Plants have sexes somewhat as animals do. Many plants carry both the male and female elements on the same individual. Other plants have the sex organs in separate plants—that is, a plant may be strictly male or female. In any case, pollen from the male part of the plant must come in contact with the female element if seed is to result.

Reproduction is the sole function of a flower. In a typical flower the essential female parts, regardless of their variable form and number, are ovary, style, and stigma. The ovary, the basal part, becomes the fruit. The style is a column of tissue arising from the top of the ovary. The expanded or otherwise modified tip of the style is the stigma. In many plants the surface of the stigma has a sticky secretion to which the pollen adheres. In a typical male part of the flower, the anther simply produces pollen, which is the functional male sex element.

Pollination is the transfer of pollen from the anther to the stigma or the distribution of pollen. Pollination must be accomplished before fertilization (the union of the male germ cell, contained in the pollen grains, with the female germ cell or egg in the ovary) and eventual reproduction can take place.

If pollen is transferred from an anther to the stigma of the same flower or to the stigma of another flower on the same plant, self-pollination is said to have taken place. The transfer of pollen from an anther to the stigma of a flower of another individual plant is spoken of as cross-pollination. Those are botanical definitions and do not consider the varietal factor, which is of such great importance to fruit production. Self-pollination, as used in fruit production, also includes the transfer of pollen from the anthers of a flower of one variety to the stigma of a flower of the same variety. Cross-pollination, in the horticultural sense, refers to the transfer of pollen from the flower of one variety to a flower of a different variety.

Charles Darwin, the English naturalist, concluded from his observations and exhaustive experiments with many plant families that plants resulting from cross-pollination generally had greater vigor, weight, and height and produced flowers earlier than those resulting from self-pollination. It has since been shown that the advantages of cross-pollination and the disadvantages of self-pollination are not always so decisive as Darwin supposed. Nevertheless, there is a long list of species and varieties of plants that are self-sterile and require cross-pollination; the advantages of hybrid vigor in some modern cropping practices also is well established.

Darwin listed several ways in which plants are constructed to avoid self-pollination and insure cross-pollination:

1. By the separation of the sexes, in which staminate and pistillate flowers are borne on separate plants, as in the hemp, willow, holly, and date.

2. By a difference in the time of maturity of the pollen and stigma in the same flower, as in the red clover, beet, plantain, and avocado.

3. By special mechanical contrivances that prevent self-pollination or that favor insect pollination, as in many orchids, legumes, and mints.

4. By producing different forms of flowers on the same plant with different lengths of stamens and pistils, as in the Chinese primrose.

5. By complete or partial sterility of the flowers to their own pollen or the prepotency of pollen from another individual or variety over the plant's own pollen, as in lobelia, mignonette, mullein, and many varieties of apple, pear, cherry, plum, and almond.

No difficulty is encountered in the...
pollination and fertilization of some self-fertile plants because both sexual elements develop so close together that pollen is directly deposited on the stigma. Wheat illustrates such a situation—it is self-pollinating and at the same time self-fertile. Self-fertile plants exist, however, which are wholly or partly incapable of fertilizing themselves without the aid of a transferring agent. Cantaloup is a prime example of this condition.

Other plants cannot fertilize themselves following self-pollination by a transferring agent even though both sexual parts mature at the same time. Varieties of sweet cherry and almond illustrate this situation; pollen from some other variety is required to effect fertilization. Not only are all the varieties of these fruits self-unfruitful; there are instances as well of interincompatible varieties.

Varieties of certain fruits, such as the apple, pear, and plum, produce some fruit as a response to self-pollination but not enough for a profitable crop. Such varieties are said to be partially self-fruitful. In such instances agents for the transfer of pollen between different varieties are essential for commercial production.

Even in many cases of self-fruitfulness, like the French prune, the activity of insects on the blossoms greatly increases fruit production through better pollen distribution. French prune trees, enclosed in tents, gave sets of 19.0 percent when bees were present and 0.34 percent when bees were absent. Similar results were obtained when trees of the self-fruitful sour cherry Montmorency were caged in Michigan.

It is perhaps significant that because California has such a large population of honey bees the yield of fruit, lint, and seed from many plants, such as plums, cotton, alfalfa, Ladino clover, onions, carrots, cantaloups, lima beans, and white mustard, often is outstanding.

A number of agents may be necessary for the distribution of pollen from plant to plant, because some pollens are dry and light and others are moist and heavy. The commonest agents of pollen distribution are gravity, wind, and insects. For example, corn pollen drops from the tassel to the silks. Date palm pollen is a fine dust, which floats away like fog. Pine pollen, with its bladderlike wings, is readily carried by wind. Deciduous fruit pollens are rather gummy and generally must be transferred by insects. The huge pollen grain of cotton is thickly dotted with sticky fluid, which makes it far too heavy to be carried by the wind but adapts it well to sticking to the hairs that cover the bodies of pollinating insects. Pollination may sometimes also be accomplished by rain, birds, and artificial means devised by man.

Even among many plants designated botanically as pollinated by wind and gravity, insects are sometimes a factor in the collection and distribution of pollen. For example, the pollens from bee colonies often contain liberal quantities from corn, oak, pine, walnut, ryegrass, Sudangrass, Canary
Island palm, date palm, juniper, cypress, elm, or redwood. Few of those plants, if any, produce visible nectar for the attraction of insects to the male blossom parts; therefore they are probably visited only by the pollen-collecting insects.

Fruits develop in many plants without pollination and fertilization or the subsequent development of seeds. A number of our cultivated plants regularly bear such parthenocarpic—seedless—fruits. Among them are seedless raisin grapes, English-forcing cucumbers, navel oranges, bananas, pineapples, and some varieties of pears, figs, and Japanese persimmons. Sometimes mere pollination without subsequent fertilization may be sufficient to start fruit development. The application of synthetic plant hormones to the flowers and leaves has also been found to stimulate parthenocarpy in tomatoes, Smyrna figs, holly, pears, and others.

Native wild bees (bumble bees, leaf-cutting bees, alkali bees, carpenter bees) are specially adapted for gathering pollen and nectar from flowers. Many other insects also do so—some beetles, flies, moths, thrips. In fact, any of the thousands of insects that visit flowers purposely or accidentally can be agents for carrying pollen grains from the anther to the stigma. But of all of them the most important by far is the honey bee, *Apis mellifera*, whose existence depends on pollen and nectar from plants. We estimate that bees accomplish more than 80 percent of the pollination by insects. Yields of fruits and legumes and vegetable seed often have been doubled or trebled simply by providing adequate numbers of bees.

The honey bee was introduced into the United States from Europe. Unlike the native wild bees, it is a colonial insect throughout the year and therefore is available in force at any season. Semidomestication in man-made hives makes it available for placement wherever needed for pollination service. (The native bumble bee is also colonial in summer, but only the queen survives the winter to establish a new colony in spring.)

Honey bees have a complete metamorphosis—they pass through egg, larva, pupa, and adult stages. Each colony has three types of individuals, the queen, a handful of drones, and many thousands of workers. The queen bee is the true female whose primary function is egg production. The drone, or male bee, has no function except to provide sperm when a young queen is mated. That done, the workers may drive him out of the hive. The mature workers are not sexual forms, although in the egg and early larval stages there is no difference between them and a queen. The kind of food and care given them causes them to develop into workers or queens. It is the worker that is familiar to all as the proverbial busy bee in orchards, gardens, and fields.

Honey bees require carbohydrates, proteins, fat, vitamins, and other elements for food. The carbohydrates are derived largely from the plant nectar, which is a liquid containing three kinds of sugars. Water is carried into the hive in quantity from various sources. The other requirements are met largely by plant pollens. Bees also sometimes seek out salt and possibly other minerals.

Pollen primarily is utilized for rearing and maturing young bees through the larval and early-adult phases. The food of the mature field bees is largely honey or the nectar from which honey is elaborated. In seeking those foods from blossoms, a bee inadvertently fulfills the required distribution of pollen so necessary to reproduction in plants.

An individual bee usually visits one plant species to collect either pollen or nectar—a fortunate provision of nature, because a pollen from one species is not effective in completely fertilizing another kind of plant. For instance, pear pollen is of no use in setting fruit on a plum tree.

Various investigators watched individual bees and found that each one
Honey Bees as Agents of Pollination

visited only a small area to collect a load of pollen or nectar. After the trip back to the hive, the bee repeatedly returned to the same area.

G. Bonnier one day marked all bees working on a strip of buckwheat, 3 by 16 feet in area, and found only marked bees there the next day. A. Minderhoud studied an area where bees were working clover, dandelion, and other plants. After marking all bees on areas of approximately a square yard, he recorded their movements on squared paper. The bees repeatedly returned to the same square or within a radius of 10 yards of it. C. N. Buzzard noted that bees working *Cotoneaster horizontalis* covered an area of only 2 square yards. From 15 observations of marked bees during the next 5 days, he concluded that the same bees returned to the same bush and strayed only where the branches intertwined.

Sardar Singh noted the honey bee's liking for a small area of alsike clover, birdsfoot trefoil, aster, dandelion, goldenrod, white sweetclover, and apple in New York State. Some individual bees devoted whole visits to a single apple tree and returned for later visits to the same tree. Other bees worked between adjacent trees. The ratio of observed exchanges of bees between trees 10 feet apart to trees more than 15 feet apart worked out at 2:1. Five bees (out of 66 observed) rambled over three to five trees.

In England, C. G. Butler, E. P. Jeffree, and H. Kalmus found that visitation areas on *Epilobium* were usually less than 5 yards across. C. R. Ribbands showed that foraging bees working in a garden with five different sorts of flowers usually attached themselves to a particular area of the most suitable crop found. The size of the foraging area varied considerably. He noted that bees changed their attachment from a pollen crop to a nectar crop, but never vice versa.

Karl von Frisch has reported in several publications that the scout bees, after locating a source of pollen or nectar, transmit their knowledge to other bees through an intricate system of "dances" within the colony.

Since foraging bees usually attach themselves to one species, bee pellets usually contain but one kind of pollen grain. However, A. D. Betts in England analyzed 915 pollen loads and found 3 percent were mixtures. Only seven of the loads showed distinct segregation of the grains into two separate areas. When pellets from trapped pollen were sorted out in the western United States, only a few segregated mixtures were apparent among many thousands examined.

It is presumed that the exhaustion of a source with advancing time of day may be a factor in obtaining segregated mixtures. For example, an orchard morningglory blossom opens at sunrise and closes before midday during bright, warm weather. On the other hand, redmaids (*Calandrinia ciliata*) unfold in late forenoon and are at their height during the heat of late afternoon. In this case a shift by a partially loaded bee from morningglory to redmaids would be expected. Colonies in the same apiary evidently choose different pollen sources or visit different areas because the trapped supply from one colony is frequently unlike that from another.

The abundance of pollen or its state of exhaustion in a source may greatly influence the rate of collection. Many bees have been seen to get full loads of pollen from one pistachio catkin. The number of visits reported to dandelion heads for a pollen load varied from 8 to 100 when dandelions were scarce and colonies numerous. Ribbands reported 47 foraging trips by 1 bee to Shirley poppy flowers during 1 day—indicating easy and rapid collection.

The legs of a honey bee are modified for handling pollen. An eye brush occurs on the inner surface of the front tibia. The large first tarsal joint is covered with long unbranched hairs, forming a body brush. At the base of the first tarsal joint is an instrument for cleaning the antennae. The hind legs of the worker bear the organs with
which it transports two large loads of pollen from the flower to the hive. The inner surface of the large basal segment of the hind tarsus is covered with sharp, stiff spines closely arranged in transverse rows. They are particularly employed for taking the pollen from the middle tarsi and holding it until it is transferred to the pollen basket. As a bee pushes in among the anthers of a flower even for nectar, the body becomes literally covered with pollen grains.

Nectar is the sweet fluid secreted in plant blossoms. Its function presumably is to attract insects to the flowering parts. When an insect gathers nectar from a blossom, its body becomes coated with pollen grains, which are transferred later to other blossoms. Nectars of different plants have a variable sugar content and aroma. Such factors result in visitation of different kinds of insects to the various plants. The blossom nectar of firethorn (*Pyracantha*) evidently has low attractiveness to honey bees although blow flies feed on it greedily. The peculiar odor may influence both insects—that is, repel the one and attract the other. Dermestid beetles are common on yarrow blossoms, but a honey bee is seldom seen on them.

The sugar concentration of the nectar is an important factor in plant visitation by bees. The nectar of oranges has about 16 percent sugar as the petals unfold. During a humid day, when the nectar continues at that concentration or is diluted with fog moisture along the southern California coastal belt, the honey bee displays little interest in it. Then they busily gather the scanty mustard nectar, which has a much higher sugar content. When the day is dry enough for evaporation of water to about 25 percent sugar, they collect the orange nectar. Before concentration increases to 40 percent, bees become so numerous that the blossoms are sucked dry. Then as humidity conditions change back to give little evaporation, bee activity on orange blossoms practically ceases.

**A POLLEN GRAIN** is somewhat like a plant seed in that it germinates to send out a rootlike projection, which is called a pollen tube. On the stigma of a flower the tube penetrates down the style into the ovary, where union with the egg cell occurs. Each seed produced requires one pollen-grain germination tube. In a many-seeded fruit like a watermelon, numerous pollen grains must be applied to the stigma. Fertilization could be effected in an almond blossom with one pollen grain.

Wide differences exist in the length of the style of flowers and in the time for growth of the pollen tube down it. An alfalfa pollen tube grows down the pistil and enters the ovule in a day. In some oaks the time is almost a year in growing one-eighth inch. With Indian corn the distance from the stigma at the end of the corn silk to the attachment of the silk to the young corn grain may be a foot or more, yet fertilization is effected within a few days. In the latter case the large pollen grain carries much starchy food material which makes possible the great length to which the tube grows.

At Davis, Calif., apricot nectar may be completely ignored for several days while honey bees are busy working almond blossoms. Under such conditions the apricot nectar contained less than 10 percent sugar when the almond had 35 percent or more. During a dry north wind, the apricot nectar lost water rapidly and then it, too, was collected by many bees.

Since sugar concentration of nectar affects bee activity, it likewise influences the pollination potential. In plum varieties a wide variation in the quality and quantity of nectar has been found, and the bees have been observed to prefer some plum varieties over others. Eight varieties growing in the same orchard at Davis had nectar averages ranging from 10 to 28 percent sugar. Three other varieties had no collectible nectar. The Kelsey, a notably shy bearer at Davis, was one of these.
The pollen grains of various plants vary greatly in size, shape, and surface structure. Some flowers produce an abundance of pollen which is fully exposed. Others produce only a scanty amount which is tightly enclosed. These differences undoubtedly affect its collection by bees. The food value also varies. Some pollen grains are evidently too sticky for easy manipulation and others are too dry. In any event, trapped pollen supplies indicate the bee’s preference for some types. For example, a trap operated in a California cotton field failed to yield pollen from the cotton although it was abundant on the plants. In an almond orchard a large supply of almost pure almond pollen was readily trapped in spite of wildflower sources. Under a condition of scarcity, bees will even collect a pollen substitute like dry mash from a chicken feeder. Also, in a greenhouse they have been observed to collect tomato and beet pollens, which are ordinarily ignored outdoors. The rather omnivorous habit of honey bees of collecting pollen from so many plants, especially under stress for a supply, is radically different from that of many other bees, which require a special kind of pollen.

To a plant breeder the variety of pollen and the resulting seed within the species is a salient factor, as it is also to a grower in the case of certain self-unfruitful varieties. In many fruits, like apples, a nearly full complement of seeds is needed to produce a shapely product. To commercial cotton producers the lint is the chief thing, but there again the production of seed is important for two reasons—the production of normal lint depends upon fertile seeds, and such seeds are the source of cottonseed oil.

Producers of package bees make use of the early and abundant supplies of pollen in deciduous fruit orchards. Where that trade is established, many colonies are regularly rented to orchardists. The possibility of getting much honey from deciduous fruit blossoms is limited by their early blossoming. The quality of this honey also is generally low; for example, almond honey is bitter and prune honey readily ferments.

On the other hand, several of the summer-blossoming species of legumes, including alsike clover, white clover, sweetclover, hairy vetch, birdsfoot trefoil, and alfalfa, are sources of high-quality honeys. Red clover is usually not even considered a source of honey in the United States. Except for alfalfa, all these legumes are medium to good sources of pollen.

The chief supply of pollinators in the country is maintained by the beekeeping industry. In the past its size and extent have been based largely on the ability of the beekeeper to make a living from the production and sale of honey. There are about 6 million colonies in the United States—one-third are in the South, one-third west of the Mississippi, and the rest in the Northeast. Properly distributed, the supply of pollinators probably would be adequate to meet the needs of agriculture. In areas having concentrated plantings of specialty crops, such as deciduous fruits and small-seeded legumes, the growers must draw upon the bee industry to meet their great requirements for pollinators during blossoming time. Maintaining the industry in a healthy condition is essential to our agricultural economy.

A hive and all its bees can be moved readily by screening the entrance after the field workers come in for the night. It should be taken at least a mile and a half from the old location—or otherwise many of the bees would return to the former location and thus be lost. During hot weather a ventilating wire screen may have to be substituted for the regular cover. Commercial beekeepers frequently move colonies without closing the entrance, but the novice should not attempt to do so.

After a colony is moved, the bees reorient themselves by flying close to the hive until they become familiar with their new surroundings. The habit may be made use of in pollina-
Bees brought into an orchard at blooming time tend to work the nearby trees first, but often it may be necessary to move the colonies in ahead of the bloom. For example, an almond orchard in the West may be almost impassable from the beginning of the winter rains to the end of blooming in early spring. Bees are ordinarily placed in such orchards following harvest in the fall because colonies are moved from the river bottoms and the mountains at that time.

Throughout the country in deciduous-fruit areas, especially where apples, sweet cherries, and plums are grown, it is common practice to rent commercial bees for pollination during blooming time. Many colonies going to fruit orchards are of local origin but some long hauls are necessary. For example, bees are moved long distances to Wenatchee, Wash., Hood River, Oreg., the Shenandoah Valley in Virginia, and the apple districts of Pennsylvania. The colonies frequently come from the neighboring States.

Developments in the small-seeded legume industry since 1945 have shown the advantage of providing more bees than are normally present. Colonies are rented and often brought in from distant places. To the seed district around Delta, Utah, with about 30,000 acres in alfalfa, 10,000 to 15,000 colonies are brought each year. Beekeeping in the area is not feasible the year around, and most of the colonies are removed to southern California after the alfalfa season, a distance of 500 miles or more. Some colonies were moved more than 1,000 miles from southern California to Colorado for alfalfa-seed pollination in 1950. A similar situation occurs in the clover-seed area of Jefferson County in Oregon, where a large acreage is grown and some 15,000 colonies were moved in in 1950. Many of the colonies came from the Sacramento Valley in California, 500 miles away. A substantial income, either from a good honey crop or from rental fees, is required to take care of the high cost of such moves.

Bees are often moved by truck in lots of approximately 100 two-story hives—perhaps 4 million potential pollinators. The truck is loaded in the evening and goes nonstop to its destination. On arrival the colonies are placed in or near the fields.

Growers of cucumbers and some other plants in greenhouses have found it necessary to supply bees for pollination. The business is rather extensive. In the production of some hybrid seeds, cages supplied with bees are in use. Colonies depreciate rapidly in both greenhouses and cages, and frequent replacement is necessary.

When a beekeeper engages his bees for pollination service he faces special problems: Extra expenses for moving and caring for the colonies, shortage of feed, and insecticidal poisoning. Ordinarily he can expect no honey in orchards, and little or no surplus honey is obtained by the large number of colonies frequently used for alfalfa. It may even be necessary to feed the colonies. The grower should make sure that enough bees are provided during the blooming period to produce the maximum set of fruit or seed.

Bee-collected pollen pellets can be obtained readily with a pollen-collecting trap consisting of a screen grid which scrapes pollen from the legs of bees as they go through it to enter their hives.

Quantities of pollen of apple, almond, cherry, plum, and pear have been collected in that way at the California Agricultural Experiment Station. During favorable periods the yields per trap approached 2 pounds daily. More than 50 pounds have been obtained from one colony in a year.

Bees add substances to the pollen to form it into pellets. Sugar—nectar or honey—is one such substance, as shown by the higher content of sugar in bee-collected pollen than in hand-collected pollen. The viability of deciduous-fruit pollen from freshly gathered bee pellets is high, but at room temperature it rapidly loses its ability to germinate. Pollen taken from the anthers by hand,
however, remains viable for a longer period. The exact reason for the difference is not known.

In testing the viability of bee-pellet pollen, one can enhance germination by dispersing the pellets in a 15-percent cane sugar sirup immediately before plating on the agar medium. Smearing the dispersed grains on the plate separates them so that they may be readily counted in determining the percentage of germination.

Storage at low temperature greatly prolongs the viable life of the pollen from the pellets of honey bees as well as hand-collected pollen. Bee-collected apple pollen, removed from the trap at 30-minute intervals, frozen with dry ice, and placed in a freezing compartment in 1949, remained highly viable for a year. In the spring of 1950 the pollen was used to hand-pollinate apple blossoms in the orchard from which it was collected in 1949. Subsequently fruits were set and matured. This demonstration of stability should assure future progress in the use of bee-collected pollen in artificial pollination.

Some beekeepers trap bee-collected pollen and dry and store it for feeding their bees when pollen is scarce. The trapped pollen is sometimes shipped from areas with mild winters to Northern States where long winters make supplementary feeding necessary. Perhaps bee-collected pollen might also be valuable for medicinal purposes or as a source of vitamins. Honey contains numerous pollen grains—the age-old belief that honey is healthful may have its basis in that fact. The pollen pellets might also be beneficial in the diet of baby chicks. We believe that these and other potential uses should be investigated.

**Controlled artificial pollination** has been used for many years in plant-breeding work and in studies to determine the pollination requirements of our cultivated plants. The usual practice is to emasculate the blossoms of the mother variety, apply the desired pollen to the stigma, and bag the flowers to exclude insects which might bring unwanted pollen. Many superior varieties of fruit, vegetable, and field crops have been developed in this way. The method also has been used in breeding varieties of forest trees, particularly pines.

Commercial hand-pollination of dates has been practiced since ancient times. The cluster of male or staminate flowers—the spadix—is removed from the male date palm and shaken gently over the flower clusters of the female tree.

L. H. MacDaniels and A. J. Heinicke in 1929 suggested using hand-pollination as a temporary expedient in apple orchards consisting of solid blocks of self-unfruitful varieties. They also thought such pollination might be worth while in years of unfavorable weather conditions even in apple orchards well provided with pollinizing varieties. Later MacDaniels put the method on a commercial basis and developed carriers for diluting the pollen for more economical use.

About that time the pollination problem had become acute in the apple-producing sections of Washington because of the heavy spray program, which practically eliminated pollinating insects, and the removal of less profitable varieties in favor of Delicious and Winesaps, both of which are self-unfruitful. Winesap produces mostly nonviable pollen and is therefore an ineffective pollinator for Delicious.

Washington apple growers quickly adopted the methods suggested by MacDaniels and Heinicke. By 1937 hundreds of acres of Delicious orchards were hand-pollinated in the Wenatchee and Yakima districts. More recently the trend has been to provide means for cross-pollination by insects by grafting over some Winesap and Delicious trees to pollinizing varieties, interplanting pollinator trees, and providing more bees. Most growers now make sure that their new plantings contain adequate pollinizing varieties.

Pollen for hand-pollination is ob-
tained by gathering flowers from a variety known to be a good pollinizer for the variety in question and removing the anthers by rubbing the flowers over 8-mesh hardware cloth. Blossoms should be gathered when most of them are in the balloon stage, just before the petals open. The pollen can be cured by holding the anthers in shallow trays at room temperature for about 2 days. The cured pollen should be placed in bottles stoppered with cotton and held in a dry, cool place until it is used.

Materials such as lycopodium spores, wheat flour, cornstarch, egg albumen, and powdered milk have been used to dilute the pollen in order to reduce the cost of hand-pollination. Lycopodium spores generally have proved to be the most satisfactory carrier, although tests have shown definite promise for powdered milk and egg albumen, which cost less than lycopodium.

To hand-pollinate an apple tree in good bloom, the usual practice is to touch the stigmas of one flower in every fourth or fifth cluster. A size 4 pig-hair brush, the rubber end of a pencil, a cork, or the bare finger can be used. The pollen should be applied 1 to 3 days after the flowers open because the flowers are no longer receptive to pollination when the tips of the styles turn brown. A skilled operator can pollinate a 20-year-old apple tree in about an hour. It would take much longer to hand-pollinate a fruit tree like the sweet cherry, in which a much higher percentage of the blossoms must set fruit in order to give a commercial crop.

Regardless of how the pollen is obtained or how much it is diluted, hand-pollination is laborious and costly—especially in light of the relatively low cost of pollination by bees. One argument in favor of hand cross-pollination is that it will greatly reduce the amount of fruit thinning needed to obtain good size where natural pollinating agents are not available. According to John C. Snyder, however, the idea of reducing thinning costs does not justify the permanent use of hand-pollination as a substitute for pollinizer varieties and honey bees.

Many labor-saving methods for applying pollen have been developed and tested. Dust and liquid mixtures of pollen have been applied from airplanes and conventional spray and dusting equipment. Bombs and shotgun shells containing pollen have been used for rapid distribution of pollen. Under controlled experimental tests conducted by R. M. Bullock and F. L. Overley, however, these rapid methods have failed to give significant increases in fruit set. They concluded that hand-pollination is the most satisfactory method of artificial pollination.

A semiartificial method of cross-pollination involves pollen dispensers designed to force honey bees to pass through prepared pollen as they leave the hive. The idea is that the bees will pick up the pollen and spread it through the orchard. Overley and W. J. O’Neill tested two types of pollen dispensers and reported that their value was questionable.

During 1951 we supplied hives of bees with pollen dispensers for almond and sweet cherry trees, which were caged to exclude outside insects. Only a few fruits were set on the trees even though the dispensers were kept supplied with viable pollen throughout the blooming period and the bees actively worked the blossoms. Satisfactory fruit sets were obtained on branches of the trees to which the same pollen was applied by hand.

A person collecting pollen by hand can usually gather only enough green anthers from fruit blossoms in an 8-hour day to produce 3 to 5 ounces of cured pollen. But bee-collected pollen can be obtained readily in almost unlimited quantities by the use of pollen traps. The pollen pellets of the common fruit species are readily distinguished by their color. Although all bees of a colony do not visit the same species, one can get a nearly pure sample by careful selection of the time and place of trapping.
Experiments at Davis, Calif., during 1948 showed that the percentage of viability of freshly trapped pellet-pollen is approximately the same as that of hand-collected pollen. It also gave fruit sets that compared favorably with those effected by hand-collected pollen when it was applied by hand with small brushes. Diluting the bee-pollen with an equal amount of lycopodium spores hardly reduced fruit set. Although viability of this pollen is rapidly lost at room temperature, it can be maintained for several days in ordinary cold storage at about 32° F., and for a much longer period at extremely low temperatures. If handled properly, therefore, the pollen in freshly trapped pollen pellets of honey bees may serve as well as hand-collected pollen in hand-pollination.

Various methods of rapid application of the pellet-pollen have been tested. The pellets have been dispersed in water and in salt and sugar solutions. The resulting mixtures have been sprayed on almonds, sweet cherries, plums, apples, and pears. The various pellet-pollens also have been applied as dusts after they were mixed with various carrying powders. Thus far commercial fruit sets have not been obtained from such rapid methods of application. J. C. Kremer suggested that bee-collected pollen from early blooming apple varieties could be mixed with lycopodium spores and stored under dry conditions at 34° to 36°. The mixture could then be used later in pollen dispensers inserted at the entrance of bee colonies for the cross-pollination of varieties that blossomed late in the spring. This method failed to give satisfactory fruit sets when tested on caged almond and sweet cherry trees at Davis during the blossoming period of 1951.

There is much more to getting results in pollination than an adequate supply of bees. The blossoms must be attractive to the pollen distributors for either pollen or nectar. For best results the specific blossoms must be more attractive than their competitors. For the self-unfruitful varieties compatible sources of pollen must be at hand. In producing seed from male-sterile varieties the same is true. The varieties providing pollen and those needing it must flower at the same time. Even after all other factors are taken into account, bad weather can cause failure by preventing insect activity. Some of those factors are brought out in the following paragraphs about some plants that need the help of insects for pollination.

Many commercial fruit varieties are propagated asexually. From the viewpoint of pollination, therefore, an orchard of a single variety is one tree, so to speak. Self-unfruitfulness in such a case creates a pollination problem that requires special consideration in the planting of an orchard.

The almond is an interesting example of self-unfruitfulness. Almonds were planted in California in 1853, but the yields of the early orchards were low and variable. The eventual failure of the first plantings was due largely to a lack of knowledge of pollination requirements and other factors of successful culture. California had 100,000 acres of almonds in 1952. According to W. P. Tufts, the pollination problem with the almond was recognized and recorded as early as 1885, when A. T. Hatch of Suisun noted that Languedoc trees growing near seedlings always produced heavier crops than those planted in solid blocks—the only plausible explanation for the many instances of crop failure was lack of cross-pollination. Tufts’ early studies indicated the self-incompatibility of some varieties. Later investigations showed that all varieties were self-unfruitful and that a few pairs of varieties were interincompatible. For example, Nonpareil and I. X. L., Languedoc and Texas, and Jordanolo and Harpareil are interincompatible pairs. Combinations of those varieties therefore should be planted without putting a pollinator with them.
The eventual recommendation was to plant the proper varieties with specific reference to pollination requirements.

Almonds may bloom from the end of January to the end of March. They may be classed as early or later in the time of blossoming. The following list gives varieties in the usual sequence of blooming from the earliest to the latest (Nonpareil is included in both groups because it occupies a position about midway): **Early**—Harriott, Jordanolo, Jordan, Ne Plus Ultra, Harpareil, King, California, Lewelling, I. X. L., Peerless, Princess, Nonpareil. **Late**—Nonpareil, Drake, Eureka, Languedoc, Texas, Reams.

Except in the instances we noted of the interincompatibility, any varieties listed as early or late will usually serve as a satisfactory pollinizer for any other variety in the same list. The blossoming periods of very early blooming varieties as Harriott and Jordanolo, however, may not overlap sufficiently in some seasons to insure adequate cross-pollination with Nonpareil. Many almond growers have planted only Jordanolo and Nonpareil because of their greater commercial value. From a pollination standpoint, however, that combination is often poor.

Because almond trees blossom early when the weather may be too cool for maximum insect activity, more bees and more trees of the pollinizing variety are needed than for later blossoming fruits. There should be at least one row of pollinizers for every three rows of the main variety. In adverse seasons it would pay to have two rows of the main variety and then two rows of the pollinizer. Two or three strong colonies of bees should be supplied per acre.

Almost all varieties of the European pear are self-unfruitful. A few (Doyenné du Comice, Flemish Beauty, Beurré Hardy, Howell) are usually self-fruitful, but even they generally will produce better crops when they are cross-pollinated. In some localities in California, Bartlett, Colonel Wilder, Beurré d'Anjou, Seckel, and Beurré Clairgeau may range from partly to completely self-fruitful in some years.

The Bartlett (or Williams' Bon Chrétien) is a widely grown variety. California had more than 36,000 acres of Bartlets in 1952. It is self-unfruitful in the East. Bartlett is said to be usually self-fruitful under interior valley and coastal conditions in California, but should not be planted without pollinizers in the Sierra Nevada foothills. Hand cross-pollination has given greatly increased fruit sets over self-pollination or open (natural) pollination, regardless of location or whether the trees were planted in solid blocks or provided with pollinizers.

Except for a few very early and late blossoming varieties, the blooming periods of most of the commonly grown pears overlap well enough for cross-pollination. Bartlett has a long, mid-season blooming period that overlaps those of nearly all the other important varieties with the possible exception of the very early Le Conte, Forelle, Kieffer, and Clairgeau.

Winter Nelis has proved to be the most satisfactory pollinizer for Bartlett under most conditions in California. In the East and Northwest, Bartlett blooms several days before Winter Nelis. In California, however, following the warmest winters, the blossoming period of the Winter Nelis may be past before the Bartlett blossoms have opened.

Nectar-collecting honey bees usually prefer flowers of other plants to those of pears. That undoubtedly is because some pear flowers provide a relatively small amount of nectar, low in sugar concentration. Bees do work pear blossoms for pollen, which most varieties produce in abundance. If the concentration of bees is great enough, therefore, effective cross-pollination will undoubtedly result in orchards that have enough pollinizing varieties. Orchardists who desire a heavier fruit set probably should provide two or three colonies of bees instead of one, as is usually recommended.
Honey Bees as Agents of Pollination

Nearly all of the commercially important pears in the United States produce viable pollen and will effectively cross-pollinate each other. Only the combination of Bartlett and Seckel has proved to be interincompatible. Other unfruitful combinations have been reported among closely related varieties. Several European varieties produce mostly nonviable pollen and therefore cannot be used as pollinizers.

Cherries are of three groups—sweet cherries, sour or pie cherries, and Duke cherries, which are hybrids of the other two.

Most of the sweet cherries grown in the United States are produced in the Pacific Coast States. California produces the bulk of the crop. Small commercial plantings of sour cherries are in western Oregon and Washington, although the main production is in the Northeast. Duke varieties are of little commercial importance anywhere in the country.

All varieties of sweet cherries are self-unfruitful and must be cross-pollinated for satisfactory yields. Not all combinations of varieties are fruitful. Examples of variety combinations that are interincompatible and therefore will not produce crops when planted together (unless other effective pollinating varieties are provided) are: Early Purple and Rockport; Advance and Rockport; Windsor and Abundance; Napoleon (Royal Ann), Bing, and Lambert; Black Tartarian, Knight's Early Black, and Early Rivers. (Some strains of Black Tartarian may be interfruitful with Knight's Early Black and Early Rivers.)

All important sweet cherry varieties produce good, viable pollen. Most variety combinations should be interfruitful therefore if their blooming periods overlap enough.

As to pollination, there are evidently different strains of certain cherry varieties, perhaps because seedlings that now exist are so similar to the original varieties that they cannot be distinguished from their parents. One should therefore select trees of strains that he knows can fertilize the desired variety. Varieties bloom at different times. One should select varieties that have overlapping blooming periods and are interfruitful. The average blooming period for most sweet cherries is about 2 weeks. Weather conditions just before and during bloom markedly influence the length of the period of bloom as well as the dates of blooming, but varieties keep approximately the same order of blooming each season. A list of most of the varieties grown in California in order of earliness of blooming is: Early—Burbank, Chapman, California Advance, Black Heart, Knight's Early Black, Early Purple Guigne, Black Republican, Black Tartarian. Late—Napoleon (Royal Ann), Windsor, Parkhill, Early Rivers, Rockport, Bing, Pontiac, Abundance, Bush Tartarian, Noir de Schmidt, Giant, Lambert, Saylor, Long Stem Bing, Gil Peck, Deacon.

The blossoming periods of the varieties within each group will usually coincide well enough for effective cross-pollination. The blossoming periods of Black Tartarian and Black Republican generally overlap well enough with those in the late group for satisfactory cross-transfer of pollen.

In the East the blooming periods of the main varieties usually coincide well enough for cross-pollination.

In general, only sweet cherries should be planted for cross-pollination of sweet cherries. Sour cherries usually bloom too late to be satisfactory pollinizers for sweet cherries, and the percentages of fruit set are low. Duke cherries are unsatisfactory pollinizers for sweet cherries, although the blooming periods of the Duke cherries coincide with those of the late sweet cherries.

The commercially important varieties of sour cherries (Early Richmond, Montmorency, Dyhouse, and the Morello group) are self-fruitful if enough pollinating insects are available. Better crops can be expected, however, if a
sour cherry orchard contains more than one variety. Almost any variety of sour cherry will serve as an effective pollinator for the other sour varieties. The later blooming sweet cherries will also satisfactorily cross-pollinate the sour varieties if their blooming periods overlap enough. The pollen of Duke cherries usually does not give satisfactory fruit sets on sour cherries.

Some of the Duke varieties, such as Royal Duke and May Duke, may be partly self-fruitful, but cross-pollination is essential for commercial crops. Duke cherries will generally set heavier crops when cross-pollinated by either sweet or sour cherries than when other Duke varieties are used as pollinizers for them. The pollen of Duke cherries gives low percentages of germination in laboratory tests. The low order of viability of their pollen undoubtedly explains why Duke cherries serve as poor pollinizers for sweet and sour cherries as well as other Dukes. Sweet cherries in the late-blossoming group make satisfactory pollinizers for such earlier blossoming Duke cherries as Olivet, Reine Hortense, and May Duke. But the sour cherry varieties may best serve as pollinizers for the later blooming Dukes, Late Duke, Royal Duke, and Abesse d'Oignies.

Keeping boxes of honey bees in the home apple orchard was a common practice even before the development of the movable frame beehive. The need for cross-pollination was not appreciated, however, until the growers started standardizing and limiting their orchards to a few varieties. Undoubtedly the decline in the activity of native wild pollinating insects also was a factor.

A few varieties (Baldwin, Early Harvest, Grimes Golden, Oldenburg, Rome Beauty, Wealthy, Yellow Transparent, Yellow Newtown) are considered to be self-fruitful in certain favorable locations. Some others (Ben Davis, Esopus Spitzenburg, Golden Delicious, Jonathan, Red Astrachan, Wagener, and York Imperial) produce varying amounts of a commercial crop when self-pollinated. It is generally agreed, however, that all varieties should be interplanted and that honey bees be put among them during the blooming periods to insure good yields.

The following are unusually good pollinizers and generally effect excellent sets of fruit on most other varieties: Ben Davis, Delicious, Fameuse, Golden Delicious, Grimes, Golden, Jonathan, McIntosh, Northern Spy, Rome Beauty, Wagener, Wealthy, Winter Banana, Yellow Transparent, and York Imperial.

Others, including Arkansas, Baldwin, Gravenstein, Rhode Island Greening, Stark, Stayman Winesap, Thompson King, and Winesap, produce mostly infertile pollen and consequently are ineffective as cross-pollinizers.

Most other commercial varieties grown in this country usually serve as satisfactory pollinizers.

Interunfruitful combinations are rare except among closely related varieties and those having infertile pollen. Parent varieties are ineffective as cross-pollinizers for their color sports or bud mutations, and the mutations, in turn, are of no value as cross-pollinizers for the parent variety. For example, Delicious is interincompatible with any of its color sports, such as Redwin, Richared, Starking, and Shotwell Delicious.

An exception is Grimes Golden, which is ineffective as a pollinizer for Arkansas but an excellent pollinizer for other varieties. Presumably it is unrelated to Arkansas.

According to present evidence, based mainly on orchard observations, color mutations of apple varieties have the same pollination requirements and value as cross-pollinizers as their parent varieties.

The blooming periods of two varieties must overlap if cross-pollination is to be accomplished. According to W. H. Chandler and others, apple trees require more chilling before their buds will open evenly in the spring than most other fruits. Mild winters may
Honey Bees as Agents of Pollination

widen the gap between the blooming dates. The relative order of blooming, however, is usually the same for any one locality. High spring temperatures following winters cold enough to meet the chilling requirements tend to shorten the blooming periods of all varieties. Under those conditions, all but the very early- and late-blooming varieties will overlap sufficiently for pollination. On the other hand, cold spring weather will tend to cause the blooming periods of the early and late varieties to be much more widely separated. In most years, however, midseason varieties would overlap with the early- and late-blooming ones sufficiently to provide an adequate pollen supply.

The pollination requirements of plums have been studied at the California Agricultural Experiment Station for more than 40 years. Beginning in 1916, A. H. Hendrickson made a series of reports showing self-unfruitfulness of many varieties of European and Japanese plums. He also showed that bees must be provided in plum orchards for commercial crops even though the varieties are highly self-fruitful. Since then, work in England, New York, Michigan, and California has shown that the European plums may be classified as usually self-fruitful, partly self-fruitful, or self-unfruitful. The self-unfruitful varieties outnumber those that may be listed as partly or completely self-fruitful. Apparently no interincompatible pairs or groups of European plum varieties exist among those grown commercially in the United States. Because most varieties produce a high percentage of viable pollen, any variety should be effective in cross-pollinating another, provided their blossoming seasons overlap sufficiently.

The blooming season of the European plums in the East usually overlaps well enough to provide cross-pollination. In California the varieties are classed as either early or late blossoming.

Most of the Japanese plums are self-unfruitful. A few varieties, such as Beauty, Climax, Methley, Red Rosa, and Santa Rosa, are partly self-fruitful, but, like the others, these five varieties will generally set much better when interplanted with other varieties for cross-pollination. Some of the earlier blossoming Japanese varieties are deficient in pollen production, and several varieties produce pollen that is low in viability. Other varieties, like Burbank, Duarte, Elephant Heart, Red Rosa, Redhart, Santa Rosa, and Wickson, are satisfactory pollinizers. The blossoming season of Tragedy, a European plum, coincides with several of the late Japanese varieties. Tragedy is also a moderately effective pollinizer for several Japanese plums, but it does not set fruit following cross-pollination by them. Certain American plums are also effective pollinizers for several Japanese varieties.

The necessity of finding a specific pollinizer is emphasized in the case of Elephant Heart. It is attractive and one of the largest of the Japanese plums. It has high quality and is a good shipper. It would undoubtedly be an important late-season plum except for its shy bearing habit. Between 1936 and 1948, workers at the California station tried 21 varieties as pollinizers for Elephant Heart. Finally in 1948, Myrobalan 5Q, a selected Myrobalan seedling and one of 47 varieties of pollen tested as pollinizers for Elephant Heart that year, gave a satisfactory fruit set. Extensive tests in 1949 proved that Elephant Heart can produce heavy crops with this source of cross-pollination. But the fruit of Myrobalan 5Q has no commercial value and the search for a suitable pollinizer was continued. In 1950 it was discovered that a promising new Japanese variety, Redheart, developed in breeding work, will also bring about heavy fruit sets on Elephant Heart.

Seed production is the object of pollination of legumes. The most familiar large-seeded legumes such as peas and beans are generally self-pol-
linated, but many of the small-seeded ones require insect pollination. Even with the self-fertile legumes, cross-pollination is desirable because greater vigor results. The seedling plants in a legume field are of mixed heredity; that is ideal for true crossing and is different from orchard trees, which are propagated asexually.

Some of the self-fertile species of legumes require tripping—release of the staminal column—by insects before they will set seed. In the process, cross-pollination is readily accomplished. An orchard presents a relatively small number of blossoms, and only some of them are required to give a commercial crop. But a legume field has a tremendous number of blossoms, and it is desirable to set the greatest possible number of pods. The orchardist may accomplish his aim with one colony to the acre, but in some legume fields five or more colonies may be needed to set maximum crops.

Alfalfa has become our leading legume hay crop. Adapted varieties are grown extensively even in the Middle West, where early attempts at production failed. The Intermountain States, particularly Utah, used to be the important producers of alfalfa seed. Since 1925, however, their yields gradually declined from 8 to 10 bushels an acre to as low as 1 bushel. Injurious insects may have been a factor, but the reduction in the number of wild bees is considered to be one of the main causes of the lowered yields.

Alfalfa blossoms require tripping (forcing the pistil out of the keel) and cross-pollination by insects for high-yields of seed. Native wild bees, notably leaf-cutting bees and alkali bees, took to alfalfa as a favorite source of pollen and nectar; where they are still abundant, tripping proceeds apace and high seed yields are maintained.

As a rule, the pollen collectors are more efficient in tripping than the nectar collectors. The presence of more easily worked pollen sources within flight range, such as mustard, sweet-clover, birdsfoot trefoil, and star-thistle, attracts the pollen-collecting bees away from alfalfa. For example, pollen trapped in the Cache Valley of Utah, which has other good pollen sources, contained little or no alfalfa pollen. A high proportion of alfalfa pollen was obtained in traps at Delta, Utah, where more attractive sources of pollen were limited.

The use of honey bees to pollinate alfalfa blossoms has increased greatly. California, which has many bee colonies, has been making rapid strides in seed production. The State produced 15 million pounds in 1949; many yields ranged from 500 to 1,600 pounds or more of seed an acre. The 1950 yield was 33 million pounds. A survey by workers at the experiment station indicated that a production of 150 to 200 pounds of seed per acre per colony of bees was not uncommon. In one instance, a 132-acre field was supplied with bees during the flowering season at the rate of 5 or 6 colonies an acre. It was inspected daily for 2 months. Almost no wild bees were seen. Only limited amounts of pollen were collected by honey bees, but nectar-collecting bees were numerous. The field averaged 896 pounds of recleaned seed to the acre. Tripping was continuous but relatively slow in comparison to the rapid tripping by wild bees or pollen-collecting honey bees, as noted in some favored areas of other States.

In earlier years bees were usually placed in large apiaries outside the field to be pollinated. The practice has been growing of scattering the colonies in small apiaries along drives crossing the field. Field experiments in 1949 and 1950 showed an increase in the rate of tripping around newly established groups of colonies—indicating the superiority of the newer arrangement.

Until recently the honey bee has not been considered an effective pollinator of red clover because measurements have shown that the length of the corolla tube of the floret exceeds the length of the honey bee’s tongue.
The longer-tongued bumble bees have often been given credit for being the important pollinators of red clover because they collect nectar and pollen from this plant in preference to many others. If bumble bees are numerous, no particular difficulty is experienced in setting seed, but they are becoming scarce in many areas.

W. E. Dunham reported that of the insects responsible for red clover pollination in Ohio several years ago, 82 percent were honey bees, 15 percent were bumble bees, and 3 percent other insects. An acre of red clover is said to contain some 216 million individual florets. A bee takes about 30 minutes to visit 346 florets to get a load of pollen.

R. G. Richmond showed that red clover caged with honey bees in Colorado produced 61.5 seeds per flower head and only 0.49 seeds per head when pollinating insects were excluded. He stated that first-cutting red clover set a good seed crop when conditions were inviting to honey bees.

A 27-acre field of Kenland red clover in the Sacramento Valley produced 616 pounds of clean seed to the acre in 1950. The field was planted that spring and no hay was cut. A large acreage of seed alfalfa was growing in the adjoining field. Honey bee colonies were in scattered groups in all fields. The grower stated that the bees worked the clover and the alfalfa about equally well.

Pollination of red clover is accomplished by the honey bee in this way: The bee approaches the floret over the keel and forces its head down directly between the keel and the standard petal. The fore and middle pairs of legs clutch and claw at the wings of the floret to spring them and the keel away from the standard, thus tripping the flower. Tripping exposes the stigma and anthers, which touch the bee on the underneath side of the head where it joins the thorax. Pollen is thus accumulated and carried to the next blossom.

White clover also needs pollination by insects for seed production. The several varieties, among them British, Dutch, and Ladino, are freely worked by honey bees. White clover is a leading source of honey in the North Central and Northeastern States, but Ladino clover (giant white) from Italy does not equal the Dutch clover (small white) in honey production. Because those two types readily cross, stands grown for seed must be far enough apart so insects cannot fly from one field to the other.

In Oregon, from Ladino plants in cages where no insects could reach them, H. A. Scullen harvested 300 seeds from a sample of 100 heads; 100 heads just outside the cages yielded 14,900 seeds. At Thornton, Calif., where three colonies of bees per acre were placed for pollinating alfalfa and red clover, heads from stray Ladino plants averaged 276 seeds each, or a total of 27,600 seeds in 100 heads.

The sweetclovers grown in the United States include many varieties, both yellow and white. Some are self-pollinating and self-fertile; others are self-fertile but require insect pollination, and still others are self-sterile and require cross-pollination. As a source of both nectar and pollen, sweetclover is highly attractive to honey bees. Variation among plants is increased by cross-pollination effected by the large number of bees that visit the plants. Increased yields of sweetclover seed have been demonstrated many times by providing at least one colony of bees to the acre.

Crimson clover, of the true clovers, is the most important winter annual cover crop in the United States. The different varieties are self-fertile, but their florets are not self-tripping, and insect visitation is required for heavy seed crops. Growers of crimson clover seed have become increasingly conscious of the benefits from introducing colonies of honey bees into their fields.

Observations in the lower Sacramento Valley disclosed that relatively few bees are required for pollination...
of all Ladino clover florets, compared to the numbers required for pollination of alfalfa. New flower buds do not open until the middle of the morning, and a concentration of two or three bees to the square yard can work all of them repeatedly in one afternoon. Following pollination, the florets turn down on the stem and close permanently at nightfall. Nectar is not secreted for 3 to 6 hours after a bud opens. In June and July the bees generally work the blossoms for pollen.

Alsike clover depends upon pollination by honey bees and also to some extent on wild insects for seed production. Alsike produces an enormous number of individual florets, all of which must be cross-pollinated for heavy yields of seed. Field experiments in Ohio demonstrated that honey bees increased seed yields from a 10-year average of 1.6 bushels an acre to 8 bushels an acre. Yields as high as 20 bushels an acre were found to be possible with maximum insect pollination.

Alsike bloom produces a relatively poor supply of nectar in some years. If the concentration of bees is heavy enough to pollinate the crop adequately under such conditions, very little honey will be produced.

**Birdsfoot Trefoil** is becoming an important permanent pasture crop. Apparently it does well on many soils where clovers and alfalfa do poorly. As it is self-sterile, seed formation depends upon cross-pollination by insects. On caged insect-free plots in Oregon, H. A. Scullen obtained no seeds on either birdsfoot or big trefoil while similar plants exposed to bees seeded freely. The flowers of trefoil have great attraction for bees as a source of nectar and pollen. Bees were observed to leave a flowering alfalfa field near Davis, Calif., and fly 1 mile to gather trefoil pollen. Exceptionally heavy seed yields have been obtained where there were many bee colonies.

**Many vegetables** do not require pollination to produce an edible crop, but of these, carrots, radishes, turnips, cabbage, celery, and many others require insect pollination for seed production. Both pollination and seed formation are essential in the production of the edible part of the pickling cucumber, cantaloup, and watermelon. Pollination of all sections of the compound ovary is evidently necessary for proper shape and quality of melons, as the deformed part of an incompletely pollinated cantaloup not only lacks seed but is also poor in sweetness and flavor. Honey bees are employed in the commercial production of the seed and fruit of several vegetable crops.

Variatel crossing is generally undesirable in producing seeds for the propagation of vegetable crops. Hence the Department of Agriculture regulations require that in the production of seed of many vegetables the plots of the different varieties must be at least one-fourth mile apart. An even greater distance would be safer because pollen grains are always found on the honey bee and its flight range exceeds one-fourth mile.

Cucumbers, muskmelons, watermelons, pumpkins, and squash have similar floral structures. The group—cucurbits—generally is characterized by having male and female blossoms on different parts of the same plant. Such an arrangement obviously requires insects for the transfer of pollen, as the plants are not wind-pollinated. Most varieties of cucurbits are self- and interfertile when pollinated by hand.

Honey bees are widely used in greenhouse and field production of cucumbers. Because the individual flowers are open for only a short time, a heavy concentration of bees is advisable whether the cucumbers are grown for the fresh market, for pickling, or for seed.

Watermelons and muskmelons often produce bisexual or complete flowers, instead of separate pistillate and staminate flowers. The complete flowers, however, do not fertilize themselves, and honey bees are as essential in their pollination as in the pistillate flowers.
Cabbage and the closely related cabbage-like plants as cauliflower, broccoli, and Brussels sprouts require cross-pollination by insects for good seed yields. Varieties of cabbage display various degrees of self-incompatibility. Cross-incompatibility is also common.

Bees are effective agents in cross-pollination. Attempts to bring about self-pollination have had little success. Besides honey bees, cuckoo bees, leaf-cutting bees, mining bees, bumble bees, and bee flies are attracted to cabbage flowers. Some are said to work at lower temperatures than the honey bee. Because cabbage for seed production is often grown in a cool location or during cool weather, some of these insects may be individually more effective than the honey bee in its pollination. The optimum temperature for pollen germination, however, is about 68°F., and bees are active in the field at temperatures as low as 60°F.

English holly trees bear their pistillate and staminate flowers on separate plants. Although a small percentage of the pistillate flowers on some trees develop parthenocarpic berries, facilities for cross-pollination are required for commercial crops. The seeded berries resulting from cross-pollination are larger, less subject to premature dropping, earlier maturing, and more resistant to withering after cutting. Bees are attracted to both staminate and pistillate holly flowers to such an extent that, when they are abundant, only one male tree is needed for pollinating 50 pistillate trees. The pollinizers should be selected for their foliage quality as well as their capacity to produce an abundance of viable pollen when the pistillate trees are blooming.

Pollination by honey bees has thus become an essential factor in producing many crops, along with the factors that are taken for granted, such as the preparation of the soil, the supplying of moisture, and cultivation, pruning, and thinning. Because beekeeping is a specialty, just as fruit growing or the production of seeds are specialties, most growers will find it advantageous to rent bees rather than to keep their own. Cooperation between grower and beekeeper thus becomes important and is mutually advantageous.

George H. Vansell, an apiculturist in the Department of Agriculture, is stationed at Davis, Calif. He has studied in the University of Kansas, Harvard and Stanford Universities, and the University of California. He has taught in the Universities of Kentucky and California. The activity of bees in collecting nectar and pollen, especially as agents of pollen distribution, has been his chief interest for many years.

W. H. Griggs is assistant professor of pomology in the University of California at Davis. He has charge of investigations into the pollination of fruits and nuts. He received his training in pomology in the University of Missouri and the University of Maryland. Dr. Griggs was assistant professor of pomology in the University of Connecticut in 1946 and 1947.

For further reference:
C. N. Buzzard: Bee Organization, Bee World, volume 17, pages 133–135, 1936; De l'Organisation du Travail chez les...


M. B. Cummings, E. W. Jenkins, and R. G. Dunning: Sterility in Pears, Vermont Agricultural Experiment Station Bulletin 408, 1936.

Charles Robert Darwin: The Effects of Cross and Self Fertilisation in the Vegetable Kingdom, D. Appleton & Co. 1877.


Olav Einset: Experiments in Cherry Pollination, New York Agricultural Experiment Station (Geneva) Bulletin 617, 1932.

S. W. Fletcher: Pollination of Bartlett and Kieffer Pears, Annual Report of Virginia Polytechnic Institute Agricultural Experiment Station for 1909, pages 213-224, 1910.


Yearbook of Agriculture 1952


A. H. Hendrickson: The Common Honey Bee as an Agent in Prune Pollination, California Agricultural Experiment Station Bulletin 291, 1918; Plum Pollination, California Agricultural Experiment Station Bulletin 310, 1919; Further Experiments in Plum Pollination, California Agricultural Experiment Station Bulletin 352, 1922.


Paul Knuth: Handbuch der Blütenbiologie, 5 volumes, Wilhelm Engeleman, Leipzig, Germany, 1896.


L. H. MacDaniels: The Possibilities of Hand Pollination in the Orchard on a Commercial Scale, Proceedings of the American Society for Horticultural Science, volume 27, 370-373, 1931; Pollination and Other Factors Affecting the Set of Fruit With Special Reference to the Apple, with A. J. Heinicke, Cornell Agricultural Experiment Station Bulletin 497, 1929.


O. H. Pearson: Observations on the Type of Sterility in Brassica Oleracea var. Capitata, Proceedings of the American Society for Horticultural Science, volume 26, pages 34-38, 1929; Breeding Plants of the Cab-
bage Group, California Agricultural Experiment Station Bulletin 532, 1932.

G. L. Philp: Cherry Culture in California, California Agricultural Extension Circular 46, revised. 1947.


R. G. Richmond: Red Clover Pollination of Honey Bees in Colorado, Colorado Agricultural Experiment Station Bulletin 391. 1932.


R. H. Roberts: Better Cherry Yields in Wisconsin, Wisconsin Agricultural Experiment Station Bulletin 344. 1922.


J. S. Shoemaker: Cherry Pollination Studies, Ohio Agricultural Experiment Station Bulletin 422. 1928.

C. E. Shuster: Pollination and Growing of the Cherry, Oregon Agricultural Experiment Station Bulletin 212. 1925.


W. P. Tufts: Almond Pollination, California Agricultural Experiment Station Bulletin 306, 1919; and California Agricultural Experiment Station Bulletins 348: Almond Pollination (1922), 373: Pear Pollination (1923), and 385: Pollination of the Sweet Cherry (1925), with G. L. Philp.

Pollination by Native Insects

George E. Bohart

The earliest flowering plants in the fossil record were related to the magnolias, which to this day depend for pollination on the visits of beetles. Beetles, which comprise the order Coleoptera, were the most abundant and adaptable insects during the dawn period of flowering plants and thus, quite naturally, were the first pollinators. The flies and the sawflies and wasps were present but poor in variety and primitively developed. In the ensuing ages, however, their adaptation to the products of flowers became a dominant feature of their structure and habits. The moths and butterflies, which first appeared in the early days of flowers, soon adapted themselves completely to floral offerings. Now nearly all of them are highly developed for taking nectar from flowers.

While the insects were thus becoming specialized to take advantage of flowers, plants were likewise becoming specialized to make more efficient use of insects. Certain flowers developed characteristics limiting them to pollination by certain types of insects, which in turn become highly adapted to these specialized flowers. Today we have many plants so constructed that only a few specially adapted insects can visit them successfully. Figs, orchids, Spanish-bayonet, and monkshood are examples.

The so-called hawk-moth orchids (in the genera Habenaria, Angraecum, and others) exemplify the many intricate modifications possessed by orchids to insure pollination by specific kinds of insects. In these flowers the nectar, lying at the bottom of a long narrow tube, is accessible only to the long-tongued hawk moths. While