are crossed with pollen of certain other cultivars of same species.

Intraspecific . . . Within species.

Involucre . . . Whorl or set of bracts around flower or crowded flower cluster.

Joint . . . Node or section of plant.

Keel . . . Two anterior united petals of papilionaceous flower.

Kernel . . . Inner soft part of nut, stone, or fruit; nucellus of an ovule.

Labellum . . . Liplike petal, particularly on orchid flowers.

Legume . . . One-celled fruit (pod) usually dehiscing down both sutures, and having the seed attached along ventral suture.

Lenticel . . . Raised breathing pore or dot.

Ligula . . . Strap-shaped corolla or ray flower of many composites.

Lobe . . . Rounded portion or segment of an organ.

Locule . . . Compartment or cell of ovary, anther, or fruit.

Matinal . . . Dawn-feeding (insects).

Melliferous . . . Honey bearing.

Mellitophilous . . . Pollinated by bees.

Mesocarp . . . Middle layer of pericarp or fruit wall.

Metaxenia . . . Effect of pollen on developing maternal tissue outside embryo and endosperm.

Micropyle . . . Pore or hole in end of egg through which sperm enters to fertilize egg.

Midrib . . . Central vein or rib of leaf.

Monoecious . . . Stamens, or male parts, and pistils, or female parts, on same plant.

Nectar . . . Sweet liquid produced in nectary of plant, usually within flower.

Nectar guide . . . Certain markings on flower that seem to guide or direct nectar feeders to nectar source.

Nectariferous . . . Having nectaries or secreting nectar.

Nectary . . . Plant gland that secretes nectar.

Nocturnal . . . Referring to plants that are open during the night and usually closed by day.

Node . . . Enlarged area of stem, where leaves and buds may originate.

Nodule . . . Small knots, especially on root of legumes.

Nucellus . . . Central body of ovule, containing embryo sac.

Nut . . . Hard, indehiscent, one-celled and one-seeded fruit, generally from compound ovary.

Operon . . . Genetic unit consisting of adjacent genes that function together under joint control of enhancer and repressor factors.

Organelle . . . Specialized part of cell performing functions analogous to those of organs in many-celled organisms.

Ornithophilous . . . Bird loving or bird pollinated.

Ovary . . . Seedcase or part of pistil, bearing ovules that develop into seed or fruit.

Ovule . . . Potential seed within ovary.

Panicle . . . Inflorescence with main axis branched into open racemose flower cluster.

Panmixis . . . High degree of random or nonselective mating within breeding population (opposite of apomixis).

Papilionaceous . . . Butterflylike, pealike flowers, with large upper petal, two lateral wing petals, and two small united keel petals.

Parasite . . . One who lives at the expense of or on another.

Parthenocarpic . . . Capable of fruit development without fertilization.

Parthenocarpy . . . Development of fruit without fertilization.

Pedicel . . . Stalk or stem of individual flower of inflorescence.

Peduncle . . . Primary flower stalk of inflorescence.

Pendent . . . Drooping.

Pendulous . . . Hanging loosely, swinging.

Pepo . . . Fruit of cucurbit family.

Perennial . . . Lasting from year to year for 3 years or more.

Perfect flower . . . Flower having both stamens and pistil, regardless of other parts.

Perianth . . . Entire floral envelope including both corolla and calyx.

Pericarp . . . Ovary or fruit wall.

Persistent . . . Remaining beyond time or period when such parts are expected to fall.

Petal . . . Leaf or unit of usually colored corolla or inner floral envelope.

Petiole . . . Leaf-stalk.

Photosynthesis . . . Conversion of carbon dioxide and water by radiant energy into carbohydrate.

"Pin and thrum" . . . Flower condition in which stamens of some flowers are longer than style, while other flowers of same species have stamens same length or shorter than style.

Pistil . . . Usually central seed-producing part of flower; usually consisting of ovary, style, and stigma.

Pistillate . . . Having or bearing pistils but no stamens.

Placenta . . . Surface or tissue part of ovary to which ovules become attached.

Plumose . . . Feathery.

Pollen . . . Usually yellow grains or fertilizing elements produced in anthers.

Pollen tube . . . Thin tubular outgrowth of pollen grain usually upon contact with stigma, and which penetrates style to ovary, permitting sperm nuclei to unite with egg cell.

Pollenization . . . See *Pollination.*

Pollenizer . . . Plant source of pollen for fertilizing receptive stigmas.

Pollinating . . . Transferring pollen from anthers to stigmas.

Pollination . . . Placement of pollen on stigma, first step in plant fertilization.

Pod . . . Monocarpellary fruit that dehisces down both sutures.

Polyembryony . . . Having more than one embryo in an ovule.

Polygamous . . . Having both perfect flowers and those of one sex (staminate or pistillate).

Polyembryonic . . . One embryo from a fertilized ovule then one to many embryos formed adventitiously from the nucellus.

Pome . . . Fleshy fruit derived from several carpels, receptacle and outer pericarp being fleshy, inner pericarp, papery.

Procumbent . . . Trailing or lying along ground but not rooting.

Prostrate . . . Lying flat upon ground.

Protandrous . . . Flower in which anthers mature and release pollen before stigma is receptive.

Protogynous . . . Flower in which stigma is receptive before anthers release pollen.

Protoplasm . . . Living matter.

Pubescent . . . Hairy or downy.

Pyrene . . . Seedlike nutlet or stone of small drupe, for example, holly berry.

Raceme . . . Inflorescence with one-flowered pedicels along sides of general peduncle.

Ray flowers . . . Showy marginal flowers on Compositae flower head.

Receptacle . . . Enlarged end of pedicel to which one or more flowers are attached.

Reflexed . . . Bent outward or backward.

Regular flower . . . One with all members of the same circle of parts alike, parts similar in shape to others of their kind; for example, each petal is identical to all other petals of the same flower.

Rhizome . . . Elongated horizontal underground stem, having nodes and capable of producing new roots or shoots at nodes.

Rostellum . . . Slender extension from upper edge of stigma of orchid flower.

Seed . . . Fertilized and matured ovule or rudimentary plant and food necessary for its germination.

Segregate . . . Separate from each other; type separated from super type.

Self-compatible . . . Capable of being fertilized within its own flower group.

Self-fertile . . . Capable of being fertilized by its own pollen.

Sef-fertilizing . . . Capable of becoming fertile by placing its pollen on its own stigma.

Self-fruitful . . . Producing fruit when pollinated with self-pollen.

Self-pollinating . . . Capable of placing its own pollen upon its own stigma.

Self-sterile . . . Incapable of becoming fertilized by its own pollen.

Sepal . . . Outermost part of flower, the parts of which form the calyx.

Sessile . . . Sitting, lacking stalk or petiole.

Sexual organs . . . Style, stigma, ovary, and stamens (filament and anther).

Sexual reproduction . . . Reproduction through union of male and female gametes, (as opposed to vegetative reproduction).

Shoot . . . Upgrowth of stem and leaves that bears reproductive organs.

Shrub . . . Woody perennial, sometimes having several stems, and smaller than usually expected of a tree.

Silique . . . Two-celled fruit, characteristic of family Cruciferae, which separates at maturity in dehiscence from framelike placenta.

Spadix . . . Thick or fleshy spike of flowers, subtended by a spathe.

Spathe . . . Large bractlike sheath inwraping an inflorescence.

Spike . . . Inflorescence with elongated main axis and sessile flowers.

Stalk . . . Main stem.

Stamen . . . Male part of flower consisting of filament and anther.

Staminate . . . Stamen-bearing.

Staminode . . . Abortive stamen.

Standard . . . Large upper petal of papilionaceous flower.

Stem . . . Main axis of plant.

Sterile . . . Barren, unfruitful, incapable of being fertilized.

Stigma . . . Receptive portion of female sexual column on end of style.

Stipule . . . Small growth on base of some leaves.

Stolon . . . Procumbent or trailing stem that bears buds and roots.

Stone (fruit) . . . One whose outer part is fleshy, inner part hard or stony.

Style . . . Part of sexual column between ovary and stigma.

Succulent . . . Juicy, fleshy plant.

Sucker . . . Shoot from side of stem.

Symbiont . . . Intimate associate or organism living with another different organism.

Syconium . . . Fruit of fig in which receptacle is hollow and succulent and lined on inside with numerous seeds.

Tendril . . . Threadlike organ on branch used for clinging.

Tetrad . . . Group of four cells, such as pollen grains.

Throat . . Opening of monopetalous corolla.

Tripping . . . Release of sexual column (in legumes).

Trunk . . . Main stem.

Tuber . . . Much enlarged fleshy underground stem or branch with eyes (buds) on sides.

Tubercle . . . Small wartlike excrescence.

Twining . . . Ascending by coiling around support.

Umbel . . . Umbrella-shaped inflorescence.

Unisexual . . . With stamens only or with pistils only.

Variety . . . See *Cultivar.*

Vegetative reproduction . . Asexual reproduction.

Vicinism . . . Natural crossing.

Whorl . . . Circular arrangement of leaves or flowers.

Wild bees . . . Pollen-storing Apoidea other than domestic honey bee.

Zygote . . . Cell formed by union of two gametes.

SUBJECT INDEX

[The superscript ® denotes registered trade names.
Bold face numerals indicate major discussion.]

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