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Basic Aspects of Pollination by Honey Bees in Hybrid Cucumber and Onion Seed Production

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ABSTRACT

Difficulties in pollen transfer have adversely affected seed production of hybrid onion (Allium cepa L.) in the United States. Six onion cultivars were examined for differential attractiveness to the honey bee (Apis mellifera L.). Honey bees clearly discriminated between the onion cultivars in both open plots and caged plots. Nectar secretion, nectar potassium content, and flower phenology were correlated with honey bee visitation.

Onion cultivars also demonstrated differential flowering potential. The cultivars produced from 176 to 359 flowers per umbel with 32 to 74 umbels per 30 onion plants. All onion cultivars examined contained viscous nectar with sugar concentrations ranging from 51 to 65% of total dissolved solids. Nectar secretion rates ranged from 0.54 to 0.84 ul per floret per day. Onion nectar was analyzed by gas chromatography to determine qualitative sugar differences among onion cultivars. All cultivars were hexose dominant with an approximately 1:1 fructose:glucose ratio. However, fructose was slightly more abundant than glucose. Sucrose was much less abundant than the hexose sugars. Nectar sugar content and composition appear to explain a major part of the honey bee visitation preferences between cultivars documented in this study.

Atomic absorption spectrophotometry revealed little difference in potassium content among the A. cepa cultivars. Nectar potassium levels ranged from 5,300 ppm to 6,900 ppm. Cultivars with higher nectar potassium levels had fewer honey bee visits.

A honey bee bioassay was conducted to simulate the sugar and potassium composition of each onion cultivar. The honey bees selectively foraged on simulated nectars with low potassium and high sugar concentrations.

Finally, seed yields of each of the cultivars were compared. Wide variations in yields were correlated with honey bee visitation, sugar composition, potassium levels, and flower phenology.

The results of this work are of immediate value to breeders of onions and other bee-pollinated crops. Monitoring nectar composition and volume as new lines and hybrids are developed will prevent inadvertent loss of attractiveness and result in improved bee visitation and pollination.

Objectives:

1. Establish relative attractiveness of genotypes, the key factors governing attractiveness, and chemically characterize those floral factors responsible for honey bee visitation in attractive and non-attractive genotypes of onions.
2. Examine the effects of varied combinations of key components of nectar and aroma by bioassaying under field and laboratory conditions mixtures simulating natural floral materials.

Objective #1 was successfully accomplished with the primary factor influencing honey bee visitation identified as the sucrose ratio in the floral nectar. Data obtained on the nectar phenolics and floral aroma were too inconclusive to determine any relationship to bee visitation behavior.

Objective #2 was not actively pursued as the role of sucrose was not definitively established until the fall of 1988. The literature on the influence of sucrose in floral nectar attractiveness is pretty clear and is in line with the results obtained in our laboratory and field studies. Therefore, as the project was terminating, floral aroma research was not undertaken.

Basic Aspects of Onion Pollination

Introduction

Plant factors affecting insect visitation have often been altered in the process of developing hybrid seed. Differences caused by male sterility (Frankel & Galan 1977, Mesquida & Renard 1978), morphological abnormalities (Grant 1949), and floral cues and rewards (Erickson & Peterson 1979) are evident between hybrid seed parents of many agronomic crops. These changes may have altered or eliminated pollinator rewards among parental lines, causing the plant to compete poorly with surrounding plant species for the attention of pollinators. This usually results in reduced pollinator visitation, reduced pollen transport, and consequently reduced seed set and yield (Erickson 1983).

This problem is nowhere more apparent than in the onion seed industry. Onion seed producers are confronted by the serious economic problem of low seed yields in onion (Allium cepa) fields as a result of insufficient insect pollination (Waller 1983). The onion flower is self-fertile but dichogamous; it relies almost entirely on insects for pollination because of the time difference between pollen shedding and stigma receptivity (van der Meer and van Bennekon 1968, Jones and Emsweller 1933, McGregor 1976).

Many potential pollinating insects are found in blooming onion fields. Of the species of Hymenoptera and Diptera common to onion fields in Utah described by Nye et al. (1973), the honey bee (Apis mellifera) was the most abundant pollinating agent. However, onion flowers appear to be less attractive to honey bees than are flowers of most competing plants (Waller et al., 1972). The unattractiveness of onion flowers to honey bees causes the bees to neglect the crop, particularly if another highly attractive plant species is in bloom (Gary 1972, 1977). This honey bee discrimination has had a deleterious effect on onion seed production in Arizona. To complicate the matter further, honey bees have been shown to discriminate between onion species and cultivars (Lederhouse et al. 1972, Shasha'a et al. 1973, Carlson 1974). This discrimination has led to differential seed yields between individual onion cultivars (Campbell et al. 1968, Carlson 1974).

Onion seed samples were solicited from several commercial seed companies in the U.S. Sixteen of these were selected to represent the various genotypes and planted in Tucson the fall of 1984. This population was observed in the spring of 1985 for honey bee visitation and six experimental lines were selected for further study in 1986-87. Comparisons of blooming phenology, honey bee visitation and nectar (quantity, sugar content and composition, potassium levels) were made on plants under open pollination and on plants grown under insect cages. Data were analyzed to determine if significant relationships between plant factors and honey bee visitation existed.

This study was designed to: (1) establish the relative attractiveness of six onion cultivars to honey bees, (2) identify the seed yield potential of the six cultivars, (3) identify key

floral factors such as flowering phenology, nectar volume, concentration, and composition, etc. responsible for honey bee visitation in both attractive and non-attractive cultivars, (4) examine the effects of key nectar components such as sugars and potassium by bioassaying mixtures simulating natural floral materials under laboratory conditions.

The data resulting from this research will provide a basic understanding of intraspecific differences between six onion cultivars. Furthermore, it should alert plant breeders about possible negative consequences of embarking on a selective breeding program. They must not overlook the importance of maintaining breeding lines that attract potential pollinators when selecting for desirable crop traits.

Three publications which report the major findings of this research are included as the main body of this report:

1. Intervarietal differences in onion (Allium cepa) seed yield in Arizona by James R. Hagler and Gordon D. Waller.
2. Production and composition of onion nectar and honey bee (Hymenoptera: Apidae) foraging activity in Arizona by James R. Hagler, Allen C. Cohen and Gerald M. Loper.
3. Honey bee (Apis mellifera L.) response to simulated onion nectars with differential sugar and potassium concentrations by James R. Hagler.

Title: Intervarietal differences in onion (Allium cepa L.) seed yield in Arizona.

ABSTRACT

Differential intervarietal seed yields were exhibited between onion (Allium cepa L.) cultivars in both open and cage pollinated experiments. Parameters examined included; total seed yield per umbel (grams), number seeds per umbel, individual seed weight, percent effective florets (i.e., florets which yielded at least one seed), and number of seeds produced per floret. In most instances all parameters of interest (except individual seed weight) favored that of the cage-pollinated experiment. This was attributed primarily to greater honey bee (Apis mellifera L.) visitation in the cage than in the open experiment. Failure of the onion flower to set full-capacity (i.e. six) seeds in both experiments seemed to be associated with some other genetic and/or physiological factors.

Recommendations/suggestions to alleviate these problems are discussed.

Title: Production and composition of onion nectar and honey bee (Hymenoptera: Apidae) foraging activity in Arizona.

ABSTRACT

Nectar characteristics of six onion (Allium cepa) cultivars were examined to assess the potential for preferential foraging by honey bees (Apis mellifera). Onion cultivars demonstrated differential flowering potential. Cultivars varied from 176 to 359 flowers per umbel with 32 to 74 umbels per 30 onion plants. All cultivars examined contained highly concentrated nectar with total dissolved solids ranging from 51 to 65%. Mean nectar amounts for six cultivars ranged from 0.54 to 0.84 ul per floret per day. Onion nectar was analyzed by gas chromatography to determine qualitative sugar differences among onion cultivars. All cultivars were hexose dominant with an approximate 1:1 fructose:glucose ratio. Fructose was usually present in slightly higher quantity than was glucose. Sucrose was the least abundant of the three determined sugars present. Data suggest that there are significant differences in sugar content between the onion cultivars. Differences in nectar sugar content and composition appear to explain a major part of the honey bee visitation preferences between cultivars documented in this study.

Title: Honey bee (Apis mellifera L.) response to simulated onion nectars with differential sugar and potassium concentrations.

ABSTRACT

Potassium concentrations from several common onion (Allium cepa L.) nectars were analyzed by atomic absorption spectrophotometry. High potassium concentrations ranging from 5,347 to 6,914 ppm were observed. Honey bee response was tested to artificial nectars with the known potassium, glucose, fructose, and sucrose concentrations of several common onion cultivars. Honey bees selected strongly in favor of those nectars lower in potassium concentration. When simulated nectars had approximately equal potassium concentrations, the honey bees foraged preferentially for onion nectars higher in carbohydrate reward.

Evaluation of the research achievements: Onions

These studies have shown that even in a crop like onions where the genetic base of much of the commercial material is narrow, there is still significant genetically influenced chemical differences which appear to be influencing honey bee visitation. The literature is correct in that onion nectar composition is basically low in sucrose, yet the most attractive lines had sufficiently more sucrose so that sensitive gas chromatographic methods and careful field observations of bee visitation were able to be positively correlated. Dr. Hagler has presented these results and conclusions to the recent National Onion Conference and has received several inquiries from the commercial onion seed research groups wanting our assistance in further chemical evaluation of nectar sugar ratios of their current selections. It is to be expected that use of this information will enable the seed industry to select genotypes of uniform sugar composition permitting more uniform visitation of pollinators between parental lines in both open pollinated and hybrid seed production.

Description of Cooperation

This project between the two countries was a little unique in that similar approaches were used in Israel and the United States but on two different crops - cucumbers in Israel and onions in the U.S. Dr. Levin visited Israel in 1985 and Drs. Lensky and Rabinowitch visited Tucson in 1986. Thus, we collaborated on the specific plans and reviewed methods, but the two studies were essentially conducted independently. The results are specific for the two crops but, in a general way, add similar information extending the basic principles of the plant factors influencing honey bee visitation and pollination in these two specific crops.

Dr. Joe Corgan, Plant Physiologist and onion breeder at New Mexico State University, Las Cruces, New Mexico, provided some "exotic" onion material which was evaluated in our tests.

Dr. Paul Bartels, Department of Plant Sciences, University of Arizona, has permitted us to use his electrical conductivity meter and spectrophotometer. In addition, the University has allowed us use of the scanning electron microscope facilities located on campus.

ARCO Seed Co., El Centro, California and Asgrow Seed Co., Sun Prairie, Wisconsin have expressed interest in our research and have supplied us with onion seed used in our experiment. These companies have also granted permission to send certain cultivars to Israel for their work.

Publications

Hagler, James R. 19 . Honey bee (Apis mellifera L.) response to simulated onion nectars with differential sugar and potassium concentrations.

Hagler, James R. and Gordon D. Waller. 19 . Intervarietal difference in onion (Allium cepa) seed yield in Arizona.

Hagler, James R., Allen C. Cohen and Gerald M. Loper. 19 . Production and composition of onion nectar and honey bee (Hymenoptera: Apidae) foraging activity. (submitted to Environ. Entomol.)

Hagler, James R. 19 . Honey bee (Apis mellifera L.) response to simulated onion nectars with differential sugar and potassium concentrations.

1
ABSTRACT

Israel - Cucumbers

Difficulties in the transfer of pollen by bees between cucumber lines used for hybrid seed production, have affected seed yields. Floral characteristics, pollen and nectar properties are the main factors contributing to the attraction of honeybees to the flower, gametes' quantity and viability have also a marked effect on productivity.

Our results show no effect of the size of the cucumber flower and of the genetic background on both, the quantity and the quality of pollen. Viability was highest during morning hours. High temperatures adversely affected germinability, both when flowers were exposed to heat and when pollen was germinated on artificial medium under temperatures of 38°C and above.

No difference in stigma receptivity was found between early morning hours and noon time. Long ovaries, however, set more seeds per fruit than short ones. Flower position (on the main axis) effects seed production, but this needs further elucidation.

Microscope observations showed significant differences in the nectary tissues, between good and poor nectar producers. The amount of vascular bundles, the density of stomata and the percentage of open stomata, are the most obvious morphological attributes that can be correlated with nectar secretion.

Cucumber genotypes vary significantly in their attractivity to honeybees, as assessed by the frequency of bee visitation in both, attached and detached flowers. The nectaries and the stamen are the only organs of the cucumber flower which initiate bee visitation.

Nectar secretion is greatly affected by the time of the day. Both, nectar volume and sugar concentration, change with the ageing of the individual flower. This may be the result of the changes in temperature, in humidity and/or in soil moisture during the day, as well as by flower age. The relative contribution of each of the above factors, requires further study. However, significant genetic differences in nectar properties: volume, sugar concentration and sugar composition are quite obvious, indicating the possibilities for plant improvement in regard to attractivity to bees.

Mineral nutrition is known to affect nectar quantities. In a number of preliminary experiments, an increase in sugar concentration was correlated with potassium application, and iron treated plants produced smaller nectar volumes. The effect of zinc application was more pronounced with genotypes secreting medium nectar volumes than with the high and poor producers. However, zinc treated plants were visited more frequently by bees and produced more seeds than the non-treated controls.

The distance between the bee colony and the flowering plants, has a marked effect on the frequency of bee visitation and pollination efficiency. Plants located at 50 to 100m away from the hive were visited at a significantly higher frequency than those at 5 or 200m distance. Male flowers are preferred by bees, over female ones, and there is a maximum of bee visitation, just before noon time. The distance between male and female flowers considerably affected productivity. A gradual decrease both, in seed set and the number of seed per fruit was observed with the increase in distance between flowers of the two sexes.

Objectives

To study the role of floral organs in honeybees' attraction, and to elucidate sex and varietal differences within the species in regard to that plant property.

To investigate the major chemical factors responsible for attractivity of plants to honeybees.

To learn the effects of field factors (distance between beehives and plants, distance between pistillate and staminate flowers, temperature, etc.) on pollination efficiency.

To examine varietal differences in regard to the potential productivity (i.e. pollen quantity and viability; stigma receptivity; potential number of ovuli).

To study possible agricultural techniques which may contribute to the improvement of plant attractivity to honeybees, and to increase seed yields.

1. The Cucumber Flower

1.1 Pollen: Quantity

In the production field, we have noticed that monoecious plants produced small (3 to 4 cm) and large (4.5 to 5.0 cm) flowers. These two types, however, did not differ in the number of pollen grains (7,000 to 7,700 grains per flower) and in their viability, which under the experimental conditions, was about 99% in both cases.

With one exception, in seven different experiments carried out in the field, in the greenhouse and in the phytotron, we have found an equal number of pollen grains per flower under all these environmental conditions. The number of pollen grains ranged between 6,400 to 7,400. In one case only, 9,500 pollen grains per flower were counted. Moreover, five different monoecious varieties differed in the number of pollen grains per flower, ranging from 6,000 to 10,000 per flower, but pollen viability in the morning hours was quite similar in all genotypes (ranging from 93 to 97%). In addition, no major differences in (morning harvested) pollen germinability were found through the production season, between mid May and the end of June. In all cases, 90 to 95% of the pollen grains germinated on artificial medium (Brewbaker and Kwack, 1963) and stained red with acetocarmin.

Pollen viability was maximal in the morning hours but dropped considerably in the afternoon (Fig. 1). In order to elucidate whether the reduction in pollen viability was the result of flower aging or the increase in temperature, we have sampled pollen grains from plants grown under controlled conditions, at 27/22°C day/night, respectively. No drop in pollen viability was detected between samples taken throughout the day at 2 hr intervals, between 8 am and 5 pm. In other experiments we exposed plants to different growth temperatures. The results are presented in Table 1. These results clearly show a significant drop of pollen viability with increased temperatures, lowest viability was recorded in plants exposed to 32/17°C day/night, respectively.

Fig. 1: Changes in the viability of cucumber pollen grains throughout the day.

Fig. 2: The effect of temperature on cucumber pollen germination. Pollen grains were germinated on artificial medium (Brewbaker and Kwack, 1963). S.D. of the means ranged between 0.25 for 24°C and 5.76 for the data examined at 24°C and 42°C, respectively.

In a different set of experiments, pollen grains sampled from plants grown at 27 to 22°C were germinated on the above mentioned artificial medium. The results in Fig. 2 show quite clearly that pollen viability drops abruptly at temperatures above 38°C. These results indicate that the decline in pollen viability during the afternoon hours is a result the adverse effects of high temperatures rather than of flower age.

1.2 Performance of Female Flowers

To elucidate differences in the stigma receptivity during the day, individual flowers were exposed to foraging bees, between 7 to 9 am, and 10 to 12 am. No difference in the number of seeds per fruit and in the seed and fruit properties of the cucumbers developed as a result of pollination during the two periods, were observed.

Significant differences were found between the length of the ovaries, ranging between 20.8 and 22.3 mm. The number of seeds developed in the longer ovaries was significantly higher than that in the shorter ones. Summation of the number of seeds and the number of unfertilized ovuli (empty seed coats) showed no significant difference in the initial number of ovuli per ovary. Seed set, however, was lower in the short ovaries being 27 to 30% as compared with 45 to 50% in the longer ones. Consequently, there was a significant decrease in the seed yield obtained from short ovaries.

1.3 Flower Position

Flower position on the main axis, may affect its productivity in regards to seed production. We have tested this hypothesis in three field experiments. In two of these, no difference in both seed number and seed weight per fruit were recorded. In the third experiment, almost linear increase in both parameters was found, with the increase node number. The figures ranged from 90 to 190 seeds per fruit and 3.0 to 6.5 gr seed per fruit from node 3 to node 8 (Figs 3 and 4).

Figs. 3 and 4: The number of seeds and seed yield per fruit as affected by the flower position on the main axis

- First, second and third field experiments

Table 1. Effect of temperature during cucumber plant development on the viability of their pollen grains(*)

Temperature C°		Relative humidity%		Pollen viability%	
Day	Night	Day	Night		
32	27	84	84	b	80.2
32	22	84	78	b	81.5
32	17	84	71	c	52.7
27	22	78	78	a	98.2
27	17	78	71	a	97.0
22	17	71	71	a	97.6

Means followed by different letters are significantly different at the 5% level.

(*)Pollen viability was established by acetocarmine staining.

2. Anatomy and Morphology of Flowers

2. 1. Optical and Scanning Microscope Studies of High and Low Nectar Secreting Genotypes

Cucumber female flowers of various genotypes and their F1 hybrids with the pollinating line M1 were examined by both, optical and electron scanning microscopy.

(1) Optical microscopy: 8 to 11 μ thick sections of nectaries belonging to G1, G2, G3, G5, G6 and G1 x M1, G2 x M1, G3 x M1, G4 x M1 were examined and the results are summarized in Table 2. Micrographs of nectary sections of genotypes G2, G3, G6, G5 x M1 are shown in Fig. 5. The data in Table 2 show that genotypes

Table 2. The nectary tissue of cucumber female flowers.

Genotypes	Thickness of nectary tissue (no. of cells)	Xylem densities	Phloem	Position of vascular bundles in relation to nectary tissue
<u>Parental Lines</u>				
G1	6-8	+++	++	attached
G2	9-10	++++	++	internal
G3	7-8	++	+	remote
G4	3-4	++	+	attached
G5	5-6	++++	++	attached
G6	8-9	++	+	attached
<u>Single Hybrid</u>				
G2 x M1	5-6	+++	++	close
G3 x M1	8-9	++++	+++	attached
G4 x M1	12-13	+++	++	internal
G5 x M1	8-9	++	+	close
G6 x M1	5-6	+	+	more remote

very high +++; high +++; medium ++; low +; none -

The optical microscope micrographs of cucumber nectary sections (G2, G3, G6, G5 x M1) are available from the authors in Israel.

G4, G5 and G2 x M1 contain stomata lined with a thin nectariferous tissue. This tissue was well developed in genotype G4 x M1. The amount of vascular bundles and their location were not consistent: in genotype G2 and the hybrid G6 x M1 they are present inside the nectary tissue, but in G3 and the hybrid G6 x M1 they are found at a distance of 3 to 5 cell layers from the nectary tissue.

(2) Scanning electron microscopy: In order to obtain a better understanding of the nectar secretion levels in high and low nectar producing genotypes, we examined the number of open stomata present in the nectaries of several female genotypes. The stomata are dispersed around the center of the nectary. Of each genotype two nectaries were examined; of each nectary, the surface of two randomly selected areas were scanned, and the number of stomata established. The results are shown in Figs. 6 and 7. It emerges from the data (Fig. 2) that the nectaries of genotype G1 and of the hybrids G4 x M1 contain but a few stomata. Other genotypes had about 150 open stomata per 0.14 mm². The density of stomata upon the surface of a nectary varied from one area to another.

No anatomical lesions or damage to nectaries were found in low-secreting genotypes. No consistent differences in the distribution of both phloem and xylem bundles in the nectariferous tissue were found in all examined genotypes. There was no direct relation between the number of open stomata on the nectary surface and the amount of secreted nectar. Therefore, the anatomical observations could not explain the difference between flowers in regard to nectar secretion.

Fig. 5: Sections of nectaries of cucumber female flowers (optical microscopy)

- A: Nectary tissue in genotype G3, consisting of 5 - 7 cells; vascular vessels are scarce and remote from the tissue.
- B: Nectary tissue in genotype G6, consisting of 8 - 10 cell layer. Vascular vessels are located near the nectariferous tissue.
- C: Nectary tissue in genotype G5 X M1, consisting of a 8 - 10 cell layer. Vascular vessels are well developed and attached to the nectary tissue.
- D: Nectary tissue in genotype G2, consisting of a 9 - 10 cells layer; bundles of phloem and xylem located inside the nectary tissue.
- E: Magnified portion of nectary tissue of genotype G2 containing phloem and xylem bundles.
- F: Thick nectary tissue of genotype G4 X M1 consisting of a 12 - 13 cell layer. The tissue is broad and elongated; it contains both phloem and xylem bundles.
- G: Magnified portion of G4 X M1 nectary tissue containing the vascular vessels.

NT - nectary tissue

PH - phloem

X - xylem

Fig. 16: Number of open stomata on the surface of nectaries in several genotypes of female cucumber flowers.

SEM studies of high and low nectar secreting genotypes showed about 15 open stomata per nectary surface of 0.01mm^2 in the high secreting flowers as compared with 4 to 5 open stomata per nectary surface of 0.01mm^2 in the low secreting ones. (Figures 8, 9, 10 11, 12, 13).

Cucumber genotypes differed significantly in the amounts of nectar secreted. Ten fold differences were found between male and female flowers: 0.3 to 3.1μ per flower, respectively, and there were changes in nectar secretion during the day. Nectar secretion declined towards noon time, in uncovered flowers.

Fig. 7: Nectaries of several genotypes of female cucumber flowers (S.E.M.)

- A A cup-shaped nectary surrounding the style base.
- B Nectary surface of genotype G6 showing but few (54) open stomata.
- C Nectary surface of genotype G3 with a medium number (135) of open stomata.
- D Nectary surface of genotype G2 with a high number (283) of open stomata.
- E,F Nectary surface of genotype G3 X M1, showing areas with high and low (99) density of open stomata.

N - Nectary
 STY - Style
 ST - Stomata

Fig. 8: SEM micrograph of male cucumber flower nectary. Arrows indicate open stomata.

Fig. 9: SEM micrograph of epidermal layer of male cucumber flower nectary. Open stomata are clearly seen.

Fig. 10: SEM micrograph of closed (CST) and open (OST) male cucumber flower nectary stomata.

Figs. 11-13: SEM micrograph of the nectaries' epidermal layer of female flower in different cucumber genotypes.

Arrows indicate stomata. Stomata density in genotypes G-12 and G-15 is much lower than that in G-11.

3. The Attractivity of Detached Cucumber Flowers to Honey Bees

3.1 Intact flowers

In order to elucidate whether flowers of different genotypes differ in their attractivity to bees, freshly picked cucumber flowers were placed inside a glass observation hive. The frequency of bee visitation to the various flowers was studied. A significant difference in frequencies of bee visitation was recorded. Flowers of some specific genotypes, were not visited by bees, others had up to 21 bee visits per 15 min in the first experiment, and up to 13 visits per 15 min in the second set of experiments (Table 3).

Table 3. Frequency of bee visitation to detached cucumber flowers inside a glass observation hive. Two independent experiments were performed in a complete randomized design at five replications.

Genotype	Experiment I		Experiment II	
	Mean $\pm$ SE	Range	Mean $\pm$ SE	Range
G ₁	8 $\pm$ 3.5	0.2 - 21	4 $\pm$ 0.9	2 - 7
G ₂	7 $\pm$ 2.0	3.0 - 14	3 $\pm$ 0.7	0 - 1
G ₃	1 $\pm$ 0.5	0.0 - 2	0	0
G ₄	2 $\pm$ 0.6	0.0 - 3	0	0
G	1 $\pm$ 0.4	0.0 - 2	0	0
G ₆	5 $\pm$ 0.9	3.0 - 7	2 $\pm$ 0.7	1 - 5
M ₁	8 $\pm$ 1.3	5.0 - 12	8 $\pm$ 1.3	3 - 5

3.2 Flower organs

The differential attractivity of various floral organs to honey bees was tested as above. Floral organs were separated and placed in an observation hive, and the number of bees' visits counted. No bee visitation to either the tepals or the stigmas was observed. Nectaries were visited more frequently than anthers, and there was quite a difference between the numbers of bee visits per 15 min to nectaries of different sources (Table 4).

Table 4. Frequencies of bee visitation to nectaries and stamens of various cucumber genotypes. Two independent experiments were performed in a complete randomized design at five replications.

<u>Genotype</u>	<u>Plant organ</u>	<u>Experiment I</u>		<u>Experiment II</u>	
		Mean $\pm$ SE	Range	Mean $\pm$ SE	Range
G ₁	Nectary	6 $\pm$ 1.0	4 - 9	3 $\pm$ 0.6	2 - 5
G ₂	Nectary	7 $\pm$ 1.3	3 - 11	3 $\pm$ 0.6	2 - 4
G ₆	Nectary	4 $\pm$ 0.9	2 - 7	1 $\pm$ 0.0	1 - 1
M ₁	Nectary	10 $\pm$ 1.1	7 - 13	5 $\pm$ 0.6	3 - 6
M ₁	Stamen	3 $\pm$ 0.6	2 - 5	1 $\pm$ 0.3	0 - 1

4. Cucumber Genotypes

4. 1 Growth Conditions

Several gynoeceous and monoecious cucumber genotypes were received both, from Israeli Seed Companies and from private breeders. Seeds were sown in speedling trays and transplanted into 5 liter pots containing methyl bromide fumigated soil, vermiculite and peat (1:1:1). Individual plants were staked and standard agricultural practice applied throughout. In addition, observations were made in several commercial F1 hybrid seed production fields. In these fields, beehives were introduced when 10% of the pollinating plants commenced their flowering. Each bee colony consisted of two fully occupied supers and they were equidistributed in the plots at 40x50m intervals. No insecticides were applied during the flowering season.

4. 2 Nectar Volume and Sugar Content

The genotypic variation in both nectar volume and nectar concentration of 7 cucumber lines, grown in the greenhouse, is described in Figure 14. No nectar could be collected from open flowers of genotypes G-12 and G-15, regardless of the time of the day and whether or not the flowers were protected by gelatin capsules. Nectar secretion of G-1, G-11 and G-14 was relatively low, ranging from 0.3 to 2.3 μ l, morning and 2pm, respectively. Samples taken at 2pm revealed high cumulated nectar volumes of G-3, and G-13, reaching 9 and

14

15

Fig. 14: Volume- and sugar concentration of nectar from genotypes grown in a green-house.

Fig. 15: Volume and sugar concentration in nectar of male and female cucumber flowers in F1 hybrid seed production fields at: A - Berurim; B - Avney Eytan.

4µl, respectively. Non-covered flowers of greenhouse plants yielded similar nectar volumes (data not shown).

G-13 and G-14, yielded nectar with low sugar concentration ranging between 25 and 30%. G-11 yielded nectar with highest sugar concentration during morning and noon hours. However, in the afternoon, the nectar of the later flowers was found to be at lower concentration. G-1 sugar concentration consistently increased from 8am to 2pm. In addition to its highest nectar volume, G-3 produced high amounts of sugars.

Both monoecious (M), M-21 plants and gynoecious (G), G-21 flowers, were evaluated under field conditions in two production fields: Avnei Eitan in the Golan Heights and Berurim and Shalem-farm in the Coastal Plain.

In the production fields, nectar volume of protected female flowers always exceeded that of similarly treated male flowers. However, sugar concentration of the later was always higher than that of the female flowers (Fig. 15). Flowers which were not covered with gelatin capsules, exhibited tiny droplets of nectar in the nectary cups only during the early morning hours, (July). No nectar was visible or collectable later in the day, due to evaporation and consumption. Plants grown under shading screen, revealed detectable amounts of nectar as late as 10:00am (data not shown).

A significant genotypic variation was found between cucumber lines, with regard to: nectar volume and its sugar concentration. Non-secreting (dry-genotypes), as well as high-nectar-producing genotypes were identified and isolated.

Figs. 16, 17 and 18: Total nectar volume (Fig. 16), sugar concentration (Fig. 17) and total sugar quantity (Fig. 18) secreted by flowers during the morning hours in several cucumber genotypes. The flowers were encupulated on the eve of anthesis. Morning and noon meteorological conditions were: Temperature 22 and 28°C, Relative humidity 74 and 55%, and Wind velocity 5 and 10 m/min, respectively. Seed Production Farm at Khavat Shalem, June 5, 6 and 8.

Selfing and intercrossing of the above material were made (based upon individual plants) for further investigations (Figs 16,17,18). Under Israeli climatic conditions, prevailing during the commercial seed production season, nectar of exposed flowers is available to bees, in the early hours of the morning, solely. Later, it dries out. Hence, sugar crystals only are available for foraging bees. In protected flowers, however, we have observed that nectar is continuously oozing during day-hours, but sugar concentration is usually decreased (dilution effect?). Total sugars secreted by the nectaries increase gradually with time.

4. 3 Sugar Composition of Cucumber Nectar: Gas Chromatography

Data presented in Fig. 19 and Table 5, show that sugar composition of different cucumber plants differ, with the genotype. Two major groups of cucumber plants can be characterized in accordance with their sugar composition: High fructose and low sucrose levels were determined in G-31, M-31 and in their F1 hybrid: F1(G-34xM-31); High sucrose and maltose, but low fructose levels were found in G-32 and the F1 hybrid between G-33 and M-3. Both groups contained low levels of alpha-glucose and some unidentified compounds with short retention-time (Fig.19!).

GLC separation of nectar sugars from several cucumber genotypes are presented in Figs. 19 b-f).

Fig. 19: Gas chromatographic analysis of the composition of sugars in the nectar of several cucumber genotypes.

Samples were separated on 3%SE-30 columns, oven temperature was programmed from 120 to 290°C at 4°C/min (E, F), 8°C/min (A, B, C), 12°C (D). Attenuation: 16x100 (B, C, D), 64x100 (E, F), and 256x100.

A. Standard Sugars: 1 - Arabinose; 2 - Rhamnose; 3 - Ribose; 4 - Xylose; 5 - Fructose; 6 - Mannose; 7 - Glucose; 8 - α glucose; 9 - β glucose; 10 - Sucrose; 11 - Maltose

B-F. Nectar Samples of genotypes: B= G1; C= M1; D= G4xM1; E= G2; F=G3xM1.

Table 5: Nectar sugars of several cucumber genotypes and their ratios with relation to fructose.

Genotype	Relative amount of sugars in cucumber nectar			
	alpha-			
	fructose	glucose	sucrose	maltose
G-31	1	0.019	0.250	0.046
H-31	1	0.000	0.120	0.000
G-34xH-31	1	0.100	0.400	0.000
G-32	1	0.068	4.300	1.970
G-33xH-31	1	0.049	1.890	0.810

4.4 Genotypic Differences in Nectar Secretion of Cucumber Flowers

Flower buds were enclosed in gelatin capsules, one or two days before anthesis. Nectar was collected with micropipettes, at 2 pm on the day of anthesis (Table 6).

Volume of extractable nectar from cucumber flowers grown in three different experimental field, and sugar composition and concentration, were studied. At sampling time, air temperature ranged between 29 to 32°C, RH ranged between 52 and 60%, and wind velocity, between 8 to 12 m/min.

Genotype G₅ was found to be a rather poor nectar producer, whereas genotype G₁ secreted large amounts of nectar throughout the summer. The results show, that cucumber genotypes vary significantly in the amount of nectar secreted, and that selection for improved and stable nectar production throughout the season.

Table 6. Nectar secretion from cucumber flowers of various genotypes. Nectar was collected with micropipettes.

Genotype	Experiment I			Experiment II			Experiment III		
	No. samples	Mean ISB	Range	No. samples	Mean ISB	Range	No. samples	Mean ISB	Range
G ₁	36	12.4 ±1.3	0.7-27.4	31	6.2 ±0.77	2.5-26.9	5	2.2 ±0.61	1.5-4.6
G ₂	32	9.8 ±1.10	2.7-25.8	33	5.7 ±0.40	0.0-9.2	29	4.9 ±0.55	0.0-9.5
G ₃	21	0.2 ±0.09	0.0-1.8	-	-	-	-	-	-
G ₄	31	0.9 ±0.25	0.0-4.9	-	-	-	-	-	-
G ₆	40	6.6 ±0.58	0.4-14.0	10	4.6 ±0.51	1.0-6.5	13	2.3 ±0.62	0.0-6.4
H ₁	101	3.1 ±0.18	0.4-8.1	60	1.4 ±0.10	0.0-3.8	13	0.9 ±0.22	0.0-2.1

It was quite easy to distinguish between two major groups of genotypes. The plants of G₃, G₄ and G₅ do not secrete any-, or produce very little nectar. The others secrete nectar in measurable quantities throughout the season. There is, however, quite a variation between the genotypes and between plants of each specific breeding line. This is not surprising, since, no selection pressure was applied for high nectar producers. The natural genetic variation was maintained in each genotype. The sugar concentration in the nectar was measured using a thermo-regulated refractometer (Table 7).

Table 7. Sugar concentration of nectar extracted from flowers of four cucumber genotypes.

Genotype	No. samples	Sugar Concentration	
		Mean±SE	Range
G ₁	21	24.1±0.99	19 - 35
G ₂	22	21.4±0.96	14 - 28
G ₆	17	20.4±1.37	15 - 32
N ₁	21	39.7±0.46	33 - 43

Gynoecious flowers of the different genotypes produced nectar of similar sugar concentration. Male flowers, however, produced significantly more concentrated nectar than any of the tested female ones.

4. 5 Effect of Mineral Nutrition Nectar Volume and Sugar Content and on Cucumber Seed Production

A foliar application of the following nutrients was given to cucumber plants (Berurim): boric acid, iron sulfate or copper sulfate at .5g/m², potassium chloride or zinc sulfate at .25g/m². Minerals were applied on either of two dates: July 19th and July 23rd.

Nectar was collected 3-4 days after the single treatment and volume and sugar concentration determined as described above.

Ripe fruits were collected, seeds extracted and counted.

Two experiments testing the effect of zinc on nectar secretion, bee visitation, and seed set were carried out.

ZnSO₄ was sprayed once, at the beginning of the flowering season at: 0, 0.5, 1.0 and 2.0% in Gedera or at 0, 0.1, 0.2, 0.3 or 0.4 g/m², in Berurim. Both nectar volume and concentration as well as frequency of bee visitation/flower and seed yield were determined.

Figs. 20 and 21 show that in some instances, potassium positively affected sugar concentration and that iron treated plants produced significantly smaller volumes of nectar.

Data presented in Table 8 show that number of seeds/fruit of zinc and to some extent boron treated plants is either significantly higher or equal to that of control plants.

Somewhat increase in sugar concentration of nectar, was found in 0.5% Zn treated plants (Fig. 22). Bee visitation was found to be markedly more intensive in flowers of plants pretreated 0.5-1.0 Zn (Fig. 23). The effect of zinc treatments on number of seeds per fruit was inconsistent and was found to be dependent on the environment (Berurim vs Gedera). It is possible that the initial level of available zinc in the soil of both places was considerably different and therefore plants also differed in their response to the treatment. In Berurim (Table 3) a 100% increase in the number of seeds per fruit was found with 0.1 to 0.4g/m². In Gedera, however, no bee visitations to male and female flowers was closely followed throughout the season.

Effect of zinc-treatment on nectar secretion of cucumber lines G2 and G4 was examined in two field experiments.

Experiment no. 1. G2 female flowers at full bloom were encapsuled one day before anthesis. The effect of treatment with 1% zinc-sulfate was assessed 1 and 4 days after zinc application. The results (Table 9) show a significant increase in nectar secretion up to 56% over the control, one day after the treatment with zinc-sulfate. Samples taken around noon, however, showed an advantage for 2% zinc-sulfate over other treatments. Four days after the zinc sulfate application no significant differences between the treatments were found.

Experiment no.2. Low nectar secreting genotype G4 was treated as above. In spite of zinc applications, the nectar secretion remained very low, i.e. less than 1 microliter/flower.

It seems that the application of zinc cannot significantly improve the nectar secretion of low nectar secreting genotypes. However, applications of zinc to genotypes secreting medium nectar volumes, can markedly increase this secretion.

The effect of Zn application on bee visitation in G2 flowers was tested and summarized in Figs. 22 and 23. The results show that frequency of bee visitation was significantly higher to flowers of zinc treated plants than to controls. This effect was also evident during the 4th day after zinc application, although, as mentioned above, nectar volume was more or less equal to the original level. This may be indicative of some other internal changes occurring as a result of zinc application.

Table 8. Effect of mineral treatment (foliage application) on number of seeds per fruit (Berurim).

Mineral (g/m ²)			
Zinc	Potassium	Boron	Iron Copper Control
.25	.25	.50	.50 —
117	54	76	57 55 72
+ 8.3	+ 6.4	+ 5.7	+ 8.4 + 6.0 + 8.3
(23)*	(30)	(57)	(14) (24) (35)

*No. fruit from which seeds were extracted (in brackets).

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Fig. 22: Flower nectar volume and sugar concentration in cucumber plants, sprayed with 0, 0.5, 1.0 or 2% zinc sulfate.

Fig. 23: Number of visiting bees in 10 female flowers sprayed with 0, 0.5, 1.0 or 2% zinc sulfate.

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Figs. 20 and 21: The effect of minerals (Zn, K, B, Fe and Cu) on nectar volume and on sugar concentration in cucumber flowers. Berurim.

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Table 9. The effect of zinc-sulfate foliar application on nectar secretion of cucumber female flowers - G2.

Zn-sulfate conc. %	no. flowers examined	Nectar volume (microliter/flower)	
		range	mean $\pm$ S.E.

(a) One day after Zn application (June 21)

09:30 hrs			
0.0	9	1.2 - 4.0	* B 2.5 $\pm$ 0.3
0.5	10	0.0 - 4.6	B 2.4 $\pm$ 0.4
1.0	10	2.3 - 5.5	A 3.9 $\pm$ 0.4
2.0	7	0.0 - 3.6	B 3.9 $\pm$ 0.4
12:30 hrs			
0.0	9	0.8 - 5.5	AB 4.3 $\pm$ 0.7
0.5	7	0.3 - 7.3	AB 4.0 $\pm$ 0.9
1.0	8	3.5 - 8.5	B 2.5 $\pm$ 0.6
2.0	9	0.4 - 5.0	A 6.7 $\pm$ 0.5

(b) Four days after Zn application (June 24)

09:30 hrs			
0.0	10	0.5 - 4.7	A 2.5 $\pm$ 0.4
0.5	9	0.0 - 3.8	A 2.5 $\pm$ 0.5
1.0	10	0.3 - 5.0	A 1.4 $\pm$ 0.5
2.0	9	0.2 - 2.4	A 1.1 $\pm$ 0.2
12:30 hrs			
0.0	10	0.0 - 8.5	A 2.4 $\pm$ 1.0
0.5	8	0.0 - 6.6	A 2.7 $\pm$ 1.0
1.0	7	0.2 - 9.1	A 4.0 $\pm$ 1.4
2.0	10	0.1 - 5.8	A 1.6 $\pm$ 0.7

* Multiple range test. Means followed by similar letter do not differ significantly at the 5% level.

The meteorological conditions prevailing during nectar sampling are listed below:

	June 21		June 24	
	09:30	12:30	09:30	12:30
Temperature (centigrade)	32	34	34	37
Relative Humidity (%)	57	39	39	31
Wind velocity (m/min)	11	23	24	26

5. The effect of distance from Bee Colonies and from Male Rows to Female Plants, on Seed Production

5.1 Distance from Bee Colonies

Bee colonies were placed in cucumber hybrid seed production fields as described above. Experiments were

carried out in Berurim and Avnei-Eitan. In addition, frequency of bee visitation to cucumber flowers as a consequence of the distance from the colony was investigated.

Field arrangements, as described in Fig. 24.

Frequency of bee visits to cucumber flowers of both sexes (10 female and 10 male flowers) was established simultaneously for 15 min, every hour.

A foraging bee was counted only if it actually landed and entered the observed flower. Duration of visits/flower was determined with a stop-watch.

Temperature, relative humidity and wind velocity during the observation hours were established with meteorological equipment.

Data presented in Fig 25 indicate significant differences in the frequency of bee visitation which were related to the distance from the bee hive. Plants located 50-100m from the bee colonies were most frequently visited by foraging bees, while the number of visitations to those planted at 5 and 200m, were considerably lower. Therefore, in all our experiments, an equidistance of 40x50m between neighbouring beehives were employed.

Bee visitations to male and female flowers was closely followed throughout the season. The data presented in Figs 26-31 show that frequencies were

higher in male flowers but that the duration of bee visits per flower were longer in the female flowers than in the male

Fig. 24: Distribution of bee colonies in cucumber seed production fields at Berurim. Cucumbers were planted at the ratio of 1:5 male to female plants, respectively.

Fig. 25: Bee visitation to 10 female cucumber flowers as affected by the distance (5, 50, 100, 200 m) from bee colonies at Berurim, (June 11). Hourly counts of bees were made for 15 mins.

ones. During the day, there is a marked peak of bee activity between 9am and 11am. The number of visits/flower at earlier and later hours was significantly lower. A considerable shift in the bee activity peak, has been observed in all experimental plots with the season. While early in the season (May) the maximal value was recorded between 9am and 1pm, late in June the maximal activity was much earlier, namely between 8 and 11am (Figs. 30-34).

5. 2 Distance from Male Rows

In an experiment carried out in commercial cucumber hybrid seed production fields, we have measured a significantly lower rate of seed set in plants being 200 m from the hives, as compared with those closer to the bee colonies. In the F1 production fields, the effect of distance between female flowers to the pollinating ones was examined during the two seasons, by measuring the effect of proximity between the pollinating and the female beds on seed set. The experimental design consisted of a sequence of 5 female plants (2 rows per bed) followed by 1 bed (2 rows per bed) of pollinating plants (Table 9). A significant reduction in seed set and no. of seed per fruit is evident in the 3rd row (5.4 m from center), compared with the first and second one (1.8 and 3.6 m, respectively). These results were further confirmed in another experiment, when 1 m sections of pollinating plants were sown in female-plant beds (Table 10). A gradual decrease both in the no. of seed per fruit and in no. of seed set was observed. Significantly low figures were found in plant samples at a distance of 10 and 20 m from the female flowers, as compared with 1 and 2-5 m.

Table 9. Effect of perpendicular distance of the female parent from the pollinating plants on seed number per fruit, seed set and thousand weight in cucumber hybrid production fields.

Distance of bed	No. seed/fruit	Seed Set (%)	Thousand weight (g)
<u>Experiment No. 1</u>			
1st	103 + 5.5 a* (57)**	57.4 + 3.1 a	33.5 + 0.7 a
2nd	72 + 5.7 b (60)	40.8 + 3.0 b	34.6 + 0.7 a
3rd	75 + 6.3 b (58)	45.6 + 3.6 b	34.6 + 0.7 a
<u>Experiment No. 2</u>			
1st	115 + 7.4 a (56)	57.9 + 2.5 a	37.3 + 1.0 a
2nd	114 + 6.1 a (60)	57.2 + 3.0 a	35.0 + 0.7 a
3rd	83 + 5.5 b (75)	46.6 + 2.6 b	36.5 + 0.6 a

(*) means followed by a similar letter do not significantly differ at 5% level.

(**) number of fruit examined.

Table 10. Effect of distance from male plants on the number of seed per fruit, seed set and thousand weight. The fruits were collected from the female plants sampled at random at the various distances from the pollinating plants' section.

Distance from male fl. (m)	No. seed/fruit	Seed Set (%)	Thousand weight (g)
1	91 + 8.9 a* (57)**	46.4 + 3.9 a	35.4 + 0.8 a
2-5	72 + 6.1 a (60)	40.3 + 3.1 a	37.2 + 1.0 a
10	65 + 7.1 a (58)	37.0 + 3.8 a	35.4 + 0.6 a
20	35 + 7.9 b (60)	21.3 + 6.9 b	36.5 + 0.8 a

(*) means followed by a similar letter do not significantly differ at 5% level.

(**) number of fruits examined.

Figs. 26 and 27: Number of visiting bees to 10 male and to 10 female flowers. Hourly counts of bees were made for 15 mins. Fig. 26 - Berurim; Fig. 27 - Avney Eytan.

Figs. 28 and 29: Duration of bee visits in cucumber male and female flowers. Fig. 28 - Berurim; Fig. 29 - Avney Eytan.

Figs. 30 and 31: Bee visitation to 10 male and to 10 female flowers throughout the growing season: May-August. Hourly counts were made for 15 min. Fig. 30 - Coastal area: Berurim; Fig. 31 - Avney Eytan.

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Figs. 32, 33 and 34: Meteorological conditions (temperature, relative humidity and wind velocity) prevailing during the experiments at Berurim (Fig. 32) and at Avney Eytan (Fig. 33) and the duration of bee visits to flowers at Berurim (Fig. 34).

Description of Cooperation

There was a fruitful exchange of ideas and technologies between the collaborating parties. Visits to the respective laboratories, and to experimental and production fields, both in Arizona and in Israel, contributed to the better understanding of the pollination problems in the investigated crops in both countries. Additionally, there was an illuminating exchange of information on efficient beekeeping, the problems involved, future hazards and possible solutions.

As a result of this collaboration, Dr Levin (AZ) was invited by the HU to spend a half a year in Rehovot. During this time, Dr Levin gave a course on Plant Pollination. Students, growers and extension officers participated and enjoyed the benefits of his vast experience.

Evaluation and Benefits to Agriculture

In accordance with the objectives of the research (detailed in our original proposal) better understanding of the interrelation between the pollinating insect and the plant was achieved. The elucidation of the main factors most important in attracting bees to the seed production fields, and the identification of genetic variability within the investigated species, have already contributed to the agricultural practice: Israeli cucumber breeders have recognized the need for selection of genotypes which better attract bees than the commonly available material, and the equidistance position of bee hives (rather than at the outermost rows) became a standard procedure in seed production fields. Consequently, hybrid seed yield obtained in Kibbutz Shoval reached a level of 50 to 60 kg/1000 m² (total production area: 50 to 60 ha), as compared with 20 to 40 kg/1000 m² on the national level.

Moreover, since production of cucurbits for fresh consumption requires adequate pollination, growers adapted the consequences of this work, to the production fields (marginal seasons) of fresh cucumbers, melons, watermelons and squashes (all of which depend on bee pollination).