NECTAR SECRETION AND HOW IT AFFECTS THE ACTIVITY OF HONEY BEES IN THE POLLINATION OF HYBRID PICKLING CUCUMBERS, CUCUMIS SATIVUS L.

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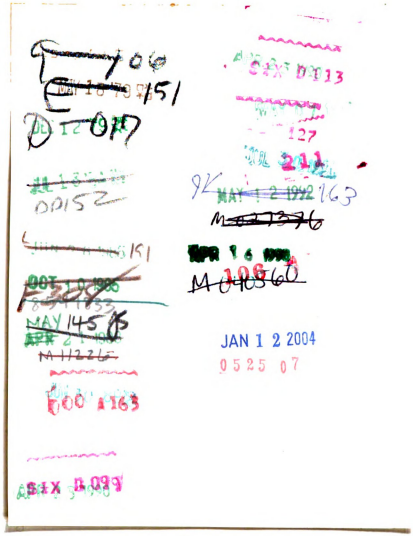
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ABSTRACT

NECTAR SECRETION AND HOW IT AFFECTS THE ACTIVITY OF HONEY BEES IN THE POLLINATION OF HYBRID PICKLING CUCUMBERS, *CUCUMIS SATIVUS* L.

By

Clarence H. Collison

Nectar secretion in both staminate and pistillate flowers of pickling cucumber was the primary attractant to honey bees. Few bees collected cucumber pollen. All cultivars tested produced a quantity and quality of nectar that was attractive to bees.

The pistillate flower nectary is cup-shaped, surrounding the base of the style, whereas the staminate flower nectary is typically a three-lobed button on the floor of the receptacle, with a few being four-lobed. The pistillate flower nectary was 1.6-1.9 times wider, had approximately twice the secreting surface and secreted 1.5-2.3 times more nectar than the staminate flower nectary. The epidermal layer of the nectary contained stomate-like pores that appeared to open and close with environmental changes.

Cucumbers basically have a one day secretion cycle with maximum production on the day of anthesis. Nectaries became moist at 16° C and measurable amounts of nectar were obtained at 21° C. Cucumber flowers have a range of nectar production from zero to over 30 ul, with 13% - 60% sugar content or 0 to 12.33 mg of sugar. The sugar concentration was

drastically reduced during the night after anthesis by sugar reabsorption. Positive correlations were found between nectary width and petal diameter, volume of nectar, total weight of sugar present and ovary length but not sugar concentration. The nectar of staminate flowers had a higher sugar concentration than that of pistillate flowers but both had approximately equal weights of sugar.

Bees spent twice as long on pistillate as on staminate flowers since the length of the visit is determined by the amount of the nectar present. Nectar replacement after removal occurred within five minutes with a decrease in sugar concentration and total weight of sugar present. Multiple visitation did not stimulate nectar production. A 40% difference in sugar concentration was found between nectar sampled from bee excluded flowers and nectar removed from the honey stomachs of bees working cucumbers.

There tended to be slight increases in flower size, nectary size and volume of nectar in flowers produced further down the vine from the base. Lateral vine flowers produced more nectar with a higher weight of sugar than main vine flowers. Only morning pollinations affected nectar secretion. After fertilization, nectar secretion appeared to cease.

Two different gas chromatography columns were needed to analyze nectar for sugar content. The nectar samples changed quantitatively within 24 hours after the silylation reagent was added. Cucumber nectar was sucrose dominant (60.5%) with fructose (25.1%) predominating over glucose (14.4%). Two unknowns were found.

Cucumber nectar would rate moderately attractive compared with other major nectar sources, but because of a relatively small number of flowers per acre, it cannot be rated as an important honey plant.

These studies indicate that important factors of attractiveness of a crop to bees could be readily monitored during a plant breeding program.

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By

Clarence H. Collison

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INTRODUCTION

Agriculturally and ecologically, nectar secretion is important to man and other species of plants and animals. Many angiosperms produce nectar to attract insect or other animal visitors to the flower. Through their visits the plant often benefits from the resulting pollination that may happen incidentally. Man relies on this flower-visitor relationship in the cross-pollinating of many agricultural crops. Honey bees alone account for about 80% of the pollination service to crops, USDA (1968), resulting in a yield of several billion dollars, McGregor (1973). Many of these crops would not be pollinated, if it were not for the nectar they produce.

Honey is a second important product of nectar secretion, since nectar is the basic raw material of honey. The honey bee collects nectar from flower and converts it into honey through the evaporation of excess water along with the addition of enzymes which change the complex sugars present into simple sugars. Some of the honey is used by the bee and the colony as a source of energy. Due to the honey bees natural hoarding instinct, they may collect 100 times their own requirements, Faegri and Van Der Pijl (1966). The surplus honey in the United States in 1972 had a value of 65 million dollars, Honey Market News, (1973). Economically though, the value of nectar secretion cannot be measured completely on the basis of commodity production

in our nations agriculture. Many wild plants, shrubs, and trees through pollination associated with nectar secretion, furnish the animal kingdom with large sources of food in the form of fruits and seeds. Nectar also serves as a food for many animals other than honey bees.

Cook (1923) reported that nectar secretion studies date back to Ruellins (1543). For many years nectar secretion was studied for academic reasons. Early researchers described nectaries and suggested that nectar was secreted to nourish the embryo, needed by the fruit buds, while others thought it was injurous to them. Recent studies have been concerned with finding the optimum conditions for nectar secretion as well as understanding the actual secretion process.

A knowledge of nectar secretion is important for many reasons. Beekeepers need this information so they can locate apiaries close to areas which will provide a surplus of honey. In order to manage bee colonies for successful honey production, knowledge of the secretion cycles for the plants in the area is needed. Such information enables the beekeeper to decide when he should install package bees, divide colonies, put on supers, remove honey, requeen and prepare colonies for winter. Orchardists and growers who rent bees for pollination need to know what plants may attract bees away from the crops to be pollinated. Knowing why bees work one species of plant while disregarding another, they should be able to more intelligently locate bees for honey production and crop pollination. Spray poisoning may be reduced if the plants attractive to bees are known.

Any improvement in nectar production of a specific crop should increase the attractiveness of the crop to bees and thus the effectiveness of pollination. Shuel and Pedersen (1953) and Shuel (1955a) suggested two ways for increasing nectar production: (1) through breeding and selection of plants for high nectar production. Studies have shown wide hereditary differences in nectar yielding ability in bee-pollinated crops. (2) by cultural means, including the provision of good conditions of soil drainage and the use of fertilizers favoring high nectar production.

Plant breeders have been actively modifying crops for many purposes, generally associated with improved yield and quality, or adaptations to mechanized agriculture. Breeding crops which are more attractive to bees has enormous possibilities. For instance, soybean industry leaders foresee great potential in developing hybrid soybeans with honey bees providing cross pollination of inbred lines. For efficient use of honey bees, nectar production would have to be built into new lines, Jaycox (1970).

Bees visit flowers to gather nectar and pollen. Research suggests that attraction to a flower is visual, with aroma helping in specific identification. A reward of nectar or pollen is necessary for continuing visits to the plant. Other factors affecting bee visits appear to be chemical attractants in pollens, Hopkins, Jevans and Boch (1969), flower structure, nectar accessibility, quantity, sugar concentration, pH, flavor, and composition.

Some plant breeders have recently become more aware of the need to keep bee-pollinated crops attractive to bees. Problems have

arisen in the production of hybrid onion seed, Bohart, Nye and Hawthorne (1970) and Gary, Witherell and Marstow (1972). Nye, Waller and Waters (1971) found that inbred lines vary in nectar attractiveness to insects.

Plant breeders have expressed a need for more information on attractiveness to bees and simplified ways of measuring it, so that significant factors of attractiveness may be readily monitored throughout breeding programs. Martin and McGregor (1973) suggested that apiculturists should be more intimately associated with breeding programs involving bee-pollinated crops, to help maintain attractiveness and usefulness to bees, and to elucidate ways in which pollination affects breeding techniques and selection of genetic material.

The production of pickling cucumbers in Michigan has recently undergone changes in cultural methods as well as breeding programs which have greatly increased the need for bees. The industry has gone from multiple hand harvest to a single destructive harvest with mechanical equipment. In order to have a single profitable harvest, plant populations have increased from less than 20,000 plants per acre to populations up to and over 200,000 plants per acre. Secondly, the development of "gynoecious" lines of pickling cucumbers, Peterson (1960), made it possible to develop commercial hybrids which are providing higher yields and more uniform growth.

With the development of new gynoecious F_1 hybrid cultivars, changes in the economics of production with new cultivation and harvesting techniques, the need for this study evolved.

Major objectives of the study were:

1. To obtain a comprehensive picture of nectar secretion in cucumber flowers as influenced by time of day, cultivar, age of flower or other factors.

2. To establish correlations between bee visits and nectar secretion.

3. To see if quantity and quality of nectar secretion is being maintained in new cultivars.

4. To progress toward a practical system of monitoring the attractiveness of new cultivars to bees during the course of a crop breeding program.

CHAPTER I

FLOWER AND NECTARY ANATOMY AS RELATED TO NECTAR SECRETION

The Cucumber Nectary

Knuth (1908) described the nectaries of flowers in the order Cucurbitaceae, as naked fleshy cups formed by the fusion of the lower parts of the calyx and corolla. The nectaries consist of a layer of secretory tissue about 1 mm thick, and are provided with water-stomata. Members of the genera Cucumis, Cucurbita and Bryonia have flowers with concealed nectar.

Staminate flower nectary.--The three-lobed button on the floor of the staminate flower is a rudimentary pistil (Figs. 1-3) and under favorable conditions, this glandular structure may develop into a fertile pistil, making the flower bisexual. Therefore, it is called a pistillodium rather than a nectary, Heimlich (1927) and Chakravarty (1958); however, in line with popular usage, the term nectary is used herein. Nemirovich-Danchenko (1964) referred to the nectary as a protuberance with three or four sections (Figs. 1-4). Four-lobed nectaries were also observed by Heimlich (1927). He found that the epidermal cells of the nectary were very small and smooth as compared with the epidermal cells lining the inner wall of the perianth tube. Cook (1923) found that staminate flowers of pumpkin, Cucurbita pepo, had the calyx

and corolla united at the base, supporting a cup-shaped disk. The sides and base of this cup secreted and held the nectar. The glandular tissue was very deep, extending into the interior for at least 1.5 mm. The epidermis was prominent, the cells being somewhat longer than in ordinary glandular tissue. The epidermal cells were somewhat broader than long, their outer walls curving only slightly, and were less granular than the underlying tissue. The epidermis was plentifully supplied with stomata which were only slightly sunken. Beneath the stomata were found the stomatal chambers and under the epidermis were many layers of sub-epidermal cells. These cells were small, 4-6 sided, and filled with granular protoplasm. Below the sub-epidermal cells were two regions of parenchymatous tissue, made up of cells larger than those of the sub-epidermis and several layers thick. Chakravarty (1958) referred to the pumpkin nectary as being trilobed.

Bohn (1961) described the nectary of the staminate muskmelon flower as being saucer-shaped whereas Free (1970) called it a cup-like gland in the center of the receptacle.

Pistillate flower nectary.--Free (1970) stated that a ring like nectary surrounded the base of the style in pistillate flowers of genus Cucurbita and in hermaphroditic flowers of Cucumis melo. Nemirovich-Danchenko (1964) and Hayward (1938) described the nectary of cucumbers as having the form of a cup or ring surrounding the style in pistillate flowers (Figs. 8-12).

Materials and Methods

The structure of the nectaries was studied using a binocular and scanning electron microscope (SEM). To prepare for viewing with an SEM, cucumber flowers of different ages were picked from Michigan State University (MSU) field plots and transported to the laboratory in a wide mouth thermos bottle, Shuel (1968). Nectaries were dissected from the staminate and pistillate flowers and placed on two faced transparent tape which was attached to aluminum pedestals. They were surrounded by Walsco Television Tube Kote, placed within the chamber of a high vacuum evaporator, dried, and coated with gold palladium. After removal, the nectaries were placed in the specimen vacuum chamber of the SEM.

Results and Discussion

When flowers were picked on the day of anthesis, the nectaries contained a high amount of moisture which required a long period of evaporation. Excessive moisture did not pose a severe problem with nectaries of staminate flowers, but those of pistillate flowers formed a large bubble in the center of the cup, while in the evaporator. When gold palladium was added, the bubble burst and destroyed a large amount of tissue. To alleviate this problem, I successfully used day old pistillate flowers (Figs. 12 and 13).

While attempting to focus the SEM on the surface of the four-lobed nectary from the staminate flower (Fig. 4), many of the stomate-like pores of the epidermis began to close as the heat and beam of electrons were striking it (Figs. 5 and 6). This may indicate that

the stomate-like openings in the nectary surface can open and close as environmental conditions around the nectary surface change.

In looking at various areas of the nectary of pistillate flowers, stomate-like pores were found only on the inner surface of the cup and not on the outer edge or surface (Figs. 13-16). From an evolutionary standpoint, it would appear advantageous for the pistillate flower to concentrate its nectar supply within the cup around the base of the style, with the stigma directly above it. Because of its location, the honey bees body must contact the stigmatic lobes in order to reach the nectar supply. The honey bee generally circles the nectary, inserting and retracting its proboscis several times, resulting in efficient pollen distribution on the stigmatic lobes.

Behrens (1879), cited by Cook (1923), divided nectar secretion into 5 classes based on the structure of different nectar secreting tissues. I believe the cucumber nectary would fit his fourth class; "secretion of nectar through the opening of stomata on the epidermal layer, which are sometimes sunken. Nectar passes from the stomatal chambers and then out through the stomata." Fahn (1952) used a similar classification. Knuth (1908) described the nectaries of Cucurbitaceae as having water-stomata and Cook (1923) described the nectary of pumpkin as having slightly sunken stomates, with stomatal chambers below. Photomicrographs from the SEM show stomate-like pores in the epidermal layer (Fig. 6). The nectary surface is irregular and the area surrounding the stomate appears to be slightly depressed.

Comparison of SEM photomicrographs (Figs. 3-7 and 12-16) with photographs taken through a dissecting microscope (Figs. 1-2 and 8-11)

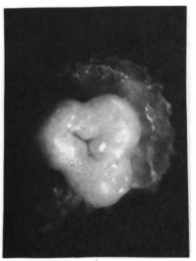
shows that the SEM is superior for examining the nectary surface in fine detail. The SEM photomicrographs have magnifications ranging from 20-800 times actual size. No references were found on use of the scanning electron microscope for studying nectary structure. However, Schnepf (1964) and Findlay & Mercer (1971) used transmission electron microscopy along with histochemical tests to study the internal structure and physiology of the nectary. The scanning electron microscope was a valuable aid in giving me a better understanding of the external surface of the nectaries.

Proportion of Three and Four-Lobed Nectaries Found in Staminate Flowers

Cultivars having staminate flowers with a higher percentage of four-lobed nectaries (Fig. 4) rather than the typical three-lobed (Fig. 3), tend to have larger nectaries. Several authors have shown a correlation between the volume of nectar and size of nectary. The phenomenon was found to be sufficiently prevalent to warrant further study.

Materials and Methods

During 1970 and 1971 the nectaries of staminate cucumber flowers were examined and the number of lobes recorded. Flowers of the cultivars SMR 58, 9805, Spartan Dawn, Spartan 27 and Piccadilly were grown at MSU research plots and the cultivar Pioneer (gynoecious F_1 hybrid) with a 10% SMR 58 blend was taken from commercial fields in Eaton County.



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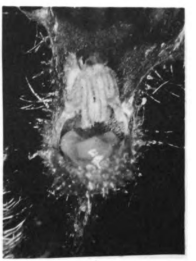

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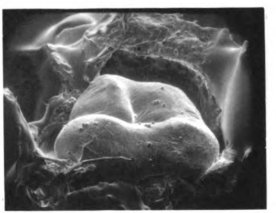

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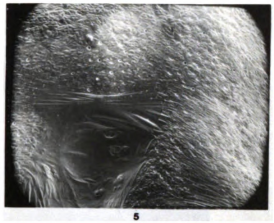
Fig. 1. Nectary of the staminate flower as seen through a dissecting microscope. 2. View of the staminate flower nectary and stamens. 3. Nectary of the staminate flower as seen by a scanning electron microscope. 20x. 4. Four-lobed nectary of the staminate flower as seen by a scanning electron microscope. 20x.



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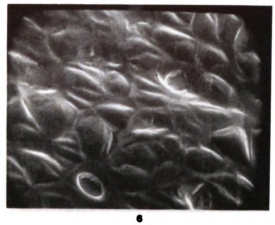

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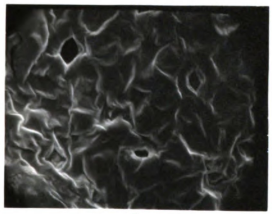

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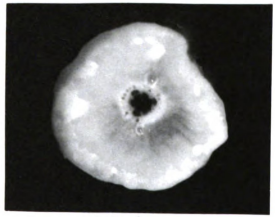

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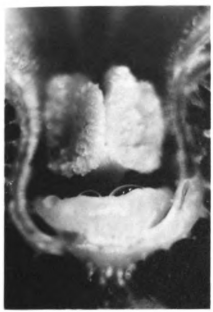
Fig. 5. Scanning electron photomicrograph of the three-lobed nectary of the staminate flower showing the stomate-like pores of the epidermis. 80x. 6. Scanning electron photomicrograph of the three-lobed nectary of the staminate flower showing the stomate-like pores of the epidermis open. 800x. 7. Scanning electron photomicrograph of the four-lobed nectary of the staminate flower showing the closing of stomate-like pores of epidermis. 800x. 8. Cup-shaped nectary of the pistillate flower with stigma and style removed as seen through a dissecting microscope.



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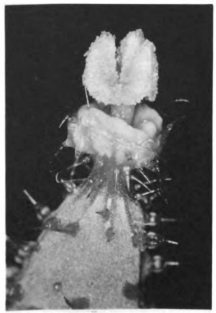

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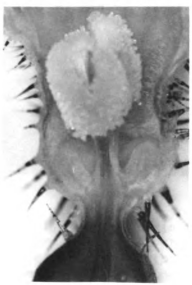

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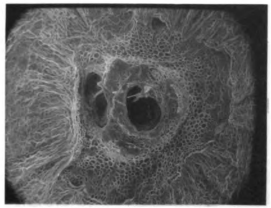
Fig. 9. Cup-shaped nectary of the pistillate flower with droplets of nectar on the nectary tissue. 10. Pistillate flower with corolla and calyx removed, showing 3 stigmatic lobes, style, and nectary. 11. Cross section through pistillate flower showing stigma, style and nectary tissue. 12. Scanning electron photomicrograph of the pistillate flower nectary with stigma and style removed. 20x.



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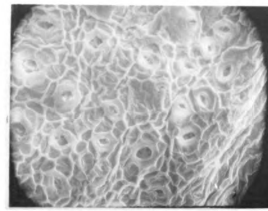

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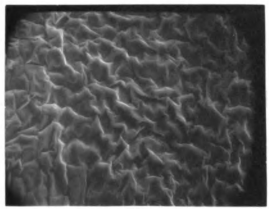

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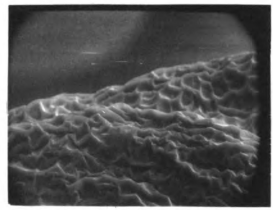

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Fig. 13. Scanning electron photomicrograph of the pistillate flower nectary showing the stomate-like pores of the epidermis and where the style was attached to the bottom of the nectary cup. 100x. 14. The stomate-like pores on the inner surface of the pistillate flower nectary as viewed through a scanning electron microscope. 15. The outer surface of the cup-shaped pistillate flower nectary showing the absence of pores as viewed by a scanning electron microscope. 500x. 16. Outer surface of the cup-shaped pistillate flower nectary showing the absence of pores as viewed by the scanning electron microscope. 500x.

Results and Discussion

Significant differences in the presence of three or four-lobed nectaries were found in different cultivars (Table 1). Three lobes were typical but of the cultivars tested, four-lobed nectaries were found to range from 0.7-12.3% of the total populations. The cultivars Pioneer and MSU 9805 contained the highest percentage of four-lobed nectaries.

Origin of the trait.--Baker (1972) suggested that the four-lobed nectary trait was inherited from the famale parent of the hybirds. Therefore, the parents of the four gynoecious hybrids sampled (Table 1) were tested to see if the source of this trait could be located. If found, then the plant breeder could possibly incorporate the four-lobed trait into new staminate lines. With the increased area of the nectary, nectar secretion might be improved and possibly the staminate flower would be more attractive to honey bees.

Materials and Methods

To test the genetic origin of the four-lobed trait, six parents that were not tested previously, SMR 18, MSU 183 G, 713-5, GY3, SMR 15 and Chipper, were planted during the summer of 1972. Thirty-seven days after planting, gibberellin (Pro-Gibb 47) at a rate of 50 ppm was sprayed on the predominately gynoecious lines to stimulate staminate flower production, Peterson and Anhder (1960). Each day the staminate flowers were picked from each of the parent stocks, and the number of three and four-lobed nectaries recorded. The gibberellin application

37 days after planting proved to be unsuccessful for staminate flower induction, therefore, the female parents MSU 183 G, 713-5 and GY3 were planted in a greenhouse on January 3 and February 9, 1973. Each planting consisted of ten plants per cultivar growing on cane poles. The first planting was treated with gibberellin at 22, 27 and 32 days after planting, and the second at 20, 25 and 30 days at a strength of 50 ppm. The staminate flowers thus produced were picked, examined, and the number of lobes recorded.

Results and Discussion

Pioneer in the original study had the highest occurrence of four-lobed nectaries at 12.3% but its parents, GY3 and SMR 18, did not produce similar results. GY3 grown in the greenhouse did not produce any four-lobed nectaries and SMR 18 produced only 3.2% in the field (Table 1). Parents of MSU 9805, MSU 183G and Chipper, also produced low numbers of four-lobed nectaries. In Chipper the four-lobed nectary occurred 0.4% of the time and in MSU 183G only 0.3%.

Of the male parents tested, SMR 15 was significantly higher than the rest, having the four-lobed nectary in 9.3% of the samples. In the greenhouse, 713-5 was the highest of the female lines with 3.7% occurrence. Both of these lines were parent stock for the hybrid Piccadilly. But in the original study, four-lobed nectaries only occurred 2.3% of the time in staminate flowers of Piccadilly. In the greenhouse only 713-5 and 183G produced four-lobed nectaries in chemically induced staminate flowers. The cultivar 713-5 produced 107

staminate flowers over a twenty day period before a four-lobed nectary appeared. In the next 22 days the plants produced 28 of them with only one day when none appeared. By that time, the chemical treatment was becoming ineffective, and the plants were reverting back to pistillate flower production. None of the 30 plants in the 2nd planting produced any four-lobed nectaries in 25 days of flowering. By that time, the effectiveness of the gibberellin had dissipated.

Difference in field and greenhouse results may indicate that production of four-lobed nectaries is a response to certain environmental conditions, similar to parthenocarpic fruit production. Teidjens (1928) found that high light intensities reduced parthenocarpic development of cucumbers. A reduction in the amount of light resulted in a vegetative response which brought about parthenocarpy and "easier fruit set," implying that the percentage of flowers which developed was higher. Connor (1969) found that the response was greatest in the fall and spring at MSU. Plants in the first planting which produced four-lobed nectaries were flowering during a time of reduced light intensity compared to those of the 2nd planting which did not produce any. Further research is needed to establish the factors which influence the expression of this trait.

The Nectary as Related to Floral Development

The floral parts of the staminate flower appear in the following sequence: calyx lobes, corolla lobes, stamen lobes and nectary lobes in Cucumis sativus and Cucumis melo, Judson (1929b, 1935).

Table 1. - Comparison of the number of three and four-lobed nectaries present in staminate flowers of various cucumber cultivars.

Variety	Sample size	% 4-lobed	Seed type	Parents Female	Parents Male
Piccadilly	691	2.3	gynoecious	713-5	SMR 15
Pioneer	302	12.3	gynoecious	GY 3	SMR 18
SMR 58	614	2.0	monoecious	--	--
M.S.U. 9805	845	5.8	gynoecious	MSU 183G	Chipper
Spartan Dawn	445	0.7	gynoecious	713-5	Spartan
Spartan 27	773	2.4	monoecious	--	--
Parent Stock 1972					
SMR 18	407	3.2			
SMR 15	442	9.3			
Chipper	680	0.4			
Greenhouse 1973					
Planting 1					
713-5	763	3.7			
GY 3	338	0.0			
183G	348	0.3			
Planting 2					
713-5	232	0.0			
GY 3	21	0.0			
183G	50	0.0			
Overall					
713-5	995	2.8			
GY 3	359	0.0			
183G	398	0.3			

McLean (1947) had the same results with Cucumis melo. Heimlich (1927) reported a different sequence for cucumbers, namely: perianth tube, stamens, nectary, calyx lobes and corolla lobes. He found that the primordia of the nectary forms in the base of the cup. The usual three lobes of the nectary arise in a low spiral arrangement, the lobes alternating with the stamens. Judson (1929b) found that immediately after the primordia of the stamens appear, three small lobes may be recognized equidistant from one another, near the bottom of the receptacle, below and within the stamen lobes. These lobes grow toward each other and form a small three-lobed nectary.

Kirkwood (1905) reported that pistillate flowers of various Cucurbitaceae have the floral parts develop in the following sequence: calyx lobes, corolla lobes, staminodium or stamen lobes and pistil lobes. Judson (1929A, 1949) while working with the pistillate flowers of Cucumis sativus and Cucumis melo reported similar findings. Judson found that the nectary tissue of cucumber is differentiated from the receptacle after the carpel lobes have extended upward into the perianth tube. Between the base of the perianth tube and the style, a group of cells become meristematic and a continuous ring of nectary tissue is formed surrounding the style. The nectary tissue is composed of cells with large nuclei and coarsely granular cytoplasm.

The Vascular Tissue of the Nectary

The concentration at which nectar leaves the nectary cells appears to depend on the anatomy of the vascular system supplying the nectar and on the sugar concentration in the phloem and/or xylem of

the nectary vascular supply, Frey-Wyssling and Agthe (1950), Agthe (1951), Zimmermann (1953), Shuel (1956), Huber (1956) and Frey-Wyssling and Hausemann (1960). Esau (1953), Agthe (1951), Frey-Wyssling and Agthe (1950) and Zimmermann (1953) found that highly concentrated nectar, essentially originates from phloem tissue whereas plants that produce high volumes of dilute nectar have only a few sieve tubes to transport sugars to the nectary, and abundant xylem.

The quantity of nectar secreted is a function of the carbohydrate supply to the nectary, Agthe (1951), Wykes (1952c), Shuel (1955b, 1956) and Waddle (1970). Wykes (1952c), Shuel (1955b), and Czarnowski (1952) demonstrated that curtailing carbohydrate synthesis and transport to the flower by defoliation and phloem ringing, reduced nectar production in various species of plants.

Miribel (1815) as cited by Cook (1923) found that the cells of nectary tissue are traversed by vascular ramifications. Caspary (1848) cited by Fahn (1952) found that nectar originated in nectary cells and not from vascular bundle secretions. Cook (1923) observed vascular bundles in all glands that he studied. They were found in close proximity to each other running either parallel or at right angles to the nectary tissue. Sometimes they extended into the nectary tissue. Beutler (1953) stated that vascular bundles ramify throughout the surrounding areas, but seldom penetrate the nectary.

Even after the vascular tissue has supplied the nectary with carbohydrates and water, it appears that ultimately nectar secretion depends on the metabolic activity of the nectary itself, Agthe (1951), Frey-Wyssling, Zimmermann and Maurizio (1954), Ziegler (1955), and Shuel (1967).

McLean (1947) while studying the staminate flowers of Cucumis melo found that the pedicel contained 10 main vascular bundles. Chakravarty (1958) while working with staminate flowers of Cucumis melo and Cucumis sativus also found that the pedicel had 10 bundles arranged in a single ring. After further branching, the bundles fuse at the receptacle forming an irregular broad ring. The outer part of this ring supplies the sepals and petals. The glandular nectary receives a number of weaker and shorter bundles from the innermost part of the vascular cylinder. In all species of Cucurbitaceae that he examined, the traces of vascular bundles for the nectary came from the inner side of the stele (vascular tissue forming a cylinder running through the stem) and ran through the inner surface of the receptacle. Traces for the nectary are far more numerous but they are smaller and weaker than those supplying the petals, sepals and stamens. These traces are arranged in a circle in the outer wall of the nectary, or sometimes scattered within where they often coalesce.

Heimlich (1927) found that the vascular bundles in the pedicel of the staminate cucumber flowers vary in number. They may form a continuous or nearly continuous ring in the lower portion of the receptacle. Slightly above this, the vascular tissue appears as a general plate or low dome-shaped expanse. Some of the branches from this plate enter the nectary. Each group supplies one of the lobes of the nectary. Within the fleshy portion, there is considerable branching and anastomosis of the vascular bundles.

Judson (1929a) found that the pistillate cucumber flower had ten main bundles at the upper extremity of the pedicel. At the narrow

neck of the flower the five bundles of the outer cycle (the main sepal bundles) fork, and five branches, extend inward and upward to the nectary tissue where they branch and anastomose freely. The nectary tissue is well supplied with branched vascular bundles.

Cook (1923) found that the two regions of parenchymous tissue in the pumpkin nectary contained extremely thick vascular bundles that ran in every direction. The vascular bundles ended in the nectary tissue and were very abundant. Chakravarty (1958) found that the pumpkin pedicel had 12 vascular bundles arranged in two rings. The bundles fused in the receptacle. From this fusion, many weak and short traces passed to the nectary.

The Procedure Used to Remove Nectar from Staminate and Pistillate Cucumber Flowers

The cucumber plants used for nectar secretion studies were grown at the Collins Road plots, Michigan State University, East Lansing, Michigan. Nectar removal from the cucumber flowers proved to be easily done since the flowers are large and the nectary accessible. Nectar was removed with Drummond microcaps, 10 microliter size (Fig. 17). To improve the action, the microcaps were attached to plastic tubing for mouth suction in addition to the capillary effect. The reverse action was used to empty the tubes. The tubes were inserted into the nectaries between the stigmatic lobes of the pistillate flowers and between the anthers of the staminate flowers (Fig. 18). Two to three insertions were needed to remove the nectar from the flowers.

The pipets were 41 mm long and held 10 microliters. By measuring the amount of nectar within the tube to the nearest mm and figuring proportionately, the volume of nectar was determined. Next, the nectar samples were placed on the prism of a Bausch and Lomb Abbe 3L refractometer to determine the refractive index and total solids present (sugars) (Fig. 19). Volumes of less than 0.49 microliters generally did not make a large enough droplet on the prism, so refractometer readings could not be taken. Corrections for temperature were made for each sample with tables found in the Association of Official Agricultural Chemist Handbook (1950).

The total weight of sugars present which takes into account both volume of nectar and sugar concentration, was figured by multiplying the volume in microliters x the specific gravity of the percent sugar present x the sugar concentration. Tables for determining the specific gravity of a sugar solution are also found in the handbook (pages 711-12).

To prevent bees from removing the nectar, plants were enclosed in nylon screened cages or the flowers were bagged one day prior to anthesis in 2.5 inch square organdy bags.

For most samples, flowers were picked and nectar removed shortly afterwards in the fieldhouse adjoining the plots. For studies that required the flowers to remain on the plants, microcaps were taken into the field in one section of a plastic petri dish, being kept separate by an index card partition (Fig. 17). After removal, the samples were taken into the fieldhouse for refractometer readings.

Nectar removal from flowers other than cucumbers may present some problems especially for compound flowers from the families Compositae and Leguminosae. Methods other than microliter pipets may have to be employed. Possibilities would include centrifuging, Swanson and Shuel (1950), absorption of nectar on weighed filter paper strips, Kenoyer (1917), and the leaching out of nectar by soaking flowers in water, Livtzeva (1954). Comparison and discussion of the various methods was done by Skirde (1960, 1961), Yakovleva (1966) and Beutler (1953).

In order to monitor the attractiveness of new cultivars to bees during the course of a crop breeding program, some refractometer readings may be required. Small, less dependable, hand refractometers are available that can be taken directly into the field.

Nectary Size and Nectar Secretion

Free (1970) stated that the size of the nectary may influence the amount of nectar secreted. Fahn (1949a, 1949b) in sampling nectar from 66 different species of plants found a definite relationship between the quantity of nectar secreted and the size of the nectary but no correlation was found between the concentration of nectar and nectary size. In Cucurbitaceae, the volume of nectary tissue is larger in the pistillate flower than in the staminate flower. Timenskii (1968) found a positive relationship between the size of the flower and nectar yield. Beutler (1953) reported that the quantity of nectar secreted and its sugar content are related to the size of the flower, which partially determines the size of the nectary. Waddle (1970) found that the rate of nectar flow, in general, was a function of the nectary area in cotton.

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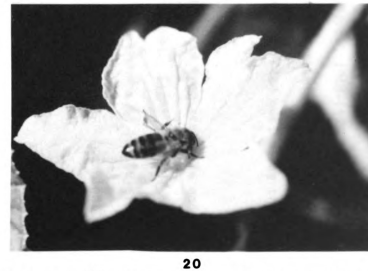

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Fig. 17. Nectar removal in the field with Drummond microcaps. 18. The insertion of the microliter pipet between the stigmatic lobes to remove the nectar from the pistillate flower. 19. The analysis of cucumber nectar with a Bausch and Lomb Abbe 3 L refractometer. 20. A honey bee removing the

nectar of a cucumber flower.

Materials and Methods

During the course of this research, 1968-1973, five studies involved the measurement of nectaries from staminate and pistillate flowers. Correlated nectar studies were carried out, using the same flowers.

1968A.--Measurement of the nectaries from staminate and pistillate flowers were made to the nearest mm. Eight seed lots of 10 plants each were used. Each morning, all flowers on the 80 plants were picked, counted, petals and nectaries measured. The eight seed lots used were:

a. Spartan 27
b. Spartan Dawn - no pollinator
c. Piccadilly - Med. I, no pollinator
d. Piccadilly - Med. II, no pollinator
e. Spartan Progress (MSU 35 G x 381)
f. MSU 35 G (Gynoecious)
g. Piccadilly - Med. II, no pollinator
h. SMR 58.

1968B.--A second replication of the previous planting was made later in the summer. Five plants from each of the cultivars f, g, and h were covered by a 6 ft^2 nylon screened cage. The plants grew upward on cane pole stakes, and the flowers were harvested at 9:30 a.m. The flower node was recorded, petals and nectaries measured before nectar removal.

1969.--Nylon screen cages 6 x 12 ft^2 were placed over plants of the cultivars SMR 58 and Spartan Progress. Pistillate flowers were picked at 11 a.m. and 4 p.m. The petal width, nectary width and ovary length were recorded prior to nectar removal.

1970.--The nectary width of staminate and pistillate flowers from the cultivar Piccadilly Med 1 were measured to the nearest mm.

1971.--To get a more accurate determination of the size differences between the nectaries of the staminate and pistillate flowers, they were measured under a dissecting microscope with an ocular micrometer. The width and depth of staminate flower nectaries were measured using 15x oculars and 0.7x objective lenses. Cultivars Spartan 27 and SMR 58 supplied the staminate flowers. The width, depth and thickness of the sides of the nectary cup of pistillate flowers of MSU 9805, MSU 35G and a parthenocarpic cultivar (MSU 6902 G) were measured.

Results

1968A.--In the cultivars that produced both staminate and pistillate flowers, the average width of the nectaries of pistillate flowers was over one and a half times that of staminate flowers (Table 2). Means of staminate flower nectaries ranged from 2.6-2.9 mm (overall mean, 2.8 mm) in diameter, whereas pistillate flower nectaries ranged from 4.2-4.6 mm (overall mean, 4.4 mm). Thus, pistillate flower nectaries were approximately 1.6 times as wide as staminate flower nectaries. The smallest pistillate flower nectary measured was 2 mm and the largest 8 mm whereas the smallest staminate flower nectary

was 1 mm and the largest, 6 mm. Of the 795 staminate flower nectaries measured, 88% were 2 to 3 mm wide and of the 1079 pistillate flower nectaries, 92% were 4 to 5 mm wide (Table 3).

The average size of petals of pistillate flowers was larger than that of staminate flowers in all cultivars but the differences were not nearly as great as was shown by the nectaries. Means of staminate petals averaged from 42.5-46.0 mm in width and pistillate ranged from 44.5-49.1 mm (Table 2). The overall means, considering all varieties, was 44.4 mm for staminate flowers and 47.2 mm for pistillate flowers. The average pistillate flower petal was approximately 1.06 times as large as that of the staminate flower.

To more fully assess relationships between nectar secretion and size of nectary, the data was sorted by nectary sizes and sex, then analyzed. A positive correlation was found between: (1) nectary size and petal diameter (Table 4), (2) nectary size and volume of nectar produced (Table 5), which is in agreement with Beutler, Fahn, and Timenskii. Overall there was a positive correlation between nectary size and total weight of sugar in the nectar, even though it was not significant in pistillate flowers (Table 7). No significant correlation was found between nectary size and sugar concentration (Table 6). When correlation coefficients were squared, there was an 18.2% association between petal size and nectary width, 11.8% between volume of nectar and the nectary size, 0.28% for sugar concentration and nectary width, and 5.1% for total weight of sugar and width of nectary.

1968B.--In this planting the staminate flower nectaries averaged 2.3 mm whereas the pistillate flower nectaries ranged from

Table 2. - The average flower diameter and nectary width of pistillate and staminate flowers for several cucumber cultivars.

Seed lot	Sample size	Staminate flower nectary (mm)	Sample size	Pistillate flower nectary (mm)	Staminate flower (mm)	Pistillate flower (mm)
Spartan 27	199	2.6 ± 0.04	45	4.5 ± 0.09	43.9 ± 0.41	45.6 ± 0.73
Spartan Dawn	93	2.7 ± 0.06	164	4.6 ± 0.05	45.3 ± 0.59	48.9 ± 0.49
Piccadilly Med I	73	2.8 ± 0.07	117	4.5 ± 0.06	46.0 ± 0.76	46.8 ± 0.51
Piccadilly Med II	120	2.7 ± 0.06	109	4.4 ± 0.07	44.6 ± 0.52	47.0 ± 0.53
Spartan Progress	1	--	179	4.3 ± 0.05	--	47.3 ± 0.50
MSU 35G	2	--	245	4.2 ± 0.04	--	49.1 ± 0.40
Piccadilly/Pollinator	97	2.9 ± 0.08	143	4.5 ± 0.05	42.5 ± 0.54	48.1 ± 0.45
SMR 58	210	2.9 ± 0.05	77	4.5 ± 0.07	44.2 ± 0.40	44.5 ± 0.75
Totals	795		1079			
Overall means		2.8 ± 0.05		4.4 ± 0.05	44.5 ± 0.50	47.2 ± 0.56

Comparison of overall means for nectary width and flower diameter found them to be highly significant at the 0.01 probability level (Student t test).

4.0-4.5 mm (Table 9). The average width of the pistillate flower was 1.7 to 1.9 times wider than that of the staminate flower. The pistillate flower nectaries ranged from 3 mm to 5 mm whereas the staminate flower nectaries ranged from 1 mm to 5 mm. Of the 366 staminate flower nectaries measured, 97% were in the 2 to 3 mm range and of the 61 pistillate flower nectaries, 95.1% were in the 4 to 5 mm range (Table 3). The average petal size of pistillate flowers was larger than that of staminate flowers in the two cultivars that produced both, but the differences were not as large as those of the nectaries (Table 9).

Correlation coefficients were established in which nectary size was compared with petal size, volume of nectar, sugar concentration and total weight of sugar in the nectar for the pistillate flowers of MSU 35G as well as staminate flowers of Piccadilly and SMR 58 (Table 9). Positive correlations were established between nectary and petal size as well as between nectary size and total weight of sugar for 2 of the 3 comparisons which is in agreement with 1968A. The 1968A study also showed a positive correlation between nectary size and volume of nectar in staminate and pistillate flowers, but in this study only pistillate flowers showed such a relationship. Also the staminate flowers of SMR 58 showed a positive correlation between nectary size and sugar concentration which was not found in the previous study. Squaring of the correlation coefficients showed ranges of 8.1 - 21.9% association between nectary width and petal size, 1.8 - 17.6% between nectary width and volume of nectar, 0.5 - 8.1% between nectary width and sugar concentration, and 5.6 - 24.0% between nectary width and total sugar present.

The values for cultivars producing staminate flowers were similar, but values for pistillate flowers were quite different (Table 9). This could be because small sample sizes of pistillate flowers were used.

1969.--In the 1968A study, the average pistillate flower nectary width was 4.5 mm for SMR 58 and 4.3 mm for Spartan Progress. In this study the values for these two cultivars were reversed and petal sizes were slightly less than before. The smallest pistillate flower nectary was 2 mm in width and the largest 6 mm. Nectary diameters of 93.6% of Spartan Progress flowers, measured in the 4 to 5 mm range while SMR 58 had 89.3% in this range (Table 8).

Since a positive correlation was found between nectary size and petal size (Tables 4 and 5), and Connor (1969) found a positive correlation between ovary length and number of ovules, the ovules of the flowers were measured to see if there was a correlation between the nectary width and ovary length. The ovary length of SMR 58 averaged 20.4 mm and Spartan Progress 18.7 mm (Table 11).

Correlation coefficients were computed comparing nectary size with petal width and ovary length. Positive correlations were found between: (1) nectary size and petal size and (2) nectary size and ovary length. The correlation coefficients showed an 11.6% - 11.8% association between nectary size and petal size and a 17.8% - 32.8% association between nectary size and ovary length (Table 11).

Analysis of the nectar secretion data showed correlations similar to the previous studies. Positive correlations were again

found between: (1) nectary size and volume of nectar and (2) nectary size and actual weight of sugar in the nectar for both morning and afternoon sampling times. A positive correlation between nectary size and sugar concentration was found only for the morning sampling period. The afternoon correlation coefficient was negative but the Student's t test showed it was not significant (Table 10).

1970.--The nectaries of pistillate flowers from the cultivar Piccadilly were 1.6 times larger than the staminate flower nectaries. Nectaries of pistillate flowers averaged 4.2 mm and those of staminate flowers 2.6 mm. The smallest pistillate flower nectary measured 2 mm and the largest 6 mm whereas the smallest staminate flower nectary was 1 mm and the largest 5 mm. Of 453 staminate flower nectaries measured 89.2% were in the 2 to 3 mm range and of 935 pistillate flower nectaries, 82.0% were in the 4 to 5 mm range (Table 3).

Again the Student's t test, showed a positive correlation between nectary size and petal width for both staminate and pistillate flowers. There was a 34.9% association between nectary and petal size for staminate flowers and 49.2% for pistillate flowers (Table 4). Significant correlations were found between mean petal size and nectary size with two exceptions (Table 4).

1971.--Again pistillate flower nectaries were wider than those of staminate flowers (Table 13). The overall average diameter of the pistillate flower nectary was 3.64 mm whereas the staminate flower nectary was 1.98 mm; therefore, the pistillate flower nectaries averaged 1.8 times as wide as those of staminate flowers.

Table 3. - Percent of the nectaries from staminate and pistillate flowers found within each size group.

	[1968 A		]		[1968 B		]		[1970		]	
Size	N	A	N	B	N	A	N	B	N	A	N	B
1mm	11	1.4%	0	---	8	2.2%	0	---	13	2.9%	0	---
2mm	225	32.1%	1	0.1%	229	62.6%	0	---	177	39.1%	7	0.7%
3mm	447	56.2%	52	4.8%	126	34.4%	3	4.9%	227	50.1%	141	15.1%
4mm	72	9.1%	550	51.0%	2	0.5%	48	78.7%	35	7.7%	446	47.7%
5mm	9	1.1%	445	41.2%	1	0.3%	10	16.4%	1	0.2%	321	34.3%
6mm	1	0.1%	28	2.6%	---	---	---	---	0	---	20	2.1%
7mm	0	---	2	0.2%	---	---	---	---	---	---	---	---
8mm	0	---	1	0.1%	---	---	---	---	---	---	---	---
Total	795		1079		366		61		453		935	

N = Sample size
A = Staminate flower nectaries
B = Pistillate flower nectaries

Table 4. - Correlation of nectary size with petal size.

Nectary width	[1968 A Sample size	Staminate flowers avg. petal size (mm)	Sample size	Pistillate flowers avg. petal size (mm)]	[1970 Sample size	Staminate flowers avg. petal size (mm)	Sample size	Pistillate flowers avg. petal size (mm)]
1mm	11	36.1 ± 1.4	0	---	13	34.0 ± 2.0	0	---
2mm	254	41.6 ± 0.3	1	---	177	41.2 ± 0.4	7	34.3 ± 2.2a
3mm	447	45.3 ± 0.2a	51	42.3 ± 1.1	227	46.8 ± 0.3c	227	46.8 ± 0.4a
4mm	72	48.9 ± 0.6b	540	46.4 ± 0.3c	35	50.9 ± 0.8	446	44.2 ± 0.2
5mm	9	46.0 ± 2.4ab	444	49.5 ± 0.2d	1	---	321	50.9 ± 0.3
6mm	1	---	28	53.8 ± 1.1e	0	---	20	54.6 ± 1.6
7mm	0	---	2	55.0 ± 8.0cde	---	---	---	---
8mm	0	---	1	---	---	---	---	---
		r = 0.3906*** (n = 794)		r = 0.3458*** (n = 1067)		r = 0.5909*** (n = 453)		r = 0.7016*** (n = 935)
Overall (1968A)		r = 0.4263*** (n = 3249)						

r = correlation coefficients
*** Significant at the .001 probability level.
Means in each column followed by the same small letter are not significantly different at the 5% probability level (Student - Newman - Keul multiple comparison test).

Table 5. - Correlation of nectary size with volume of nectar produced.

Nectary width	Sample size	Staminate flowers vol. of nectar (microliters)	Sample size	Pistillate flowers vol. of nectar (microliters)
1mm	2	0.86 ± 0.39abcd	0	---
2mm	46	1.22 ± 0.12 def	1	---
3mm	55	1.41 ± 0.16 c fg	10	2.32 ± 0.50 ij
4mm	10	2.56 ± 0.63a h	163	2.01 ± 0.16 i
5mm	2	2.06 ± 1.12 b e gh	145	2.94 ± 0.20 j
6mm	0	---	4	7.67 ± 0.96
		r = 0.2688** (n = 115)		r = 0.178*** (n = 323)

Overall r = 0.3440*** (n = 438)
** Significant at the .01 probability level.
*** Significant at the .001 probability level.
Means in each column followed by the same small letter are not significantly different at the 5% probability level. (Student-Newman-Keul multiple comparison test)

Table 6. - Correlation of nectary size with sugar concentration of nectar.

Nectary width	Sample size	Staminate flowers % sugar	Sample size	Pistillate flowers % sugar
1mm	2	38.0 ± 6.95a	0	---
2mm	42	41.8 ± 0.82a	0	---
3mm	51	42.6 ± 1.16a	9	41.6 ± 2.01 bcd
4mm	10	41.3 ± 1.41a	159	42.9 ± 0.39 c e
5mm	2	34.1 ± 7.55a	141	43.5 ± 0.43 de
6mm	0	---	4	36.2 ± 2.14 b
		r = 0.0213 n.s. (n = 107)		r = 0.0295 n.s. (n = 213)

Overall r = 0.0536 n.s. (n = 320)
n.s. = Not significant
Means in each column followed by the same small letter are not significantly different at the 5% probability level. (Student - Newman - Keul multiple comparison test).

Table 7. - Correlation of nectary size with total weight of sugar in the nectar.

Nectary width	Sample size	Staminate flowers wt. of sugar (mg)	Sample size	Pistillate flowers wt. of sugar (mg)
1mm	2	0.32 ± 0.11a	0	---
2mm	42	0.59 ± 0.06a	0	---
3mm	50	0.72 ± 0.08a	9	1.17 ± 0.17 bc
4mm	10	0.97 ± 0.14a	159	1.34 ± 0.07 cd
5mm	2	0.68 ± 0.24a	141	1.46 ± 0.09 b d
6mm	0	---	4	3.16 ± 0.31
		r = 0.2101* (n = 106)		r = 0.1096 n.s. (n = 313)

Overall r = 0.2258*** (n = 419)
n.s. = Not significant.
* = Significant at the .05 probability level.
*** = Significant at the .001 probability level.
Means in each column followed by the same small letter are not significantly different at the 5% probability level. (Student - Newman - Keul multiple comparison test).

Table 8. - Percent of the pistillate flower nectaries found within each size group. (1969)

Size	SMR 58 Sample size	SMR 58 % of group	Spartan Progress Sample size	Spartan Progress % of group
1mm	0	0.0	0	0.0
2mm	1	1.0	0	0.0
3mm	7	6.8	1	3.2
4mm	45	43.7	14	45.2
5mm	47	45.6	15	48.4
Totals	103		31	

Table 9. - *The correlation* of nectary size with petal size, volume of nectar, sugar concentration and total weight of sugar in the nectar. (1968 B)

Cultivar	Sample size	Average nectary width (mm)	Sample size	Average petal size (mm)	Sample size	Average nectar volume (microliters)	Sample size	Average sugar conc. %	Sample size	Average wt. of sugar (mg)
MSU 35G										
Staminate flowers	--	--	--	--	--	--	--	--	--	--
Pistillate flowers	35	4.0 ± 0.06	35	45.0 ± 0.97	25	2.90 ± 0.40	23	41.0 ± 1.40	23	1.47 ± 0.17
				r = 0.4683**		r = 0.4198*		r = 0.0685		r = 0.4895*
Piccadilly										
Staminate flowers	116	2.3 ± 0.05	116	39.2 ± 0.54	68	2.63 ± 0.15	68	45.2 ± 0.30	68	1.40 ± 0.07
				r = 0.2852**		r = 0.1499		r = 0.1107		r = 0.2361
Pistillate flowers	13	4.1 ± 0.08	13	41.1 ± 2.25	6	3.25 ± 0.28	6	45.1 ± 1.92	6	1.78 ± 0.20
SMR 58										
Staminate flowers	250	2.3 ± 0.04	193	40.9 ± 0.42	128	2.66 ± 0.10	121	45.1 ± 0.27	121	1.53 ± 0.05
				r = 0.2884***		r = 0.1326		r = 0.2843**		r = 0.2702**
Pistillate flowers	13	4.5 ± 0.14	11	42.4 ± 1.54	7	4.15 ± 0.96	6	45.9 ± 1.19	6	2.69 ± 0.51

* = Significant at the .05 probability level.
** = Significant at the .01 probability level.
*** = Significant at the .001 probability level.

Table 10. - Correlation of nectary size with volume of nectar, sugar concentration and total weight of sugar in the nectar (1969).

Cultivar	Sample size	Avg. nectar vol. (ul)	Avg. sugar conc. (%)	Avg. weight of sugar (mg)
SMR 58				
11:00 AM	82	5.22 ± 0.43	41.0 ± 1.42	2.34 ± 0.18
4:00 PM	20	9.54 ± 1.19	44.1 ± 2.10	4.93 ± 0.58
Spartan Progress				
11:00 AM	15	6.41 ± 0.88	32.1 ± 1.58	2.27 ± 0.31
4:00 PM	16	7.24 ± 1.19	42.3 ± 1.70	3.35 ± 0.48
Correlation Coefficients				
11:00 AM	97	r = 0.3239**	r = 0.2543*	r = 0.5130***
4:00 PM	36	r = 0.4682**	r =-0.1524 n.s.	r = 0.4399**

n.s. = Not significant.
* = Significant at the .05 probability level.
** = Significant at the.01 probability level.
*** = Significant at the .001 probability level.

Since scanning electron micrographs showed that the stomate-like pores through which nectar was secreted were found only on the inner surface of the cup in the pistillate flower nectary, the secreting area can be calculated. Figs. 8 and 11 show that the style takes up 24.4% of the total area of the nectary in the bottom of the cup. Therefore, a hypothetical model for figuring the secreting surface area of the pistillate flower nectary, would be a cup-shaped structure with an inner width of 2.30 mm at the top and .89 mm at the bottom with a depth of 1.04 mm (Table 13).

Two different geometric models were used for figuring the surface area. The inner surface of the cup was considered as a hemisphere. By using the depth from a central point as the radius of that sphere and subtracting the area taken up by the base of the style, an area of 6.17 mm^2 was calculated. The radius at the top of the cup was found to be 1.15 mm which was greater than the depth; therefore, a radius of 1.095 was considered a reasonable estimate and gave an area of 6.91 mm^2.

Another way to calculate the area is to consider the curved surface as a frustrum of a right cone with a base radius of 1.15 mm and the lower radius equal to .445 mm which would represent the base of the style. The frustrum would have an altitude equal to the depth. This gives an area of 6.30 mm^2 which probably is the best estimate.

The upper surface of the staminate flower nectary constitutes a circle with a diameter of 1.975 mm, if there were complete fusion of the 3 lobes that make up the nectary. Figs. 1 and 3 show that this is

not quite the case. Graphically, the nectary in Fig. 1 contains approximately 85.7% of the total area of the circle with a diameter equal to the width of the nectary. This hypothetical surface has an area of 3.06 mm^2. Subtracting 14.3% of the area, which was not part of the actual nectary, yields an area of 2.62 mm^2. From Fig. 3 it appears that stomate-like pores occur on the overlapping edge of the staminate flower nectary, along with an observed unevenness of the nectary surface; both of these factors would increase the nectary area; therefore, the value of 3.06 mm^2 would provide a reasonable estimate of secreting area.

From these values it would appear that the pistillate flower nectary has approximately twice as much secreting surface as the staminate flower nectary. Overall the staminate flower nectary measured 1.98 mm wide and .98 mm thick whereas the pistillate flower nectary measured 3.64 mm wide, with the edges .67 mm thick and a depth of 1.04 mm (Table 13).

Discussion

The following points summarize the results of the 5 studies dealing with nectary size.

1. In all cases the nectaries of pistillate flowers ranged 1.6-1.9 times as wide as the nectaries of staminate flowers.

2. The average width of the staminate flower nectaries was from 2.0-2.9 mm whereas the pistillate flower nectaries averaged from 3.6-4.6 mm.

3. The smallest pistillate flower nectary measured 2 mm and the largest 8 mm.

Table 11. - Correlation of nectary size with flower size and ovary length (1969).

Cultivar	Sample size	Avg. nectary width	Avg. petal width	Avg. ovary length
SMR 58	103	4.3 ± 0.07 mm	46.7 ± 0.57 mm r = 0.3404***	20.4 ± 0.30 mm r = 0.5729***
Spartan Progress	31	4.5 ± 0.11 mm	47.5 ± 0.69 mm r = 0.3435 n.s.	18.7 ± 0.39 mm r = 0.4225*
		Overall	r = 0.3416***	r = 0.5159***

n.s. = Not significant.
* = Significant at the .05 probability level.
*** = Significant at the .001 probability level.

Table 12. - Average petal size and ovary length of SMR 58 and Spartan Progress (1969).

	[SMR 58]			[Spartan Progress]	
Size	N	Avg. petal size	Avg. ovary length	N	Avg. petal size	Avg. ovary length
2mm	1	---	---		---	---
3mm	7	43.9 ± 2.42	18.1 ± 1.01	1	---	---
4mm	45	45.3 ± 0.94	19.1 ± 0.36	14	47.0 ± 1.13	18.0 ± 0.44
5mm	47	48.3 ± 0.66	22.0 ± 0.37	15	48.3 ± 0.80	19.1 ± 0.56
6mm	3	52.7 ± 2.60	24.7 ± 1.33	1	---	---

Table 13. - The average dimensions of the pistillate and staminate flower nectaries of several cucumber cultivars as measured by an optical micrometer.

Cultivar	Sex	N	Diameter (mm)	Thickness (mm)	Depth (mm)
SMR 58	M	101	1.95 ± 0.02	1.08 ± 0.02	---
Spartan 27	M	101	2.00 ± 0.03	0.88 ± 0.02	---
MSU 35G	F	109	3.33 ± 0.05	0.57 ± 0.01	0.97 ± 0.02
9805	F	115	3.80 ± 0.03	0.65 ± 0.01	1.05 ± 0.02
MSU 6902 G	F	28	3.78 ± 0.08	0.78 ± 0.03	1.10 ± 0.04

4. The smallest staminate flower nectary measured 1 mm and the largest 6 mm.

5. The diameters of the staminate and pistillate flower nectaries tend to fall within 2 class sizes. From 88% - 97% of the staminate flower nectaries were from 2 to 3 mm and 82% - 95% of those from pistillate flowers were 4 to 5 mm wide.

6. Consistently, I found positive correlations between: (a) nectary size and petal diameter, (b) nectary size and volume of nectar, (c) nectary size and actual weight of sugar in the nectar, (d) nectary size and ovary length but not for nectary size and sugar concentration.

7. The secreting surface area of the pistillate flower nectary measured approximately twice that of the staminate flower.

8. The squaring of correlation coefficients showed an 8% - 49% association between nectary size and petal diameter, 1% - 18% association between nectary size and volume of nectar, .3% - 8% association between nectary size and sugar concentration, 5% - 24% association between nectary size and total weight of sugar and 18% - 33% association between nectary size and ovary length.

Other research workers have shown positive correlations between: (a) nectary size and petal size and (b) nectary size and volume of nectar in several other plants. Since consistent positive correlations were found between actual weight of sugar and volume of nectar to nectary size, these characteristics should be usable in a breeding program. Nectar volume and sugar concentration present in flowers largely determine attractiveness of a plant to bees. These studies indicate

that attractiveness of a crop to bees could be readily monitored during a plant breeding program in that they have demonstrated a correlation between nectary size and nectar production which might provide the breeder with an additional indicator of attractiveness to bees. In a cultivar known to secrete nectar, selection for larger nectaries could further increase attractiveness. Plant breeders and growers have encountered major problems in production of adequate seed yields in hybrid onion and carrot. Adequate pollination appears to be an important part of the problem. In general, in past breeding of bee-pollinated crops, no adequate tools for measuring potential attractiveness to bees have been available, so this aspect of a breeding program has been largely overlooked. I feel that these studies now indicate that certain factors related to bee attractiveness may be readily monitored.

In addition to the usefulness of these studies to the plant breeder, it is conceivable that honey production and prosperity of the beekeeping industry could be vastly improved if nectar secretion could be even slightly improved in a few of our major honey plants such as alfalfa or potential honey plants such as soybeans. Again further monitoring of nectar production in breeding programs of such plants would be fully justified and could be of inestimable value in maintaining a prosperous beekeeping industry and an adequate nation-wide force of pollinating bees. I feel that my studies of nectar secretion in cucumbers could be expanded and applied to any crop which is bee-pollinated or a source of honey.

CHAPTER II

CUCUMBER NECTAR AND ITS SECRETION

Watkins (1926) listed cucumber as one of Michigan's important sources of nectar. Edgecombe (1946) on the other hand mentioned that honey bee colonies placed beside a cucumber field obtained very little honey from it. McGregor and Todd (1952) recorded that with only one colony per 5.7 hectares of cantaloupes, colonies lost weight. Wilson, Moffett, and Harrington (1958) reported that bees collected both nectar and pollen from cucumbers in Colorado. They also concluded that even though large acreages of cucumbers were grown, it was not an important source of nectar. Oertel (1967) reported that cucumber is considered a nectar and pollen plant in all regions of the United States except Alaska and Hawaii.

Cucumber nectar is almost colorless, Wilson, Moffett and Harrington (1958) and the honey is reported to be light amber or pale yellow in color, Watkins (1926), Milum (1943) and Wilson, Moffett and Harrington (1958). Watkins (1926) described the honey as having a mild and pleasing flavor. Milum (1943) stated that the honey was strong, later becoming mild, whereas Wilson, Moffett, and Harrington (1958) stated that it did not have an objectionable flavor.

Fahn (1949a, 1949b) in Palestine found that a single flower of Cucumis sativus secreted a daily average of 3.25 mg of nectar with

30.7% sugar (dry weight of 1.00 mg), whereas Cucurbita maxima (Winter Squash) produced 201.25 mg with 16% sugar (dry weight 32.37 mg) and Cucurbita pepo (pumpkin) 98.40 mg with 28% sugar (27.60 mg dry weight). Vansell (1941a, 1942) found that cantaloupe nectar averaged 46% - 46.7% sugar in California and Oregon. Wilson, Moffet and Harrington (1958) in analyzing the honey stomach contents of 18 bees, found cucumber nectar to average 42.2% sugar with a minimum of 37.8% and maximum of 49.2% in Colorado. In Wisconsin, Kauffeld and Williams (1972) took 10-20 hand refractometer readings of nectar from the honey stomachs of bees working cucumbers and found the average to be 36% - 41% sugar, depending on weather conditions. Shaw (1953) found the sugar content of nectar from Cucurbita maxima (Winter Squash) ranged from 18% - 38% with an average of 29.7%. Montgomery (1958) found that Citrullus vulgaris (watermelon) nectar averaged 26.6% sugar and Cucumis melo averaged 31.6% - 32.7% sugar by analyzing honey stomach contents. Cirnu, Tone and Coteanu (1967) found that Cucurbita maxima flowers secreted from 56 to 558 mg of nectar with a mean sugar concentration of 38%.

Even though individual cantaloupe and cucumber flowers secrete nectar abundantly, there are so few flowers per acre in comparison to other major sources, that one would not anticipate that the crop would be an important source of honey.

Nectar Secretion of Different Aged Flowers

Both staminate and pistillate cucumber flowers secreted most actively on the first day of anthesis Veprikov (1936) quoting Gorski as

cited by Beutler (1953). On the second day only half as much nectar was secreted and on the third day still less. Nemirovich-Danchenko (1964) found nectar secretion in both staminate and pistillate flowers to be greatest 3-4 hours after opening whereas Kaziev and Seidova (1965) reported that cucurbit flowers produced the largest quantity of nectar after the first day of flowering.

Bailey, Fieger and Oertel (1954) stressed the importance of considering the age of the flower in nectar work. They found that blossoms of equal age, grown under equal conditions, produced similar quantities of nectar. Blossoms picked at random contained varying quantities of nectar that differed greatly in sugar content.

Materials and Methods

Plots in which to study the nectar secretion of different aged flowers, were planted on June 7, 1968. Pistillate flowers of the cultivar Piccadilly were sampled from July 23 to August 23. Four different aged flower groups were used in this experiment.

1. Flowers 2 days after anthesis
2. Flowers 1 day after anthesis
3. Flowers on the day of anthesis
4. Flowers 1 day prior to anthesis.

Five bagged flowers were picked from each of the different aged groups each day at 1 p.m. EST and nectar removed.

Results and Discussion

The cucumber flower basically has a one day secretion period. None of the 93 flowers sampled one day prior to anthesis produced any

nectar by 1 p.m. Eighty five per cent of the flowers produced nectar on the day of anthesis and 31% of the day old flowers produced nectar. Only 3% of the two day old flowers contained nectar (Table 14). Flowers on the day of anthesis produced 1.1 times as much nectar as one day old flowers and 3.8 times that of the two day olds. The one day old flowers averaged only 16.7% sugar compared to 35.4% sugar for flowers on the day of anthesis (Table 14). The total weight of sugar in the nectar was also greatest on the first day. Flowers on the day of anthesis averaged 2.39 mg of sugar or 2.5 times as much as flowers the day after anthesis and 11.6 times those measured two days after anthesis. The actual weight of sugar present is a preferred indicator since it takes into consideration both the volume of nectar present and its sugar concentration.

Since the cucumber flower basically secretes for only one day, factors such as weather or cultural practices that prevent the bees from flying that day, essentially prevent pollination of that days flower output. Fruit already pollinated, will be one day closer to maturity and gaps in flower pollination will lessen uniformity of pickle production for machine harvest.

Further observations have shown that honey bees do not visit flowers the day after anthesis.

The Commencement of Nectar Secretion

Percival (1946) reported that the same stimulus which causes the opening of the flower likely stimulates the exudation of nectar from the nectary. Banadyga (1949) reported that anther dehiscence and nectar

Table 14. - The comparison of nectar secretion in different aged cucumber flowers.

Age	Sample size	% Producing nectar at 1:00 PM	Sample size	Avg. vol.	Avg. % of sugar	Avg. wt. of sugar
1 Day prior to anthesis	93	0.0	93	0.00	0.00	0.00
Day of anthesis	92	84.8	78	5.71 ± 0.51	35.4 ± 0.82	2.39 ± 0.19
1 Day after anthesis	88	30.7	27	5.23 ± 0.99	16.7 ± 1.33	0.92 ± 0.14
2 Days after anthesis	91	3.3	3	1.51 ± 0.36	13.1 ± 0.69	0.20 ± 0.05

Volume of nectar expressed in microliters.

Weight of sugar expressed in milligrams.

Data based only on those flowers that produced nectar.

secretion in cucumber starts from 17-18°C. Shuel (1961) found that anther dehiscence coincided with the beginning of secretion in Streptosolen jamesonii. He was able to show that the period of secreting activity of the nectary and stigma coincide.

Many plants have a threshold temperature below which they will not begin to secrete, Haupt (1902). This was 8° C for Prunus avium and 18° C for Prunus laurocerasus and these continue to secrete even if the temperature falls below the threshold temperature, Behlen (1911) cited by Beutler (1953). Wilson (1881) found the threshold temperature for Prunus laurocerasus to be 12° C or greater. Wilson and Haupt are cited from Kenoyer (1916, 1917). Demuth (1923) found that basswood begins secreting nectar at 18° C.

Materials and Methods

In 1969, continuous observations of flowers were started at 6 a.m. EST for 13 mornings to determine the temperature at which nectar secretion began. A centigrade thermometer was placed in a small cardboard box and set among the vines so that an accurate temperature reading could be recorded. Ten pistillate flowers (MSU 35G) were picked each time the temperature increased one degree. The flowers were checked under a dissecting microscope, for nectar exudation and if present, attempts were made to collect it.

Results and Discussion

The previous study showed that a flower one day prior to anthesis did not secrete nectar. This study showed that nectar secretion began on the day of anthesis and appeared to be temperature

dependent. Below 16° C all nectaries were dry. At 16° C, the nectaries looked moist or wet under the microscope but not with the naked eye. When the temperature was 17° C one or two small beads of nectar formed on the inside of the psitillate flower's cup-shaped nectary. From 18° C to 21° C the percentage of the nectaries containing beads of nectar increased as well as the number and size of the beads. The first nectar measurable in a microcap was observed at 21° C and the volume was equal to 0.24 ul.

Percival (1946) suggested that the opening of the flower and commencement of nectar secretion were dependent on the same stimulus. This study would indicate that this is not so. On August 19, 1969, at 6 a.m. at a temperature of 22° C in the field the flowers were closed tight and bees were desperately trying to work them. In breaking the pistillate flowers open, 90% of them contained many large beads of nectar and the staminate flower anthers of SMR 58 were completely dehisced even though the flowers were closed. By 6:30 the sun was beginning to break through the haze. At this time the flowers started to open slowly.

My observations during the 13 mornings showed that anther dehiscence started at approximately the same time as the pistillate flower nectaries became moist (16° C) whereas Seaton and Kremer (1939) and Banadyga (1949) reported that anther dehiscense did not occur until the temperature reached 17 to 18° C. It appears that the commencement of nectar secretion and anther dehiscense are temperature dependent whereas the opening of the flower is at least partially light dependent.

Temperature readings from the MSU south farm and tree research center which were close to the cucumber plots showed that air temperature may vary within short distances. By using a thermometer within the plant canopy the precise temperature to which the flowers were exposed was obtained.

Connor (1969) found that bee flights to cucumbers started at an average temperature of 16° C in East Lansing. Seaton and Kremer (1939) made similar observations. Since the nectary begins to get moist with nectar at 16° C, bee flights are likely associated with an attractive force such as aroma present in the flower at the time of nectar secretion.

A Comparison of Nectar Secretion in Staminate and Pistillate Flowers

Fahn (1949b) reported that the pistillate flower is the chief producer of nectar in the family Cucurbitaceae. He considered the volume of nectary tissue the determining factor and pistillate flowers are larger than staminate flowers. The following data from Fahn shows relative nectar secretion of staminate and pistillate flowers of cucumber, pumpkin and squash.

	Fresh Nectar in mg		Dry Sugar in mg	
	Staminate	Pistillate	Staminate	Pistillate
Cucumis sativus	2	4.5	0.5	1.5
Cucurbita pepo	54.5	142.5	15.0	40.25
Cucurbita maxima	60.5	342.0	9.75	54.0

Cirnu, Tone and Coteanu (1967) found that the pistillate flowers of *Cucurbita maxima* secreted more nectar than the staminate flowers.

Foster, Levin and McGregor (1965) found that staminate muskmelon flowers (Cucumis melo) produced .001-.002 ml of nectar whereas hermaphroditic flowers produced .019 ml. McGregor and Todd (1952) found that the sugar concentration of the nectar of staminate cantaloupe flowers was greater than that of pistillate (56:17%).

Nemirovich-Danchenko (1964) reported that nectar secretion in both staminate and pistillate cucumber flowers was greatest at 3-4 hours after opening, when pollen was most abundant and bee visitation greatest. The average daily nectar yield was 1.290 $\pm$ 0.038 mg in pistillate flowers and 0.687 $\pm$ 0.054 mg in staminate flowers; depending on temperature, it could rise to 2 mg in warm weather. Kaziev and Seidova (1965) found that a pistillate cucumber flower averaged between 1.1 and 2.4 mg of nectar compared to 0.9 and 1.6 mg for a staminate flower, depending on cultivar and environmental conditions. Under excellent conditions pistillate flowers reached 3.3 mg and staminate 2.0 mg. Staminate flowers of cucumbers, melons, and watermelons all secreted a much smaller quantity of nectar than pistillate flowers. Veprikov (1936) reported that staminate flowers on the main stems of cucumber produced 3.1 mg of nectar whereas the pistillate flowers produced only 2.5 mg. On the other hand, the pistillate flowers on lateral stems produced 3.4 mg and the staminate flowers only 2.1 mg.

Caspary (1848) found more nectar in staminate than in pistillate flowers of several species including Bryonia dioica, (gourd), Cucurbita pepo, and Cucumis melo. Kurr (1833) found that pistillate flowers of Bryonia dioica when placed in water, secreted less nectar than similarly treated staminate flowers. Veprikov, Caspary and Kurr were cited by Beutler (1953).

Kaziev and Seidova (1965) found that flowers of cucumbers, melons, and watermelons began to secrete nectar between 8-9 a.m. The greatest quantity of nectar accumulated between 11 a.m. and 2 p.m. The sugar content at noon and during the second half of the day was greater than during the morning. In staminate cantaloupe flowers nectar secretion ceased at 11 a.m. but continued until late afternoon in hermaphroditic flowers.

Materials and Methods I

The pistillate flower.--Plants of the cultivar MSU 35G were planted June 7, 1968. Each day, from 7 a.m. to 4 p.m., a minimum of two flowers were picked on the hour from July 26 to August 26. The nectar was removed for measurement from bagged and caged pistillate flowers.

Results

Because temperature as well as other weather factors vary from day to day, pistillate flowers began to secrete nectar at different times of the day. On August 12, measurable amounts of nectar did not appear until 1 p.m. whereas on August 20, 21 and 22 all of the flowers sampled were producing nectar at 7 a.m. The number of flowers producing nectar at each hourly interval increased throughout the day until noon (Table 15). For the rest of the afternoon the values were not significantly different.

The average volume of nectar increased throughout the day averaging from 1.40 to 9.92 ul. On the other hand, the average sugar concentration decreased throughout the day from 44.5% to 27.4%. The

actual weight of sugar increased during the day until 2 p.m., then began to decrease (Table 15). Pistillate flowers produced from 0.0 to 34.15 ul of nectar with a mean of 6.05 ul/day. The sugar concentration of the nectar ranged from 13.6% to 57.1% with a mean of 36.3%. The total weight of sugar in the nectar ranged from .06 to 12.33 mg with a mean of 2.29 mg/day (Table 17). Mean values were based only on those flowers which produced nectar.

Materials and Methods II

The staminate flower.--Flowers of the cultivar SMR 58 were picked daily from August 14 to August 29, 1969. Each day from 7 a.m. to 4 p.m. six caged flowers were picked on the hour and nectar removed.

Results

During the sampling of pistillate flowers (MSU 35G) in 1968, there were five days when the temperature was in the 70's by 6 a.m. Therefore, there was a measurable amount of nectar present by 7 a.m. During 1969, there were no days when the temperature was high enough to have a measurable amount of nectar by 7 a.m. Therefore, nectar production in staminate flowers in 1969 started later in the day than in pistillate flowers in 1968 (Table 15). Overall, there was an increase in the percentage of flowers producing nectar from the time secretion started until noon. For the rest of the day the values were not significantly different.

The average volume of nectar increased throughout the day averaging from .73 to 6.79 ul. The average sugar concentration decreased through the morning from 46.1% to 43.7% and had a similar

Table 15. - The percent of the pistillate flowers producing nectar throughout the first day of bloom and the average volume of nectar, sugar concentration and total weight of sugar present.

Time (EST)	Sample size	% Producing nectar	Sample size	Avg. vol. (ul)	Avg. sugar conc. (%)	Avg. total wt. of sugar (mg)
7:00 AM	146	17.1	25	1.40 ± 0.21	44.5 ± 1.01	0.72 ± 0.10
8:00	111	36.9	41	1.83 ± 0.22	42.5 ± 0.66	0.97 ± 0.11
9:00	86	50.0	43	2.89 ± 0.37	41.0 ± 0.49	1.52 ± 0.20
10:00	78	71.8	56	4.44 ± 0.45	40.0 ± 0.66	2.06 ± 0.21
11:00	69	73.9	51	6.08 ± 0.61	38.1 ± 0.80	2.70 ± 0.26
Noon PM	80	88.7	71	6.98 ± 0.61	35.8 ± 0.56	2.83 ± 0.24
1:00	68	91.2	62	7.61 ± 0.89	33.5 ± 0.69	2.78 ± 0.32
2:00	61	91.8	56	9.77 ± 1.05	30.3 ± 0.55	3.26 ± 0.35
3:00	64	90.6	58	9.59 ± 0.96	29.8 ± 0.90	3.08 ± 0.30
4:00	64	89.0	57	9.92 ± 0.87	27.4 ± 0.78	2.95 ± 0.26
Overall	--	--	--	6.05	36.3	2.29

Data based only on those flowers that produced nectar.

decline in the afternoon from 47.0% to 44.3%. The actual weight of sugar in the nectar generally increased during the day from .42 to 3.63 mg (Table 16).

The flowers had a potential production from 0.0 to 14.88 ul with a mean of 4.01 ul/day. The sugar concentration of the nectar ranged from 27.8% to 60.2% with a mean of 45.3%. The total weight of sugar in the nectar ranged from .09 to 8.36 mg with a mean of 2.23 mg/day (Table 17).

Discussion

Data showed that pistillate and staminate flowers of pickling cucumbers differ in nectar secretion, though their secreting rhythms are similar. Some flowers do not secrete any nectar and the percentage of both staminate and pistillate flowers starting secretion increased until noon. Without bee visitation, the average volume of nectar and total weight of sugar increased until late afternoon for both types of flowers. The average sugar concentration for both staminate and pistillate flowers did not significantly change throughout the day.

The average mean values for the first day of bloom showed that pistillate flowers produced approximately 1.5 times more nectar than staminate flowers (Tables 15 and 16). The maximum values obtained in the two studies showed an even greater difference, 34.15 ul for the pistillate flowers compared to 14.88 ul for the staminate (Table 17). The literature review showed that several other authors found the pistillate cucumber flower to be the predominant producer. Fahn, felt the volume of nectary tissue was the determining factor. Measurements

Table 16. - The percent of the staminate flowers producing nectar throughout the first day of bloom and the average volume of nectar, sugar concentration and total weight of sugar present.

Time (EST)	Sample size	% Producing nectar	Sample size	Avg. vol. (ul)	Avg. sugar conc. (%)	Avg. total wt. of sugar (mg)
7:00 AM	46	0.0	46	---	---	---
8:00	60	16.7	10	0.73 ± 0.22	46.1 ± 3.22	0.42 ± 0.10
9:00	66	47.0	31	2.28 ± 0.30	45.7 ± 0.65	1.35 ± 0.18
10:00	66	69.7	46	2.58 ± 0.22	44.6 ± 0.61	1.42 ± 0.12
11:00	66	83.3	52	3.52 ± 0.29	43.7 ± 0.79	1.90 ± 0.17
Noon	66	98.5	65	3.86 ± 0.27	47.0 ± 0.59	2.27 ± 0.16
1:00 PM	60	95.0	57	5.32 ± 0.37	46.0 ± 0.56	3.03 ± 0.22
2:00	65	98.5	64	4.97 ± 0.34	45.6 ± 0.55	2.76 ± 0.20
3:00	67	98.5	66	6.04 ± 0.30	44.8 ± 0.51	3.31 ± 0.18
4:00	60	98.3	59	6.79 ± 0.45	44.3 ± 0.54	3.63 ± 0.25
Overall	—	—	—	4.01	45.3	2.23

Data based only on those flowers that produce nectar.

Table 17. - The range of values within the cycle of nectar secretion for pistillate and staminate cucumber flowers throughout the first day of bloom.

Time (EST)	Lowest volume (ul)	Highest volume	Lowest % sugar	Highest % sugar	Lowest wt. sugar (mg)	Highest wt. sugar
			Pistillate flowers			
7:00 AM	0.24	4.15	29.9	55.0	0.14	2.23
8:00	0.24	6.10	28.3	47.8	0.14	2.94
9:00	0.24	9.51	34.0	46.5	0.33	5.36
10:00	0.24	12.20	26.4	57.1	0.11	5.19
11:00	0.16	17.32	13.6	49.2	0.07	6.92
Noon	0.94	21.46	28.5	50.5	0.39	7.68
1:00 PM	0.49	31.95	21.9	48.1	0.28	11.93
2:00	0.16	34.15	22.1	43.6	0.06	11.40
3:00	0.31	32.44	20.0	52.5	0.08	12.33
4:00	1.71	28.05	21.3	47.0	0.56	8.03
			Staminate flowers			
7:00	--	--	--	--	--	--
8:00	0.24	2.44	31.3	57.0	0.14	0.87
9:00	0.24	8.54	37.7	50.9	0.43	4.94
10:00	0.24	7.56	31.6	54.2	0.33	4.16
11:00	0.24	12.69	27.8	50.0	0.09	7.29
Noon	0.24	10.24	27.8	60.2	0.19	6.30
1:00 PM	0.73	12.44	30.1	55.9	0.79	8.28
2:00	0.73	13.66	31.0	54.4	0.43	7.97
3:00	1.22	10.98	30.5	54.8	0.50	6.24
4:00	1.22	14.88	33.9	55.2	0.58	8.36

Data based only on those flowers that produce nectar.

reported earlier showed the pistillate flower nectary was 1.6-1.9 times wider and had a secreting surface area approximately twice that of the staminate flower nectary. Therefore one would expect the pistillate flower to be capable of greater production.

Staminate flower nectar had a higher average sugar concentration, 45.3% compared to 36.3%, for pistillate flowers, but in total weight of sugar produced the two types of flowers were similar. The pistillate flower averaged 2.29 mg compared to 2.23 mg for the staminate flower. Beutler (1949) cited by Ribbands (1953) estimated the weight of sugar secreted per flower per day in major nectar plants ranged between 0.02 mg to 7.6 mg. From these values, the cucumber flower would appear to be intermediate in nectar secreting ability. In assessing the significance of the crop as a honey producer, we must consider that there are a small number of flowers per acre relative to some plants.

Since the cucumber requires insect pollination, it is necessary that the pollinator visit both staminate and pistillate flowers. From an ecological consideration, the pistillate flower produces a greater volume of nectar but the staminate flower produces nectar of higher sugar concentration. Heinrich and Raven (1972) found that the specific amounts of nectar per flower, in terms of calories of food energy are related to the characteristic rates of energy expenditure of the pollinator. The honey bee has to visit many more staminate then pistillate flowers to get a load of nectar. But even though there is greater energy expenditure, the honey bee is about equally rewarded by the staminate

flower, because of the higher concentration of sugar. This should help ensure that both pistillate and staminate flowers will be visited.

Connor (1969) found the peak activity of honey bees on cucumber flowers to occur at 11 a.m. and maximum bee flights in the field extended from 9 a.m. to 2 p.m. These data reinforce Connor's findings in that availability of nectar coincides with bee flights. However, bee visits seem to drop off in late afternoon when nectar should be plentiful. It is possible that nectar replacement after visitation may slow up later in the day or the replaced nectar may become less attractive.

Nectar Secretion During the Night

Kaziev and Seidova (1965) stated that nectar secretion, in Cucurbitaceae ceased during the night. Kenoyer (1916) found that sugar excretion was markedly diminished when photosynthesis stopped because of limited food reserves in the plant. Fahn (1949b) while studying 66 species of plants found that nectar secretion peaked for most in the fore or afternoon, but Capparis sicula reached maximum secretion during the night. In some, secretion was low or ceased during the night.

Materials and Methods

The secreting rhythm of cucumber flowers during the night was investigated by the author during the summer of 1970. Caged staminate and pistillate flowers of the cultivar Piccadilly on the day of anthesis were divided into two groups. One half of them were picked and their nectar supply removed at 4:30 p.m. The other half were sampled the next morning at 8 a.m.

Results

Most of the flowers sampled the morning after anthesis were pale yellow and closed. Ninety three per cent of the pistillate flowers and 100 % of the staminate flowers sampled were producing nectar at 4:30 p.m. The following morning showed slight decreases, with 87% of the pistillate and 95% of the staminate producing nectar.

Comparison of the two sampling times showed that during the night the nectar volume remained about the same. The pistillate flowers average volume decreased from 11.44 to 8.29 ul and the staminate flowers increased from 6.83 to 7.06 ul. The sugar content of the nectar on the other hand showed a drastic change. The average sugar concentration of the pistillate flowers changed from 34.8% to 12% and in staminate flowers from 41.2% to 18.9% during the night. Decreases were also found in the actual weight of sugar present, from 4.61 to 1.34 mg in the pistillate flowers and from 3.30 to 1.72 mg in the staminate (Table 18). Pistillate flowers produced approximately 1.68 times more nectar than staminate flowers on the day of anthesis. On the other hand, staminate flowers had a higher sugar concentration, 41.2% compared to 34.8%. In a previous comparison, pistillate and staminate flowers had similar weights of sugar in their nectar supplies. This study showed that the weight of sugar in the nectar of the pistillate flower was approximately 1.4 times greater than in the staminate flower. Previously, the pistillate flower was 1.03 times greater. On the morning after anthesis, the differences were not as great. Apparently the rates of reabsorption are not equal. Pistillate flowers contained 1.17 times more nectar and staminate flowers still had

a higher sugar concentration, 18.9 compared to 12.0%. Once again the total weight of sugar in the nectar was similar for both.

Discussion

The literature shows that other researchers have observed losses of sugar from nectar. Bravois (1842) quoted by Beutler (1953) believed that old flowers reabsorbed sugar secreted in nectar. Bonnier (1878) cited by Pedersen, Le Fevre, and Wiebe (1958) observed the reabsorption of nectar, if it were not removed from the flower before pollination. Pankratova (1950) found that no reabsorption of nectar occurred in clover florets from which insects were excluded, whereas reabsorption appeared to take place in non-protected florets. Boetius (1948) cited by Raw (1953) on the other hand, observed the reabsorption of sugar and suggested that nectar removal might retard the process of reabsorption. Shuel (1964) was able to show with snapdragon that no reabsorption of water from the nectar took place. Now, direct evidence of reabsorption has been shown. Pedersen et al. (1958) by supplying C^{14}- labelled sucrose to pollinated alfalfa florets, Ziegler and Luttge (1959) using C^{14}- labelled glutamic acid on secreting nectaries, Agthe (1951) by using fluorescent dyes was able to show reabsorption only in old glands and suggested it was related to the general metabolic state of the plant, Luttge (1962) using S^{35} and C^{45} as tracers and Shuel (1961) using C^{14}- sucrose was able to show that reabsorption occurred throughout the secretory period.

From the results of this study it appears that the cucumber nectary begins to reabsorb the sugar from its nectar supply and the

Table 18. - The average volume of nectar, sugar concentration and total weight of sugar which remains in staminate and pistillate cucumber flowers during the night.

Time (EST)	Sample size	Avg. vol. (ul)	Avg. sugar conc. (%)	Avg. weight of sugar (mg)
Day of anthesis (4:30 PM)				
Pistillate flowers	67	11.44 ± 0.85	34.8 ± 0.92	4.61 ± 0.34
Staminate flowers	61	6.83 ± 0.48	41.2 ± 0.49	3.30 ± 0.23
Day after anthesis (8:00 AM)				
Pistillate flowers	73	8.29 ± 0.86	12.0 ± 0.78	1.34 ± 0.18
Staminate flowers	66	7.06 ± 0.56	18.9 ± 1.11	1.72 ± 0.20

Data based only on those flowers that produced nectar.

corolla starts closing during the night after anthesis. At night the sugar supply was diminished by 48% - 71% depending on the flowers sex (Table 18). The morning after anthesis, pistillate flowers averaged 1.34 mg sugar with 87% of the flowers having nectar. A previous study (Table 14) showed that by 1 p.m. on the day after anthesis, the average weight of sugar had dropped to 0.92 mg with 30.7% of the flowers containing nectar and at the same time 2 days after anthesis only 0.20 mg of sugar remained in 3.3% of the flowers.

Pedersen et al. (1958) showed that reabsorbed sugar is distributed primarily to growing parts of the plant, such as leaves, flowers and pollen. He showed that sugar was translocated and secreted in flowers that developed later. Ecologically then, even though the cucumber flower has only a one day secreting cycle, the flower's sugar supply is still potentially available to the bee at a later time due to reabsorption and resecretion. Connor and Martin (1970) found that delaying pollination to flowers on the 6th and 7th node resulted in larger pistillate flowers, more ovules per fruit, better shaped fruit and a larger yield. They suggested that stronger root and vine growth were responsible. Since the cucumber flower reabsorbs its uncollected sugar supply, through delayed pollination, the plant would be able to build up larger sugar supplies for nectar production through a longer period of photosynthesis and reabsorption before collection. Also through delayed pollination, larger flowers would provide larger volumes of nectar with more sugar as was pointed out by the positive correlations found in Chapter I.

As previously stated, the maximum nectar production for a staminate flower was 14.88 ul found in the cultivar SMR 58 (Table 17). In this study, staminate flowers of the cultivar Piccadilly produced a maximum of 17.07 ul, indicating that sufficient levels of nectar production were maintained in the development of this cultivar.

Comparison of Nectar Secretion in Different Cucumber Cultivars

Kaziev and Seidova (1965) stated that the range of values for nectar secretion in staminate and pistillate cucumber flowers depended to some extent upon the cultivar and environmental conditions.

Materials and Methods

Two plantings of eight different seed lots including six cultivars were studied during the 1968 summer. Each planting contained 10 plants from each seed lot. Flowers were picked from the first planting at 7:30 a.m. and from the second at 1:30 p.m. As time allowed, nectar was removed and analyzed. The eight seed lots used were:

a. Spartan 27
b. Spartan Dawn - no pollinator
c. Piccadilly - Med 1, no pollinator
d. Piccadilly - Med 11, no pollinator
e. Spartan Progress - (MSU 35G x 381)
f. MSU 35G
g. Piccadilly - Med 11, with pollinator
H. SMR 58.

Results

Comparison of nectar yields of different cultivars was complicated by their different production of staminate and pistillate flowers but the data was used to reinforce the knowledge of these differences. Spartan Progress and MSU 35G rated highest in nectar production while SMR 58 and Spartan 27 rated lowest when samples included nectar from both staminate and pistillate flowers (Table 19). Both Spartan Progress and MSU 35G are gynoecious cultivars, whereas SMR 58 and Spartan 27 are monoecious, producing predominantly staminate flowers. SMR 58 and Spartan 27 averaged from 3-4 ul of nectar per flower compared to 7-9 ul for the top producers. The commercial gynoecious hybrids which produce more pistillate than staminate flowers rated between the above two extremes in nectar production.

The rankings were somewhat reversed for sugar concentration (Table 19) since staminate flowers produced nectar of a higher concentration than pistillate flowers. SMR 58 was highest averaging 40.9% sugar and MSU 35G lowest averaging 34.3%. SMR 58 produced no pistillate flowers and MSU 35G no staminate flowers during the sampling period. Spartan Progress and MSU 35G rated high in total sugar production averaging over 4 mg per flower with SMR 58 and Spartan 27 at the bottom with less than 2 mg per flower.

However, the large differences in nectar production, sugar concentration and total weight of sugar present may not be due to differences between cultivars but rather differences in staminate and pistillate flower production. Earlier in the chapter, I found that the pistillate flowers produced approximately 1.5 - 1.7 times more nectar

Table 19. - The average volume, sugar concentration and total weight of sugar present in nectar from flowers of eight different seed lots of various cultivars (2nd planting).

Seed lot	Sample size	Avg. vol. of nectar (ul)	Avg. % sugar	Rank	Avg. wt. of sugar (mg)
Spartan Progress	30	9.91 ± 1.04	40.1 ± 1.0	2	4.40 ± 0.39
MSU 35G	17	7.65 ± 1.86	34.3 ± 1.3	8	4.17 ± 0.80
Piccadilly Med 11/pollinator	16	6.78 ± 1.49	40.1 ± 1.6	2	2.86 ± 0.51
Spartan Dawn	31	6.59 ± 0.72	36.0 ± 0.9	7	2.61 ± 0.25
Piccadilly Med 11	26	5.89 ± 0.90	37.1 ± 1.2	5	2.53 ± 0.31
Piccadilly Med 1	28	5.41 ± 0.83	37.1 ± 1.2	5	2.32 ± 0.27
SMR 58	25	4.06 ± 0.38	40.9 ± 1.0	1	1.94 ± 0.17
Spartan 27	32	3.09 ± 0.43	39.2 ± 0.8	4	1.38 ± 0.15

than the staminate flower. Therefore, differences in flowering pattern and sex ratio between cultivars could result in erroneous conclusions.

By separating data on the two types of flowers, it was again found that pistillate flowers averaged more nectar per flower than staminate (Table 20). The pistillate flowers of the second planting averaged from 7.31-10.67 ul and the staminate flowers from 2.48-5.02 ul. Overall the pistillate flowers of the second planting averaged 9.02 ul compared to 3.88 ul for the staminate, or the pistillate flowers produced 2.3 times more nectar. The pistillate flowers of the first planting averaged from 1.61-3.39 ul whereas the staminate flowers averaged 1.28-1.66 ul. Overall, for the planting staminate flowers averaged 1.50 ul and pistillate flowers 2.74. From these values, the pistillate flowers produced approximately 1.8 times more nectar.

All previous studies showed that staminate flowers produced nectar of a higher sugar concentration. But in the first planting, staminate flowers overall, averaged 41.9% and the pistillate flowers 43.0% sugar (Table 21). However, the differences were not significant. All staminate flower groups of planting two contained a higher sugar concentration than similar groups of pistillate flowers. In the planting overall, the staminate flowers averaged 40.2% sugar and the pistillate flowers 33.9%.

In both plantings the average total weight of sugars present in the nectar of pistillate flowers was greater than staminate flowers (Table 22). Staminate flowers averaged from 0.66-0.79 mg whereas pistillate flowers contained 0.82-1.72 mg in planting one. Overall the

Table 20. - The average volume of nectar produced by staminate and pistillate flowers from eight different seed lots of various cultivars.

	[1st Planting			]	[2nd Planting			]
Seed lot	Sample size	Staminate flowers (ul)	Sample size	Pistillate flowers (ul)	Sample size	Staminate flowers (ul)	Sample size	Pistillate flowers (ul)
Spartan 27	27	1.28 ± 0.21	21	1.61 ± 0.27	28	2.48 ± 0.22	4	7.31 ± 2.43
Spartan Dawn	11	1.32 ± 0.24	60	3.10 ± 0.31	19	4.02 ± 0.44	12	10.67 ± 0.80
Piccadilly Med I	19	1.66 ± 0.25	52	3.16 ± 0.34	16	3.63 ± 0.52	12	7.78 ± 1.61
Piccadilly Med II	21	1.50 ± 0.21	40	3.39 ± 0.40	21	5.02 ± 0.60	5	9.54 ± 3.86
Spartan Progress	--	No flowers	69	2.76 ± 0.23	--	No flowers	30	9.91 ± 1.04
MSU 35G	--	No flowers	55	2.25 ± 0.18	--	No flowers	17	7.65 ± 1.86
Piccadilly Med II/ pollinator	11	1.62 ± 0.39	42	2.98 ± 0.24	9	4.06 ± 0.55	7	10.29 ± 2.93
SMR 58	27	1.59 ± 0.31	17	2.65 ± 0.53	25	4.06 ± 0.38	--	No flowers

Table 21. - The average sugar concentration of nectar produced by staminate and pistillate flowers from eight different seed lots of various cultivars.

	[1st Planting			]	[2nd Planting			]
Seed lot	Sample size	Staminate flowers (%)	Sample size	Pistillate flowers (%)	Sample size	Staminate flowers (%)	Sample size	Pistillate flowers (%)
Spartan 27	23	39.3 ± 2.22	20	43.3 ± 0.76	28	40.3 ± 0.5	3	29.5 ± 3.2
Spartan Dawn	10	40.8 ± 1.57	58	41.9 ± 0.71	19	39.1 ± 0.6	12	31.2 ± 1.1
Piccadilly Med I	18	42.0 ± 1.49	50	40.1 ± 0.90	14	40.6 ± 0.9	12	33.1 ± 1.9
Piccadilly Med II	21	42.4 ± 1.26	38	42.1 ± 0.75	20	37.7 ± 0.8	5	32.3 ± 3.4
Spartan Progress	---	No flowers	67	45.4 ± 0.49	---	No flowers	30	40.1 ± 1.0
MSU 35G	---	No flowers	55	43.1 ± 0.66	---	No flowers	12	34.3 ± 1.3
Piccadilly Med II/ pollinator	11	42.8 ± 1.73	42	44.8 ± 0.51	9	42.6 ± 1.5	7	36.9 ± 2.7
SMR 58	25	44.2 ± 0.78	16	43.0 ± 0.73	25	40.9 ± 1.0	---	No flowers

Table 22. - The average weight of sugar found in the nectar produced by the staminate and pistillate flowers from eight different seed lots of various cultivars.

Seed lot	[1st Planting			]	[2nd Planting			]
	Sample size	Staminate flowers (mg)	Sample size	Pistillate flowers (mg)	Sample size	Staminate flowers (mg)	Sample size	Pistillate flowers (mg)
Spartan 27	22	0.66 ± 0.11	20	0.82 ± 0.13	28	1.19 ± 0.11	3	3.13 ± 0.27
Spartan Dawn	10	0.66 ± 0.11	58	1.48 ± 0.14	19	1.86 ± 0.20	12	3.80 ± 0.36
Piccadilly Med 1	18	0.79 ± 0.11	50	1.43 ± 0.14	14	1.99 ± 0.23	12	2.71 ± 0.50
Piccadilly Med 11	21	0.69 ± 0.09	38	1.72 ± 0.19	20	2.35 ± 0.25	5	3.23 ± 1.24
Spartan Progress	--	No flowers	67	1.49 ± 0.12	--	No flowers	30	4.40 ± 0.39
MSU 35G	--	No flowers	55	1.13 ± 0.09	--	No flowers	12	4.17 ± 0.80
Piccadilly Med 11/ pollinator	11	0.78 ± 0.20	42	1.57 ± 0.13	9	2.03 ± 0.26	7	3.93 ± 1.02
SMR 58	25	0.74 ± 0.11	16	1.16 ± 0.22	25	1.94 ± 0.17	--	No flowers

staminate flowers averaged 0.72 mg compared to 1.35 for pistillate flowers or 1.9 times more sugar. The nectar of pistillate flowers of planting two contained 1.9 times more sugar than that of staminate flowers. The pistillate flowers averaged 3.62 mg compared to 1.89 for the staminate flowers.

Discussion

There were no significant intervarietal differences in nectar secretion between staminate and pistillate flowers. In selecting cultivars for attractiveness to bees the plant breeder needs to be aware that staminate and pistillate flowers differ in their nectar secreting characteristics. The relative numbers of staminate and pistillate flowers produced by different cultivars may affect their attractiveness to bees due to variations in their available nectar supply. In general there would be concern with keeping staminate and pistillate flowers equally attractive so as to ensure cross pollination. There must of course be a balance between the numbers of pistillate and staminate flowers to ensure enough pollen to do the job without having bees spend excess time on staminate, non-reproductive flowers, Connor and Martin (1971).

Currently, commercial seed companies mix 10% - 15% seed of monoecious lines with gynoecious hybrids to insure a sufficient supply of cucumber pollen. If nectar supplies of the two cultivars being mixed were significantly different in attractiveness, the honey bees might fail to cross over. However, at the present time, no reports have been received or observations made of cultivars that appear to be unattractive to the honey bee. Any significant increases in quantity or

quality of nectar produced, by cucumbers would help to lessen the competition that exists between cucumbers and other nearby nectar sources Collison and Martin (1970).

The Influence of Flower Position on Nectar Secretion

Kaziev and Seidova (1965) found that flowers of all species of Cucurbitaceae located at or near the base of the main stem secreted between 12% - 21% more nectar than flowers located on lateral stems. Veprikov (1936) cited by Beutler (1953) reported that staminate flowers on the main stem of cucumber produced more nectar than those on the lateral stems. The opposite results were found for pistillate flowers.

Materials and Methods

During the summer of 1968 three studies were done involving flower position and nectar secretion.

1968A.--Eight different seed lots were used in the experiment, 10 plants for each. The flowers were picked at 7:30 a.m., nodes recorded and nectar removed. The eight seedlots used were:

a. Spartan 27
b. Spartan Dawn - no pollinator
c. Piccadilly - Med I, no pollinator
d. Piccadilly - Med II, no pollinator
e. Spartan Progress (MSU 35G x 381)
f. MSU 35G
g. Piccadilly - Med II, with pollinator
h. SMR 58.

1968B.--A second planting of the above seed lots was made later in the summer. Five plants from each of the cultivars f, g and h grew upward on cane pole stakes within a cage and the flowers were harvested at 9:30 a.m. The node of the flower was recorded and nectar removed.

1968C.--Using similar plants grown on the ground flowers were picked at 1:30 p.m.; sorted by seed lot, main vine or lateral and nectar removed.

Results

1968A.--Since the flowers were sampled at 7:30 a.m. nectar secretion was just getting under way. Staminate flowers produced 4.2 times more nectar and pistillate flowers 2.1 times more on lateral vines than on main vines (Table 23).

Sugar concentration of the nectar of pistillate flowers was not significantly different between the main and lateral vines. Staminate flowers on lateral vines showed a higher concentration than those on the main vines, 45.0% compared to 41.4%. These differences are reflected in the total weight of sugar present since both volume of nectar and sugar concentration are involved. Both staminate and pistillate flowers on the main vine contained more sugar than those on lateral vines; the staminate 1.8 times more and pistillate 1.6 times more.

To look for further trends, the data were sorted by sex and node position. Tables 24 and 25 show that there is a tendency towards slight increases in flower size, nectary size and volume of nectar further down the vine from the base of the plant. Differences in sugar concentration

and total weight of sugar present were not significant. Staminate flower averages ranged from 37.9 to 43.9 mm wide, averaging overall 40.6 mm compared to a range of 42.9 to 51.0 mm and a mean of 47.9 for pistillate flowers. In both cases node one had the smallest flowers and node two the second smallest. Differences in nectary size were not as large. The staminate flower nectaries averaged from 2.4 to 2.9 mm with an overall mean of 2.6 mm. On the other hand, the nectaries of pistillate flowers averaged from 4.1-4.6 mm with an overall mean of 4.4 mm.

Nectar production of staminate flowers averaged from 1.47-2.18 ul and 3.01-5.27 for pistillate flowers. Overall mean for staminate flowers was 1.8 ul and 3.9 for pistillate ones. The average sugar concentration for staminate flowers ranged from 37.3% to 41.8% and pistillate flowers fluctuated from 37.8% to 44.4%. Likewise the total weight of sugar fluctuated from 0.68-0.90 mg for staminate flowers and 1.44-2.27 mg for pistillate flowers.

Within this study, overall the pistillate flower was larger, the nectary was 1.7 times wider, produced 2.2 times more nectar of a higher sugar concentration and it contained 2.2 times more sugar than the staminate flower.

1968B.--The three cultivars used had completely different flowering patterns. MSU 35G produced only 49 pistillate flowers. Piccadilly 158 staminate, 17 pistillate, and SMR 58, 265 staminate and 11 pistillate. Besides genetic differences in the staminate-pistillate flower ratio, basically only one pistillate flower was produced at each node, whereas several staminate flowers were produced at each node. Since the

Table 23. - A comparison of the average volume of nectar, sugar concentration and total weight of sugar produced by staminate and pistillate cucumber flowers located on main and lateral vines (1968A).

Flower position	Sample size	Avg. vol. (ul)	Sample size	Avg. sugar conc. (%)	Avg. weight of sugar (mg)
Staminate flowers					
Main vine	95	0.18 ± 0.09	90	41.4 ± 0.77	0.74 ± 0.53
Lateral vines	20	0.76 ± 0.12	17	45.0 ± 0.85	0.42 ± 0.08
Pistillate flowers					
Main vine	226	0.90 ± 0.11	223	42.8 ± 0.34	1.58 ± 0.06
Lateral vines	98	1.92 ± 0.18	91	43.6 ± 0.52	1.00 ± 0.09

staminate-pistillate flower ratio varied greatly between the cultivars, the data were sorted by flower sex. Due to the small number of pistillate flowers produced, the data for nodes 1-4, 5-8 etc., were combined (Table 25).

Even the lumping of data for the pistillate flowers shows no significant trends (Table 25). Likewise no significant trends were found for staminate flowers (Table 24), though at times it appeared that petal size, nectary size, volume of nectar and total weight of sugar gradually increased further from the plant base.

The overall means (Tables 24 & 25) show that pistillate flowers were larger, contained a wider nectary that produced a larger quantity of nectar which contained more sugar than staminate flowers. The only difference from the 1968A study was that staminate flowers contained a higher sugar concentration, 45.6% compared to 42.0%. This is in agreement with earlier resuls in Chapter II where staminate and pistillate flowers were compared.

1968C.--After sorting the data of the eight seed lots that produced flowers on both main and lateral vines, analysis showed that all seven had a larger volume of nectar in flowers on the lateral vines than on the main vines (Table 26). Flowers on lateral vines of cultivars Spartan Progress and MSU 35G produced significantly more nectar than other seed lots tested. Spartan Progress averaged 16.42 ul and MSU 35G, 15.74 compared to 9.64 ul or less for the rest. Six of the seven seed lots had a lower per cent sugar in the lateral flowers but a larger amount of sugar. These can only be used as trends since the flowers

Table 24. - Effect of node position on flower size, nectary size and nectar secretion of staminate cucumber flowers.

Node	N	Avg. flower size (mm)	N	Avg. nectary size (mm)	N	Avg. vol. (ul)	Avg. % sugar	Avg. wt.of sugar (mg)
1968 A								
1	8	37.9 ± 1.62	8	2.4 ± 0.18	5	1.47 ± 0.34	37.3 ± 0.85	0.74 ± 0.14
2	35	39.8 ± 0.75	35	2.4 ± 0.11	27	2.00 ± 0.16	38.5 ± 0.82	0.90 ± 0.08
3	24	43.9 ± 0.73	24	2.6 ± 0.12	18	2.18 ± 0.41	40.5 ± 1.00	0.85 ± 0.11
4	13	41.0 ± 1.60	13	2.9 ± 0.27	6	1.51 ± 0.57	41.8 ± 1.72	0.68 ± 0.25
1968 B								
1	1	34.0 ± --	1	2.0 ± --	0	---	---	---
2	16	39.6 ± 1.58	15	2.1 ± 0.07	10	2.05 ± 0.23	45.0 ± 0.59	1.09 ± 0.08
3	27	42.1 ± 1.19	32	2.2 ± 0.08	17	2.08 ± 0.21	45.6 ± 0.65	1.25 ± 0.12
4	27	40.6 ± 1.25	31	2.3 ± 0.09	18	1.86 ± 0.23	44.1 ± 0.99	1.04 ± 0.14
5	40	38.5 ± 0.89	41	2.3 ± 0.07	25	2.00 ± 0.21	44.4 ± 0.50	1.16 ± 0.12
6	34	40.2 ± 0.92	38	2.4 ± 0.09	19	2.27 ± 0.22	44.7 ± 0.66	1.30 ± 0.16
7	26	39.6 ± 0.93	37	2.4 ± 0.10	22	2.55 ± 0.29	44.9 ± 0.65	1.48 ± 0.17
8	27	40.9 ± 0.92	28	2.4 ± 0.11	17	2.54 ± 0.27	45.6 ± 0.60	1.50 ± 0.15
9	20	37.7 ± 1.31	26	2.4 ± 0.11	14	3.08 ± 0.28	44.7 ± 0.69	1.62 ± 0.21
10	15	41.7 ± 1.17	26	2.4 ± 0.16	10	3.29 ± 0.31	45.2 ± 0.77	1.76 ± 0.22
11	18	42.7 ± 1.49	25	2.6 ± 0.10	9	2.95 ± 0.18	45.8 ± 0.58	2.07 ± 0.17
12	14	42.0 ± 1.66	20	2.4 ± 0.11	9	3.06 ± 0.21	46.0 ± 0.82	1.16 ± 0.15
13	13	39.5 ± 1.93	19	2.2 ± 0.10	8	3.14 ± 0.42	44.3 ± 1.23	1.59 ± 0.26
14	7	42.3 ± 3.18	10	2.1 ± 0.10	3	3.74 ± 0.08	46.9 ± 0.85	2.13 ± 0.09
15	12	40.7 ± 1.59	13	2.3 ± 0.13	7	3.59 ± 0.41	47.1 ± 0.56	2.16 ± 0.35
16	3	42.3 ± 4.91	4	2.3 ± 0.25	1	2.93 ± --	45.6 ± 0.05	1.61 ± --
17	4	41.5 ± 3.78	11	2.4 ± 0.15	2	4.39 ± 0.24	48.9 ± 1.40	2.58 ± --
18	3	41.0 ± 4.00	5	2.0 ± 0.00	2	3.54 ± 0.36	46.4 ± 0.95	2.14 ± --
19	2	34.0 ± 3.00	3	2.3 ± 0.33	--	---	---	---
20	1	40.0 ± --	2	2.5 ± 0.50	--	---	---	---
Overall mean		40.0 ± 0.55		2.3 ± 0.04		2.89 ± 0.17	45.6 ± 0.30	1.65 ± 0.11

Table 25. - Effect of node position on flower size and nectar secretion of pistillate cucumber flowers.

Node	N	Avg. flower size (mm)	N	Avg. nectary size (mm)	N	Avg. vol. (ul)	Avg. % sugar	Avg. wt. of sugar (mg)
1968 A								
1	7	42.9 ± 1.26	7	4.3 ± 0.18	2	3.91 ± 2.03	44.3 ± 1.40	2.11 ± 1.16
2	77	44.7 ± 0.67	64	4.1 ± 0.05	32	3.01 ± 0.36	42.8 ± 1.11	1.44 ± 0.15
3	99	48.9 ± 0.58	83	4.3 ± 0.07	34	3.77 ± 0.28	44.3 ± 0.65	1.97 ± 0.14
4	76	49.7 ± 0.62	70	4.3 ± 0.06	32	3.69 ± 0.30	44.4 ± 0.86	1.91 ± 0.14
5	58	48.8 ± 0.65	58	4.4 ± 0.07	30	4.17 ± 0.40	42.5 ± 0.79	2.06 ± 0.19
6	34	47.5 ± 0.91	34	4.4 ± 0.11	25	4.24 ± 0.53	40.7 ± 0.11	1.92 ± 0.21
7	26	47.8 ± 1.39	26	4.5 ± 0.11	14	3.65 ± 0.48	41.5 ± 0.12	1.74 ± 0.20
8	16	46.2 ± 2.04	16	4.6 ± 0.12	4	5.27 ± 1.59	37.8 ± 3.46	1.46 ± 0.57
21	5	51.0 ± 2.61	5	4.6 ± 0.25	3	3.91 ± 0.83	44.4 ± 1.30	2.07 ± 0.41
22	9	48.9 ± 1.86	9	4.4 ± 0.17	5	4.87 ± 1.29	41.5 ± 1.72	2.27 ± 0.54
31	7	50.3 ± 1.51	7	4.1 ± 0.26	6	3.36 ± 0.61	40.9 ± 2.25	1.66 ± 0.38
32	10	48.1 ± 2.39	10	4.6 ± 0.22	7	3.36 ± 0.50	43.2 ± 0.82	1.68 ± 0.23
1968 B								
1-4	3	47.3 ± 0.88	3	4.0 ± 0.00	2	3.18 ± 0.98	42.0 ± --	2.07 ± --
5-8	14	42.7 ± 1.67	14	3.9 ± 0.07	7	2.23 ± 0.68	38.6 ± 3.95	1.01 ± 0.16
9-11	25	43.6 ± 1.40	27	4.1 ± 0.09	18	2.91 ± 0.43	41.5 ± 1.31	1.48 ± 0.18
13-16	17	46.7 ± 1.24	21	4.3 ± 0.10	13	4.39 ± 0.50	46.0 ± 0.62	2.43 ± 0.28
17-20	3	34.3 ± 0.67	7	4.1 ± 0.26	--	---	---	---
Overall means		42.9 ± 2.33		4.1 ± 0.07		3.18 ± 0.45	42.0 ± 1.52	1.75 ± 0.31

Table 26. - Comparison of main and lateral vine flower position on nectar secretion of eight different seed lots (1968 C).

Seed lot	Main or lateral vine	N	Avg. nectar vol. (ul)	Avg. % sugar	Avg. total wt. sugar (mg)
Spartan 27	M	24	2.28 ± 0.17	40.4 ± 0.54	1.10 ± 0.09
	L	8	5.52 ± 1.40	35.2 ± 2.43	2.35 ± 0.40
Spartan Dawn	M	22	6.46 ± 0.88	37.5 ± 0.93	2.70 ± 0.32
	L	9	6.91 ± 1.28	32.7 ± 1.75	2.39 ± 0.38
Piccadilly Med I	M	23	4.94 ± 0.92	37.4 ± 1.47	2.16 ± 0.30
	L	5	7.56 ± 1.82	36.1 ± 1.94	3.01 ± 0.52
Piccadilly Med II	M	22	5.21 ± 0.91	37.7 ± 1.05	2.32 ± 0.33
	L	4	9.64 ± 2.70	34.1 ± 3.03	3.60 ± 0.83
Spartan Progress	M	24	8.28 ± 0.97	41.2 ± 1.10	3.84 ± 0.38
	L	6	16.42 ± 1.83	35.5 ± 1.46	6.63 ± 0.68
MSU 35G	M	15	6.57 ± 1.92	33.3 ± 1.39	3.55 ± 0.78
	L	2	15.74 ± 3.54	39.2 ± 0.80	7.28 ± 1.80
Piccadilly/pollinator	M	15	6.10 ± 1.42	40.6 ± 1.61	2.61 ± 0.48
	L	1	---	---	---
SMR 58	M	23	3.92 ± 0.38	41.0 ± 1.03	1.87 ± 0.16
	L	2	5.61 ± 1.95	39.7 ± 1.90	2.67 ± 1.06

Table 27. - Comparison of staminate and pistillate cucumber flowers located on the main and lateral vines of eight different seed lots (1968 C).

Seed lot	Position	Sex	Sample size	Avg. vol.	Avg. % sugar	Avg. total wt. sugar (mg)
Spartan 27	M	S	24	2.28 ± 0.17	40.4 ± 0.54	1.10 ± 0.09
	M	P	0	---	---	---
	L	S	4	3.72 ± 1.03	39.4 ± 1.30	1.76 ± 0.51
	L	P	4	7.32 ± 2.43	29.5 ± 3.15	3.13 ± 0.27
Spartan Dawn	M	S	15	4.19 ± 0.48	39.5 ± 0.65	1.97 ± 0.22
	M	P	7	11.32 ± 1.27	32.4 ± 1.54	4.27 ± 0.54
	L	S	4	3.36 ± 1.16	37.8 ± 1.24	1.44 ± 0.46
	L	P	5	9.76 ± 0.73	28.7 ± 1.00	3.15 ± 0.26
Piccadilly Med I	M	S	15	3.53 ± 0.54	40.5 ± 0.93	1.95 ± 0.24
	M	P	8	7.59 ± 2.24	32.2 ± 2.78	2.49 ± 0.70
	L	S	1	---	---	---
	L	P	4	8.17 ± 2.22	34.8 ± 1.75	3.13 ± 0.65
Piccadilly Med II	M	S	19	4.89 ± 0.65	38.3 ± 1.29	2.30 ± 0.28
	M	P	3	7.24 ± 0.03	34.2 ± 5.75	2.46 ± 1.86
	L	S	2	6.22 ± 0.12	38.8 ± 3.05	2.82 ± 0.20
	L	P	2	13.05 ± 4.51	29.4 ± 1.25	4.38 ± 1.70
Spartan Progress	M	S	0	---	---	---
	M	P	24	8.28 ± 0.97	41.2 ± 1.10	3.84 ± 0.38
	L	S	0	---	---	---
	L	P	6	16.42 ± 1.83	35.5 ± 1.46	6.63 ± 0.68
MSU 35G	M	S	0	---	---	---
	M	P	15	6.57 ± 1.92	33.3 ± 1.39	3.55 ± 0.78
	L	S	0	---	---	---
	L	P	2	15.74 ± 3.54	39.2 ± 0.80	7.28 ± 1.80
Piccadilly Med II/ pollinator	M	S	9	4.06 ± 0.55	42.6 ± 1.45	2.03 ± 0.26
	M	P	6	9.15 ± 3.19	37.4 ± 3.14	3.48 ± 1.09
	L	S	0	---	---	---
	L	P	1	---	---	---
SMR 58	M	S	23	3.92 ± 0.38	41.0 ± 1.03	1.87 ± 0.16
	M	P	0	---	---	---
	L	S	2	5.61 ± 1.95	39.7 ± 1.90	2.67 ± 1.06
	L	P	0	---	---	---

were not sorted by sex and the sample sizes of the lateral flowers were rather small.

Comparison of cultivars that produced staminate and pistillate flowers on both lateral and main vines showed that staminate flowers on lateral vines produced more nectar than those on main vines 4 out of 5 times. Similar findings for pistillate flowers were found 5 out of 6 times (Table 27). The concentration of sugar from the nectar of staminate flowers on the main stem was greater than that on lateral stems 3 out of 4 times. Pistillate flowers on the main stem had a higher concentration 3 out of 5 times. As a result, the total weight of sugar in the nectar of staminate flowers on lateral vines was greater 3 out of 4 times and for pistillate flowers it was greater 5 out of 6 times.

Pistillate flowers produced a larger quantity of nectar than staminate flowers on both the lateral and main vines. Likewise, in both positions staminate flowers contained a higher concentration of sugar than pistillate. The nectar of pistillate flowers contained a higher weight of sugar than staminate flowers in similar locations.

Discussion

Studying the association of nectar secretion with position of the flower on the stem proved to be difficult because the various cultivars differ greatly in the number and sequence of staminate and pistillate flowers produced. Some of the new hybrids produced only pistillate flowers. Basically only one pistillate flower is produced at each node, whereas several staminate flowers are produced at each node on the same day or more often on different days. Therefore, sampling data were

affected by unavoidable differences due to weather, carbohydrate supply, vine age, etc. With the flowering pattern peculiar to staminate flowers you might have an older vine with staminate flowers on nodes 3,8,12,18 and 21 all on one day, whereas pistillate flower production would be on node 24 only.

Flowers on lateral vines tended to produce a larger quantity of nectar containing a higher weight of sugar than those on the main vine. This may be explained by the relative length of vascular tissue leading to the flowers sampled.

Connor (1969) found that fruits from a higher node position, and thus older plants contained more seeds and were longer than fruits from lower nodes (i.e., younger plants). He also found the effect of node position was most noticeable in highly gynoecious varieties. His results indicated that pistillate flowers found on the early nodes were smaller, had smaller ovaries with less ovules and developed into shorter fruits, often misshapen. As a result, Connor and Martin (1970) proposed delayed pollination. Their studies have shown that a delay up to 11 days after the first appearance of pistillate flowers resulted in higher yields of cucumbers with a greater dollar value. My studies, (Tables 24 & 25) show that there tends to be slight increases in flower size, nectary size and volume of nectar as you move down the vine away from the base. With the positive correlations found in Chapter I relating to: (1) nectary size and volume of nectar, (2) nectary size and actual weight of sugar in the nectar, (3) nectary size and ovary length and (4) nectary size and petal size, by delaying pollination the

bees should be visiting larger flowers, which in turn offer larger quantities of nectar with more sugar. This makes the flowers more attractive to the bees and through pollination, the grower should have a higher yield with a greater dollar value. Not only will the flowers' nectar supply be more attractive, but there will be a larger number of flowers per acre which is advantageous to the bees. Also, as was suggested earlier in the chapter, nectar not collected during the waiting period before bees become active, may be reabsorbed and resecreted at a later time. This may allow the plant to increase its stored carbohydrate supply and favorably affect nectar secretion.

CHAPTER III

THE NECTAR SECRETION CYCLE AND HOW IT IS AFFECTED BY HONEY BEE VISITS AND THE PROCESS OF FERTILIZATION

Honey bee pollination has been recognized as necessary for normal cucumber production by several authors. The flower's nectar supply appears to be the primary attractant since very few honey bees have been observed packing pollen pellets in the corbiculae; those observed being small in size compared to the pellets from major pollen sources. Bohn and Mann (1960) found that a nectarless strain of muskmelon was not visited by bees; therefore, nectar may be the primary attractant in Cucumis melo.

A honey bee seldom returns to a flower that it recently visited. When this does occur, the bee leaves immediately for another flower, apparently sensing a prior visit. In following bees, I have noticed that the honey bee tends to work a group of flowers in a small area. Then it starts moving around a great deal, just visiting a flower now and then. It would appear that the honey bee has nearly a full load of nectar and visits a few flowers at random before returning to the hive.

The honey bee in removing nectar from a pistillate flower generally inserts and withdraws her proboscis 2-3 times. She inserts her proboscis at the periphery of the stigma, between the lobes, to reach the cup-shaped nectary below (Fig. 20). The cup generally holds the

entire nectar supply since secretion only takes place on the inner surface (Chapter I). Occasionally, through lack of visitation, the cup becomes full, spills over the sides and nectar collects between the corolla wall and the nectary. In moving around the stigma and inserting her proboscis, the bee keeps her hind legs on the corolla. As she moves, the hind legs step from petal to petal (Fig. 20).

In order to reach the nectar of a staminate flower, the bee inserts her proboscis between the central mass of five anther lobes and the wall of the corolla. The anthers are attached to the wall of the corolla, providing an obstacle to a bee trying to get nectar from the flower. In addition the nectar encircles the nectary at its base and is found between the nectary and the corolla wall, thus forcing the bee to move around the anthers several times, inserting and withdrawing her proboscis. Occasionally, in attempting to visit a flower, the bee is confronted with competition, such as another bee, a cucumber beetle or syrphid fly. When confronted with a beetle or fly, the honey bee moves away to another flower. If a honey bee lands on a flower being worked by another honey bee, the working bee is generally chased away.

Nectar Removal by the Honey Bee

Meyerhoff (1958) in studying bee visitation to inner and outer nectaries of rape, concluded that bees are unable to distinguish empty nectaries from full ones. Park (1954) came to a similar conclusion. He suggested that the bee can only tell by inserting her proboscis and when nectar is found, she remains to suck until all nectar within reach of her proboscis has been taken up.

Materials and Methods

Bagged pistillate flowers of the cultivar MSU 35G were sampled in the afternoon on the day of anthesis during the summer of 1969. Some of the flowers were unbagged and one honey bee was allowed to visit each flower. Immediately after the visit, the flower was picked and the nectar that remained was removed. The remaining unvisited flowers served as controls. They were picked and the nectar collected to determine approximately how much nectar the honey bee removed.

Results

In the 25 recorded visits, honey bees removed all the nectar present with one visit (Table 28). The small number of controls substantiated that the flowers contained nectar prior to visitation. Honey bees averaged 60.1 seconds in their initial visit and removed a mean of 9.64 ul of nectar.

Discussion

Connor (1969) found that honey bees averaged 36.2 seconds on their first visit to cucumber flowers. He also noted that the duration of a first visit to a flower varied with the time of day of the visit. For 12-1 p.m. first visits lasted 39.9 - 43.1 seconds, 1-2 p.m. 37.3 - 37.1 seconds and from 2-3 p.m. 37.9 - 38.3 seconds. These values are lower than reported here, since his values included both staminate and pistillate flowers.

Honey bees constantly revisit cucumber flowers throughout the day; therefore, the cucumber flower must resecrete nectar fairly rapidly after each visit. If it were not for this replacement of nectar, the

Table 28. - The amount of nectar removed from a pistillate flower in one visit.

Date	Time spent in one visit	Measurable amount remaining	Controls - vol. of nectar (ul)
8/20/69	55	0.00	
(3:30 - 4:30)	67	0.00	
	50	0.00	No Controls
	59	0.00	Measured
	66	0.00	
8/28/69	110	0.00	14.40
(3:00 - 4:00)	110	0.00	8.54
	40	0.00	12.20
	35	0.00	6.83
	40	0.00	19.52
	65	0.00	13.91
	75	0.00	13.91
	55	0.00	--
9/4/69	45	0.00	6.34
	40	0.00	5.85
(2:00)	50	0.00	4.15
	32	0.00	--
	34	0.00	--
9/5/69	105	0.00	6.83
	95	0.00	3.17
(3:00)	85	0.00	--
	75	0.00	--
	50	0.00	--
	25	0.00	--
Overall mean	60.1 ± 5.0		9.64 ± 1.45

flowers would become unattractive to bees soon after anthesis, since the nectar supply is the primary attractant.

The Rate of Nectar Replacement after Removal

That removal of nectar by bees and other nectar gathering insects may increase nectar secretion was suggested by Free (1970), Koreshkov (1967), and Wykes (1950). Melnichenko (1963) found that multiple bee visits normally increased nectar productivity of flowers by 50% - 75%. Bogoyavlenskii and Kovarskaya (1956) cited by Free (1970) and Maksymiuk (1958), reported that flowers from which nectar was removed three times per day produced more sugar than those from which it was removed once a day. Raw (1953) found that artificial removal of nectar increased the amounts of nectar and sugar secreted, but the average sugar concentration of the nectar was markedly lowered. He suggested this might be due to differences in the osmotic relations of the nectary tissues and secreted nectar. Wykes (1915a) had similar findings.

The sugar concentration of nectar in flowers visited by bees was lower than in those protected from bees according to Pedersen and Todd (1949) in alfalfa. Pedersen (1953b) showed that the use of heavy concentrations of bees had a tendency to reduce the sugar concentration. Meyerhoff (1958) cited by Free (1970) observed that after bee visits, the inner nectaries of rape were empty. Five minutes later the nectaries had secreted a small amount of nectar and 30 minutes later they were full again.

Materials and Methods I

Nectar replacement in pistillate cucumber flowers with removal at hourly intervals.--Caged pistillate flowers of the cultivar MSU 35G

were sampled from July 29 through August 29, 1969. Each morning at 9:30 four pistillate flowers were marked and the nectar removed carefully so not to injure the nectary tissue. At hourly intervals from 9:30 a.m. to 2:30 p.m., nectar was removed from the same four flowers. Each hour, starting at 10:30 a.m. and ending at 2:30 p.m. two different flowers were picked as controls and their nectar removed.

Results

When nectar was removed from pistillate flowers at hourly intervals over a six hour period, the flowers replaced approximately the same volume of nectar that was removed the hour before (Table 29). Nectar replacement was slightly higher in the morning than in the afternoon. The overall mean value for the morning was 1.34 ul and 1.10 ul for the afternoon. The volume of nectar of the controls on the other hand increased throughout the day going from an average of 1.40 ul at 9:30 a.m. to a high of 10.38 ul at 1:30 p.m. Table 15 dealing with the secretion cycle of the pistillate flower shows similar results. The sum of the average values for the experimental group over the six hour period of removal was 7.33 microliters. This is less than three of the hourly average values for the control group. Therefore, it would appear that multiple visitation in the cucumber does not stimulate nectar secretion. To look at this in a different way, the production of nectar for each flower, being sampled six times, was totalled. The total production for each flower over the six hour sampling period was from 0.49 to 21.71 ul with a mean of $7.18 \pm .55$ ul/flower. Once again this value is less than three hourly average production values for the control group.

Therefore, nectar removal did not stimulate nectar production in pistillate cucumber flowers.

Even though the flower was able to almost replace the volume of nectar that was removed the hour before, the sugar concentration and actual weight of sugar in the nectar decreased sharply over the six hour removal period. The sugar concentration of the experimental group dropped from 42.3% at 9:30 a.m. to 13.8% by 2:30 p.m. (Table 30). The hourly sugar concentrations of the control group did not change significantly, falling within a range of 39.3% - 42.8% sugar. The significant decrease in sugar concentration following nectar removal is substantiated by the literature review.

The weight of sugar in the nectar decreased from .76 mg of sugar at 9:30 a.m. to .15 mg at 2:30 p.m. for the experimental group (Table 31). While the flowers that had hourly nectar removal showed a steady decrease in sugar weight, the controls had an increase, going from .76 mg at 9:30 to a high of 4.98 mg at 1:30. The sum of the average values over the six hour period during removal, showed the mean weight of sugar being replaced hourly was 2.36 mg, which is less than four average values for the control group (Table 31). Thirty eight of the flowers having nectar removed hourly had sugar production values for all six of the sampling times and produced from .21 to 5.03 mg of sugar with a mean of 2.19 mg. This value is less than five of the average readings for the control group. Therefore, it would again appear that nectar removal does not stimulate sugar production in cucumber nectar.

The reason that there are only 38 flowers with six sugar production values, is that a sample of .49 ul of nectar, seldom makes a large enough drop on the prism of the refractometer to be read.

Table 29. - The average volume of nectar replaced in pistillate cucumber flowers after removal at hourly intervals.

Time	Removal Sample size	Avg. vol. nectar (ul)	% of flowers producing nectar	Control Sample size	Avg. vol. nectar (ul)
9:30	89	1.40 ± 0.11	83%	89	1.40 ± 0.11
10:30	88	1.21 ± 0.08	89%	24	4.42 ± 0.48
11:30	88	1.41 ± 0.12	93%	24	5.75 ± 0.76
12:30	78	1.12 ± 0.10	82%	22	9.22 ± 0.96
1:30	69	1.14 ± 0.15	77%	20	10.38 ± 1.20
2:30	65	1.05 ± 0.22	51%	20	9.58 ± 0.85

Table 30. - The average sugar concentration of nectar replaced in pistillate cucumber flowers after removal at hourly intervals.

Time	Removal Sample size	Avg. % sugar	Control Sample size	Avg. % sugar
9:30	67	42.3 ± 0.53	67	42.3 ± 0.53
10:30	73	34.3 ± 0.81	21	42.8 ± 1.20
11:30	74	26.4 ± 0.82	24	42.2 ± 1.15
12:30	58	21.9 ± 0.87	20	41.4 ± 1.68
1:30	43	17.8 ± 0.79	20	39.3 ± 1.80
2:30	28	13.8 ± 0.76	20	42.4 ± 2.48
Overall		26.1 ± 4.35		41.7 ± .52

Discussion

Possibly the pistillate cucumber flower does not respond to multiple visits by secreting more nectar and sugar since it has basically only a one day secretion cycle. Most of the plants used by other researchers in this area had secreting cycles of more than one day. Since recent work suggests that nectar secretion results from metabolic activity of the nectary, we might anticipate that nectar removal may set up a physiological response that would affect the metabolic rate of secretion for flowers secreting for more than one day. If a bee visit results in pollination, then an opposing response may be stimulated. Shuel (1961) found that the stigmatic surfaces of flowers Streptosolen jamesonii from which multiple collections of nectar had been made, remained comparatively dry. A later study showed that periodic removal of nectar caused a 50% reduction in the yield of stigmatic exudate. Therefore, he suggested that under normal circumstances part of the stigmatic exudate is derived from nectar which has been reabsorbed into the flower. Pollination may have a drying effect on the stigma, which might decrease the need for nectar and sugar production by the nectary tissue for this reabsorbing process.

Materials and Methods II

Nectar replacement every fifteen minutes.--Since the previous study showed that a flower could replace approximately the same volume of nectar that was removed one hour before, a small pilot study was set up to determine how rapidly nectar replacement takes place after removal. On August 21, 1969, four pistillate flowers of the cultivar MSU 35G were

selected within the cage used in the previous study. Instead of removing the nectar once every hour, it was removed every 15 minutes.

Results

Twenty six per cent of the original volume of nectar was replaced in the first 15 minutes, 15% was returned during the second 15 minutes and 13% during the third 15 minutes. As in the previous study, the sugar concentration and total weight of sugar present decreased with removal (Table 32).

Materials and Methods III

Nectar replacement every 5 minutes.--Starting on September 1, 1969, caged pistillate flowers of the cultivar MSU 35G were sampled in the afternoon for five days. The nectar was removed from each flower every five minutes.

Results

Nectar replacement in a cucumber flower is a rapid event. Forty per cent of the original volume of nectar was replaced in the first five minutes after removal (Table 33). Thirty two per cent was replaced in the second five minutes and 29% after the third removal. Since the study only covered 20 minutes, decreases in sugar concentration and total weight of sugar were not as large as with removal every hour.

Discussion

Even though nectar secretion appears to be related to metabolism in the nectary tissue, there may also be an osmotic relationship between

Table 31. - The average weight of sugar in nectar replaced by pistillate cucumber flowers after removal at hourly intervals.

Time	Removal Sample size	Avg. wt. sugar (mg)	Control	Avg. wt. sugar (mg)
9:30	80	0.76 ± 0.06	80	0.76 ± 0.06
10:30	82	0.51 ± 0.04	21	2.20 ± 0.21
11:30	80	0.45 ± 0.05	24	2.76 ± 0.30
12:30	72	0.27 ± 0.02	20	4.62 ± 0.36
1:30	59	0.22 ± 0.03	20	4.98 ± 0.61
2:30	59	0.15 ± 0.03	20	4.80 ± 0.56

Table 32. - The average volume of nectar, sugar concentration, and total weight of sugar in the nectar replaced after removal at 15 minute intervals.

Time	N	Avg. vol. (ul)	N	Avg. sugar concentration (%)	N	Avg. weight of sugar (mg)
2:45	4	2.81 ± 1.28	4	30.3 ± 1.98	4	0.95 ± 0.40
3:00	4	0.73 ± 0.28	2	27.2 ± 2.80	2	0.37 ± 0.04
3:15	4	0.43 ± 0.21	2	23.8 ± 0.05	2	0.19 ± 0.06
3:30	4	0.36 ± 0.21	1	18.5 ±	1	0.19 ±

N = Sample size

Table 33. - The average volume of nectar, sugar concentration, and total weight of sugar in the nectar replaced after removal at 5 minute intervals.

Visit number	N	Avg. vol. (ul)	N	Avg. sugar concentration (%)	N	Avg. weight of sugar (mg)
1	54	3.04 ± 0.24	53	35.9 ± 0.86	46	1.21 ± 0.08
2	54	1.23 ± 0.12	43	33.4 ± 0.87	37	0.48 ± 0.04
3	54	0.98 ± 0.11	36	31.7 ± 1.44	33	0.33 ± 0.03
4	36	0.87 ± 0.11	28	32.0 ± 1.23	23	0.33 ± 0.04

the secreted nectar and nectary tissue as was suggested by Raw (1953). Without rapid replacement of nectar, cucumber flowers would become unattractive to bees and since there are few flowers per acre bees would soon leave cucumbers for other, more attractive sources. Rapid replacement of nectar allows bees to revisit the same flowers thus keeping cucumber flowers competitive in attracting pollinating bees.

The Concentration of Cucumber Nectar at the Time of Collection by the Bee Throughout the Day

Kauffeld and Williams (1972) found the honey stomach contents of bees working cucumber ranged from 36% - 41% sugar, depending on weather conditions. Wilson, Moffett and Harrington (1958) in analyzing the honey stomach contents of 18 bees, found that cucumber nectar averaged 42.2% sugar with a minimum of 37.8% and maximum of 49.2% in Colorado. Pedersen (1953b) found that when bees were caged with plants, the sugar concentration of the nectar appeared to be lower than under natural conditions.

The method of removing and analyzing honey stomach contents has been questioned and studied by several researchers. The method was used by Nye and Pedersen (1962), Pedersen (1953b), Scullen (1940,1942) and Butler (1945). Shaw, Farr and Goldstein (1953) tested the method and found that after killing the bees with cyanide, there was no significant difference in the sugar concentration of the nectar within 15 minutes after the bee had died. They did, however, find that a reduction in sugar concentration occurred if the nectar was analyzed 30 minutes after the bee was dead. Montgomery (1958) on the other hand reported that no change occurred in the sugar concentration of the nectar up to 42 hours.

Park (1932) is generally given credit for disproving the theory that honey bees extract and get rid of water from the nectar while carrying it back to the hive. He found that the concentration was altered only very slightly, in the form of a decrease of about one per cent. This decrease appeared to be greater for nectar of high concentration than low. Simpson (1964) and Free & Durrant (1966) found that the dilution was due to the bees mixing saliva with it from the labial glands. The dilution was greater for the more concentrated nectar. Bailey, Fieger and Oertel (1954) stated that the honey stomach contents were a mixture of honey and nectar and that rapid hydrolysis of sucrose took place in the honey stomach of the bee which could account for a slight reduction in water content.

Vansell (1934,1942) found that the average concentration of nectar in the honey stomachs of collecting bees corresponded closely to the concentration in the flowers. Woodrow (1968) recorded ranges as great as 25% in the sugar concentration of nectar in individual bees foraging on a single natural source. Bees having small amounts of nectar in their nectar sacs were discarded by Shaw, Farr and Goldstein (1953) and Wilson, Moffett and Harrington (1958), since data from such samples were found to vary and usually indicated extremely low sugar concentrations. Oertel (1946) on the other hand combined 2 or more bee samples when one sample was too small.

Materials and Methods

Honey bees were collected from cucumber flowers during the first two weeks of August, 1970. When a bee was observed working a

cucumber flower, it was caught and killed in a cyanide killing jar. Within five minutes after collection, the head of the bee was removed and honey stomach contents squeezed onto the prism of the refractometer for analysis. A total of 495 bees were collected and the data sorted by the hour to see how the sugar concentration varied throughout the day.

Results

The sugar concentration of the honey stomach contents did not vary a great deal during the day. The average values ranged from 17.1% to 28.3% sugar (Table 34). Overall the average was 24.5%. The morning values were highest averaging 26.0% and the afternoons 23.0%. Values peaked at 9-10 a.m. and 12-1 p.m. with a decrease throughout the rest of the afternoon. The lowest averages were at 8-9 a.m. and 3-4 p.m. which would generally be expected. The range of values shows that the lowest concentration carried by a bee was 2.6% and the highest 46.5%.

Discussion

Tables 15 and 16 show that nectar taken directly from pistillate flowers averaged 36.3% and from staminate flowers 45.3% sugar during the day, when bees were excluded from the blossoms. The overall mean of the two values is 40.8% while the overall average sugar concentration of nectar from bee's honey stomachs was 24.5%, a 40% decline (Table 34). In an earlier study on the concentration of nectar removed from flowers at hourly intervals (Table 30), the sugar concentration dropped from 42.3% to 13.8% with a mean of 26.1%. Since the average concentration of the contents of the bee's honey stomachs was so close to the mean

value obtained from the nectar replacement study, it can be assumed that if bees are properly chosen, honey stomach content of bees working cucumber provides a legitimate and simple means of obtaining nectar for analysis. The method might well be suitable for monitoring nectar secretion in a plant breeding program. These studies have brought out the important point that nectar replaced after removal is of lower sugar concentration than nectar which has not been removed from the nectary. Errors in interpreting nectar analysis could result from ignoring this phenomenon.

Cucumber flowers would typically be visited several times an hour by honey bees. Each bee load is an accumulation of small quantities of nectar from many individual flowers and the range of values shown in Table 34 would lead one to suspect a wide variation in sugar concentration is acceptable to foragers repeatedly visiting the same field. Woodrow (1968) made similar observations.

Connor (1969) found maximum bee flights in the field to extend from 9 a.m. to 2 p.m. During this period, the sugar concentration values averaged 26.6% compared to 21.0% for early morning and late afternoon. This study indicates a correlation between nectar concentration and the presence of bees on the crop. Brett and Sullivan (1972) said that the most attractive flowers have sugar concentrations above 20% and the sugar concentrations of nectars have been found to range between 5% - 74% Percival (1965). On this basis, cucumber nectar would be rated moderately attractive to honey bees. Collison and Martin (1970) noted that bees located near cucumber fields visited many other plants in the area for nectar.

Since some authors discarded small samples with low sugar concentrations, the data used in Table 34 was reanalyzed, excluding any values less than 10% (Table 35). No new trends were found.

The Effect of Pollination on Nectar Secretion

Davidson (1922) claimed that osmotic pressure within the plant forces open the flowers, keeps them open and supplied with nectar until pollination takes place. Pollination results in reducing the pressure, the nectar flow ceases, the floral parts fade and wither or fall off. Swanson and Shuel (1950), Oertel (1956), Melnichenko (1963) and Barbier (1962) all reported that secretion by floral nectaries decreased soon after pollination and ceased with fertilization. Veprikov (1936) quoting Gorski as cited by Beutler (1953) found that nectar secretion in cucumbers ceased after pollination, and the corolla fell at the same time. Kaziev and Seidova (1965) found that pistillate flowers of Cucurbitaceae secrete nectar intensely before pollination and after this process nectar secretion ceased. If pistillate flowers of cucumbers, melons and watermelons were isolated from pollination, they could secrete nectar continuously for 2-3 days.

Materials and Methods

Three studies, with different approaches, were run to find the effects of pollination on nectar secretion.

1968A.--Pistillate flowers of the cultivar Piccadilly Med. II were used in the greenhouse during this study. Each day at 7 a.m. the plants were checked for newly opened flowers on vines where no fruit

Table 34. - Concentration of cucumber nectar in the honey stomachs of honey bees throughout the day.

Time	Sample size	Avg. sugar concentration	Range of values
8:00 - 9:00	58	22.7 ± 1.43	6.3 - 38.6
9:00 -10:00	94	28.3 ± 0.98	6.9 - 46.5
10:00 -11:00	70	27.0 ± 1.19	6.5 - 38.7
11:00 -12:00	76	26.2 ± 1.30	6.8 - 40.0
12:00 - 1:00	97	27.5 ± 0.97	7.7 - 39.9
1:00 - 2:00	41	23.9 ± 1.77	7.1 - 38.3
2:00 - 3:00	27	23.3 ± 1.41	10.0 - 32.0
3:00 - 4:00	32	17.1 ± 1.55	2.6 - 33.7
Overall		24.5 ± 1.28	

Table 35. - Concentration of cucumber nectar in the honey stomachs of honey bees after removal of low values.

Time	Sample size	Avg. sugar conc.
8:00 - 9:00	45	26.9 ± 1.28
9:00 -10:00	84	30.7 ± 0.74
10:00 -11:00	64	28.8 ± 1.06
11:00 -12:00	66	28.8 ± 1.18
12:00 - 1:00	88	29.4 ± 0.83
1:00 - 2:00	34	27.0 ± 1.67
2:00 - 3:00	27	23.3 ± 1.41
3:00 - 4:00	22	21.2 ± 1.60

had been previously set or growing. Due to lack of plants without fruit, an equal number of flowers to serve as controls were used on vines where only one fruit was developing. At 7:30 a.m. the nectar was removed from the flowers. Following the removal of nectar, the first group of pistillate flowers were hand pollinated with a camel hair brush. The controls were not pollinated after nectar removal. The nectar of all flowers was again removed at 11:30 a.m. and at 3:30 p.m. from both groups. The flowers were tagged and clipped shut after the last nectar removal to see if fruit developed.

1968B.--Field studies commenced on August 14 and ended on September 10. Groups of four pistillate flowers of the cultivars Piccadilly and MSU 35G were bagged the evening before anthesis. Each morning at 8:30 two of four flowers in a group were hand pollinated with a camel hair brush and re-covered with cloth bags. At 2:30 one of the pollinated flowers and one of the controls were picked by removing the flowers at the perianth with attached style and stigma. The nectar was removed, volume determined and refractometer readings taken. The other pollinated flower and control were picked at 8:30 a.m. the next day and the nectar removed. After the flowers were removed at the perianth, the remaining ovary was left on the vine to check for fruit development.

1969.--This field study used pistillate flowers of the cultivar MSU 35G. Bagged flowers were pollinated on the day of anthesis at 4:30 p.m. with staminate flowers from the cultivar SMR 58. The flowers were picked the following morning at 8:30 a.m. by removing them at the perianth. The nectar was removed, measured and refractometer readings

taken. Seed counts were taken on the fruit that developed from the ovaries that were left on the vine.

Results

1968A.--Since the first nectar was removed at 7:30 a.m. not all of the flowers had started to secrete (Table 36). When the nectar was removed from the same flowers at 11:30 a.m., 5% fewer of the pollinated group and 3% more of the control group contained nectar. Therefore, it would appear that pollination had affected nectar replacement. Going back to the data on the study dealing with nectar removal once every hour; at 9:30, (time of first removal), 83% of the flowers were producing nectar, at 10:30 (second removal), 89% and at 11:30 (third removal), 93% were producing nectar (Table 29). Since the percentage of flowers producing nectar increased even though the nectar was being removed hourly and now with removal and pollination, the per cent decreased, it would appear that the observed decrease was not due to nectar replacement but rather to pollination. By 3:30 p.m. both the pollinated and control groups were similar again in the percentage of flowers producing nectar. This was probably due to the previous removals and natural decrease in secretion rate in late afternoon (Table 34). Possibly the pollinated group reached a secretion decline earlier in the day. To know for sure, the sampling times would have to be changed. The average volume of nectar secreted at 11:30 by the two groups partially supports the hypothesis of earlier secretion decline due to pollination (Table 37). The pollinated group secreted 4.88 ul compared to 5.16 ul for the controls. But at 7:30 a.m. the controls had secreted less than the

pollinated group. Looking at the differences of the two periods for each group shows that controls produced 3.50 ul for the four hour period compared to 2.40 for those pollinated. These values further support the proposed hypothesis. Also, when you look at the production of nectar at 3:30 the pollinated group again has less, 0.32 ul compared to 0.66 for the controls.

When looking at the total secretion pattern for the day, the differences no longer show up, (Table 37). The pollinated group produced 7.68 ul for the day and controls 7.48. A possible explanation for this, is that the control flowers came from vines where a fruit was developing. Therefore, large amounts of the plants carbohydrate supply was being used for fruit and seed development. This suggests a need for further research dealing with the effects of fruit development on nectar secretion. The total weight of sugar produced by the two groups was in agreement. The controls produced 3.13 mg and the pollinated group 3.80 mg. When the zero values were averaged in (Table 38), the pollinated group produced 2.94 mg and the controls 2.61 mg.

Both groups showed similar decreases in sugar concentration as the nectar was removed throughout the day. The pollinated group decreased from 41.9% - 19.3% and control group from 45.3% - 18.1%. A similar decline was shown in Table 30 where the nectar was removed at hourly intervals. A significant difference was observed in the total weight of sugar that was produced at 11:30 a.m. The pollinated group produced 1.5 times more sugar than the control group. Once again this may be attributed to the presence of fruit on the control vines.

The study shows that nectar replacement will continue even though the flower has been pollinated. The average volume of nectar produced by the pollinated group at 11:30 was almost twice the volume produced at 7:30. The average sugar weights reported in Table 37 are based only on those flowers that were producing enough nectar to measure on the refractometer. Including the unmeasurable samples in the analysis as having 0.00 mg of sugar did not significantly change the results (Table 38). Both the average values and the differences between them were smaller.

In Chapter II some work dealing with the flower's position on the vine was reported. The positions on the vine of the hand pollinated flowers in this study were recorded and the results are shown in Table 39. As was found in previous studies, flowers found on lateral vines tended to produce a larger quantity of nectar, containing a higher weight of sugar than those on the main vine. But with nectar removal and pollination the flowers on the lateral vines were more definitely affected than those on the main vines. From 7:30-11:30 the main vine flowers increased their nectar production 2.98 times compared to 1.02 times for lateral vines. Similar results are seen in total weight of sugar present. Total production over the entire day showed the main vine flowers to be slightly more productive in volume and sugar weight than lateral ones. For each time period, the sugar concentrations between the two positions were not significantly different.

In the above study all hand pollinated flowers developed fruit except two.

1968B.--Even though every mean value for nectar secretion was lower in the hand pollinated group than the equivalent one in the control group, the t-test shows that all but two of the comparisons were not significantly different (Table 40). The lack of significant differences may be due to the fact, that in this study, only pollination is involved, not nectar removal too. Nectar was removed only once, at 6 or 24 hour intervals after pollination and the 0.00 values for the total amount of sugar as well as volume were included in the data analysis.

Nectar volume values for both the pollinated group and the controls were significantly lower for the 24 hour sampling than the 6 hour. This would be expected since there was an overnight involved to complete the 24 hour period after pollination. Sugar concentration and total weight of sugar was drastically reduced for both groups also. This was probably due to the reabsorption of sugar during the night.

In this study after 24 hours the pollinated group had significantly less nectar and sugar than the unpollinated controls. Therefore, it would appear that nectar secretion was affected sometime between 6 and 24 hours after pollination. None of the flowers that were removed at the perianth at the end of 6 hours after being pollinated developed fruit, whereas 40% of those removed after 24 hours developed normal fruit.

There was a large difference in the two cultivars used in the experiment, only this time it was not due to the sex of the flower and the cultivars flowering pattern, since only pistillate flowers were sampled. Within the six hour period after pollination, MSU 35G produced 1.67 times more nectar and in the 24 hour period 2.13 times more than

Table 36. - The percentage of the flowers producing nectar throughout the day after the nectar is removed and the flower pollinated (1968 A).

Time	Pollinated group	Control group
7:30	85%	92%
11:30	80%	97%
3:30	32%	30%

Sample sizes for both groups was 40.

Table 37. - The volume of nectar, sugar concentration and total weight of sugar produced after the nectar was removed and flowers pollinated in the greenhouse.

Time	N	Avg. vol. (ul)	N	Avg. sugar conc. (%)	N	Avg. wt. of sugar (mg)
Pollinated group						
7:30	40	2.48 ± 0.52	33	41.9 ± 1.38	33	1.25 ± 0.17
11:30	40	4.88 ± 0.72	28	28.5 ± 1.26	28	2.33 ± 0.29
3:30	40	0.32 ± 0.11	10	19.3 ± 1.60	10	0.22 ± 0.05
Total	40	7.68				3.80
Control group						
7:30	40	1.66 ± 0.26	28	45.3 ± 1.16	28	1.12 ± 0.15
11:30	40	5.16 ± 0.62	38	25.5 ± 0.97	38	1.53 ± 0.19
3:30	40	0.66 ± 0.26	8	18.1 ± 2.31	8	0.48 ± 0.12
Total	40	7.48				3.13

N = Sample size.

Table 38. - The average weight of sugar produced after the nectar was removed and flowers pollinated with zero values included.

Time	Sample size	Pollinated Avg. wt. sugar	Sample size	Control Avg. wt. sugar
7:30	39	1.06 ± 0.16	31	1.01 ± 0.15
11:30	36	1.82 ± 0.28	39	1.49 ± 0.19
3:30	37	0.06 ± 0.02	36	0.11 ± 0.04
Total		2.94		2.61

Piccadilly (Table 41). The controls likewise showed MSU 35G producing 1.94 times more nectar at 6 hours and 1.33 times more after 24 hours. In three out of four comparisons Piccadilly had a slightly higher sugar concentration. In total, MSU 35G produced more sugar three of the four times. At six hours it contained 1.60 times more sugar when pollinated and 1.43 times more when not pollinated. After 24 hours it contained 2.12 times more sugar when pollinated.

Every mean value for the pollinated group was lower than the equivalent for the controls, except one (Table 41). The Student's t test, however, showed only one comparison to be significant at the .05 probability level. The cultivar Piccadilly, 24 hours after pollination contained significantly less nectar than the controls. The cultivar MSU 35G was found to contain significantly less nectar and weight of sugar than the controls at the .10 probability level. Table 40 shows that there were significant differences in both volume of nectar and total weight of sugar present after 24 hours when the data of both cultivars was combined. Separation by cultivars, made the sample sizes too small for differences to be detectable.

From the group of flowers that were pollinated and flowers removed 24 hours later, comparisons were made between those that developed fruit and those that did not, to see if there was a difference in nectar secretion (Table 42). Even though the values in the group that developed fruit were lower than the group that did not, the t test showed that they were not significantly different at the .05 probability level.

The percentage of flowers containing nectar at the time of sampling, would tend to indicate that sometime between 6 and 24 hours

Table 39. - The influence of flower position on nectar secretion in flowers where the nectar supply is removed and the flower pollinated.

Time	N	Avg. vol. (ul)	N	Avg. sugar concentration	N	Avg. wt. of sugar (mg)
Main vine						
7:30	26	1.84 ± 0.30	23	43.3 ± 1.24	25	0.94 ± 0.14
11:30	26	5.48 ± 0.91	19	28.5 ± 1.73	23	2.10 ± 0.36
3:30	26	0.41 ± 0.15	8	19.7 ± 1.65	23	0.08 ± 0.03
Total		7.73				3.12
Lateral vine						
7:30	14	3.68 ± 1.36	10	38.8 ± 3.51	14	1.26 ± 0.38
11:30	14	3.76 ± 1.15	9	28.6 ± 1.57	13	1.31 ± 0.40
3:30	14	0.14 ± 0.11	2	17.5 ± 5.90	14	0.02 ± 0.02
Total		7.58				2.59

N = Sample size

Table 40. - The effect of pollination on nectar secretion (1968 B).

	N	Pollinated - 6 hours	N	Control - 6 hours
Avg. volume	25	9.73 ± 1.39 ul	25	11.68 ± 1.60 ul
Avg. sugar concentration	25	30.4 ± 1.30 %	24	30.8 ± 1.55 %
Avg. amt. of sugar	25	3.14 ± 0.42 mg	25	3.79 ± 0.50 mg
	N	Pollinated - 24 hours	N	Control - 24 hours
Avg. volume	25	2.30 ± 0.77 ul*	25	6.58 ± 1.50 ul*
Avg. sugar concentration	10	12.2 ± 1.12 %	18	15.1 ± 2.31 %
Avg. amt. of sugar	23	0.31 ± 0.11 mg*	24	0.91 ± 0.21 mg*

N = Sample size

* = Comparisons significantly different at the 0.05 probability level. (Students t test)

Table 41. - The effect of pollination on nectar secretion for the cultivars MSU 35G and Piccadilly.

	N	Pollinated 6 hrs.	N	Control 6 hrs.
Piccadilly (Avg. vol.)	7	6.55 ± 1.24 ul	7	6.97 ± 2.80 ul
MSU 35G (Avg. vol.)	18	10.96 ± 1.80 ul	18	13.51 ± 1.79 ul
Piccadilly (Sugar conc.	7	32.2 ± 3.11 %	6	35.4 ± 2.39 %
MSU 35G (Sugar conc.)	18	29.3 ± 1.80 %	18	29.3 ± 1.80 %
Piccadilly (Sugar wt.)	7	2.19 ± 0.40 mg	7	2.89 ± 1.18 mg
MSU 35G (Sugar wt.)	18	3.51 ± 0.54 mg	18	4.14 ± 0.53 mg
	N	Pollinated 24 hrs.	N	Control 24 hrs.
Piccadilly (Avg. vol.)	7	1.27* ± 0.57 ul	7	5.30* ± 1.70 ul
MSU 35G (Avg. vol.)	18	2.70 ± 1.04 ul	18	7.07 ± 1.99 ul
Piccadilly (Sugar conc.)	4	11.6 ± 2.34 %	5	19.7 ± 6.77 %
MSU 35G (Sugar conc.)	6	12.5 ± 1.23 %	13	13.4 ± 1.92 %
Piccadilly (Sugar wt.)	6	0.17 ± 0.09 mg	6	1.02 ± 0.46 mg
MSU 35G (Sugar wt.)	17	0.36 ± 0.14 mg	18	0.87 ± 0.25 mg

N = Sample size
* = Comparisons significantly different at the 0.05 probability level. (Students t test)

Table 42. - Nectar secretion in cucumber flowers 24 hours after pollination comparing successful pollination (fruit formed) with unsuccessful pollination (no fruit formed).

	N	Developed fruit	N	No fruit development
Avg. volume	10	1.62 ± 0.94 ul	15	2.75 ± 1.13 ul
Avg. sugar conc.	4	11.8 ± 1.45 %	6	12.4 ± 1.71 %
Avg. sugar weight	9	0.23 ± 0.13 mg	14	0.37 ± 0.16 mg

No statistical differences at 0.05 probability level. (Students t test).

after pollination nectar secretion was affected by pollination (Table 43). Twenty four hours after pollination, only 48% of the pollinated flowers contained nectar compared to 76% for the controls.

1969.--Since it seemed that the effects of pollination showed up some time between 6 and 24 hours after pollination, this study sampled the flowers 16 hours after pollination. With this timing it was impossible to avoid an overnight, therefore, the reabsorption of sugar is incorporated into the data for both groups.

Because the cucumber flower has basically a one day secretion cycle, pollination at 4:30 in the afternoon may be too late to detect any effects due to pollination (Table 44). No significant differences were found in nectar volume, sugar concentration, or amount of sugar between the pollinated and control groups.

Of the 99 flowers that were pollinated, 29 developed fruit. They contained 10-461 seeds and averaged 188 seeds per fruit. Since only 29% of the pollinated flowers that were removed at the perianth developed into fruit, the pollinated group was sorted on the basis of fruit development (Table 45). The Student's t test shows that only the comparison of sugar concentration between the two groups was significant at the .05 probability level. Differences in volume of nectar and total weight of sugar were not significant. Sixty four per cent of the pollinated flowers contained nectar and 67% of the controls which shows no significant difference.

Table 43. - The effect of pollination on the percentage of flowers producing nectar.

Group	Sample size	% Producing nectar
Pollinated - 6 hours	25	100%
Control - 6 hours	25	96%
Pollinated -24 hours	25	48%
Control -24 hours	25	76%

Table 44. - The effect of pollination on nectar secretion 16 hours later (1969).

	N	Pollinated	N	Control
Avg. volume	99	2.74 ± 0.44 ul	81	2.44 ± 0.36 ul
Avg. sugar conc.	50	17.8 ± 0.80 %	47	17.8 ± 0.83 %
Avg. wt. of sugar	86	0.63 ± 0.11 mg	74	0.51 ± 0.09 mg

N = Sample size
No statistical differences at 0.05 probability level. (Student t test)

Table 45. - Comparison of the pollinated flowers with regard to fruit development when the flower was removed and nectar sampled 16 hours after pollination.

	N	Developed fruit	N	No fruit development
Avg. volume	28	1.98 ± 0.59 ul	71	3.04 ± 0.56 ul
Avg. sugar conc.	15	14.3 ± 0.92 %*	35	19.4 ± 0.97 %*
Avg. sugar weight	25	0.34 ± 0.11 mg	61	0.75 ± 0.14 mg

N = Sample size
* Comparisons significantly different at the 0.05 probability level. (Student t test)

Discussion

The results of the three studies indicated that only morning pollination affected nectar secretion. Pollinations late in the afternoon failed to affect nectar secretion. The 1968B study indicated that possibly no new nectar was produced after fertilization. These studies also showed, using stigma and style removal at the perianth as an indicator that some fertilization takes place between 6 and 16 hours after pollination. Connor (1969) found with a similar procedure that no fruit developed three hours after pollination but 2 of 5 fruit developed 12 hours after pollination, averaging 64 seeds per fruit. In another study which will not be reported at this time, a minimum of 7 1/2 hours was needed before any fruit developed that contained seeds. The literature search and these studies suggest that nectar secretion ceases after fertilization, which requires at least 7 1/2 hrs. after pollination. From the time of bee pollination to fertilization, the cucumber flower continues to secrete nectar and replenish its supply after each visit. Any nectar remaining at the time of fertilization may change in sugar concentration due to changes in the relative humidity and may be partially reabsorbed during the night. Another study in which pollinations were done in the early morning and nectar samples taken at night would be desirable to verify this hypothesis.

It is advantageous for the crop not to cease nectar secretion at the time of pollination. Otherwise, the crop would be unattractive to bees in the afternoon. Instead of bee activity peaking at 11 a.m., it would be on a rapid decline. If nectar secretion were to cease with

the first visit resulting in pollination, chances are the level of pollination needed in the field would not be accomplished and fruit set would decrease.

Comparison of the Attractiveness of Staminate and Pistillate Cucumber Flowers to the Honey Bee

Sanduleac (1959) found that staminate flowers were visited more frequently than pistillate, indicating that many bees were collecting pollen in cultivars of Cucurbita maxima, C. pepo and C. moschata. Mann (1953) found that bees collecting nectar from flowers of Cucumis melo spend about 8-9 sec/flower/visit. Staminate flowers have shorter corolla tubes and honey bees can more easily reach the nectaries. Hermaphroditic flowers have deeper corolla tubes and the entrances are more constricted, so that honey bees have to squeeze between the anthers and stigmas to reach the nectary and in so doing transfer pollen to the stigmas. Although bees passed readily from one type of flower to the other, there was a slight preference for hermaphroditic flowers when equal numbers of each were present. Such a preference probably also existed in the field after mid-day as pollen collection was found to reach a peak at about 11 a.m. and then rapidly diminish, whereas nectar collection declined much less abruptly. Bees remained at perfect flowers longer than at staminate ones. The average time spent on perfect flowers (1 visit per bee) was 8.54 sec. and on staminate flowers (2 visits per bee) was 5.66 sec. Bees spent about one and one-half times as long visiting perfect flowers as they did staminate flowers.

Materials and Methods

Relative attractiveness of staminate and pistillate flowers is partly indicated by the average time spent on each type of flower. To obtain data on this in 1968 honey bees working the cultivar Piccadilly were followed and timed with a stopwatch. Since this cultivar produced more staminate than pistillate flowers each day, more data was taken from staminate than pistillate flowers. The honey bees were timed at different periods during the day from July 22 to August 23, 1968. The time started when they began working the center of the flower for nectar and ended when they finished removing nectar from the flower. Often a honey bee will stop and groom itself after removing nectar from a flower before moving on to the next one. The time spent in grooming was not included in our timings.

Results

Throughout the entire day honey bees spent more time per visit on pistillate flowers than on staminate flowers (Table 46). Honey bees averaged from 7.8 - 16.0 sec. on pistillate flowers with an overall mean of 12.6 sec. compared to a range of 5.0 - 7.3 sec. and a mean of 6.3 for staminate flowers. For the entire day honey bees spent twice as long on pistillate as on staminate flowers. The average maximum time spent on pistillate flowers was between 7-8 a.m. and on staminate flowers from 8-9 a.m. Comparison of the morning and afternoon values shows that honey bees spent 1.86-2.25 times longer on pistillate than on staminate flowers in the morning compared to 1.42-2.73 times longer in the afternoon.

Discussion

In Chapter I it was found that the nectaries of pistillate flowers were 1.6-1.9 times wider and had secreting surfaces approximately twice as large as nectaries of staminate flowers. Also in Chapter II it was found that pistillate flowers produced from 1.5-2.3 times more nectar than staminate flowers. These values help to explain why the honey bee spent twice as long on pistillate as on staminate flowers. This study indicates that the length of the visit is dependent on the amount of nectar present. As was shown earlier, honey bees if not disturbed, will remove all of the nectar present in one visit. Pedersen (1953b) showed that honey bee visitation was correlated with the amount of nectar available per plant.

Connor (1969) found the activity of honey bees on cucumber flowers peaked at 11 a.m. and maximum bee flights in the field extended from 9 a.m. to 2 p.m. In this study, prior to 9 a.m. the average time spent on each flower was greater than values for the rest of the day (Table 46). Until 9 a.m. fewer bees were observed in the field working the flowers. Due to the lower level of competition for flowers and the fact that flowers were being visited for the first time, the flowers contained a larger supply of nectar which required a longer time for removal.

As bee density increased after 9 a.m., the average time per visit began to decrease because flowers being visited had only partially replenished their nectar supply following removal by earlier bee visits. Connor (1969) found that the length of a bee visit to a pistillate flower

decreased as the number of the visits increased. The first visits to a cucumber flower lasted an average of 36.2 sec., while the average length of subsequent visits dropped sharply. Also, as shown earlier, successive removal and replacement of nectar reduces sugar concentration and actual weight of sugar which should make the flower less attractive to the bee. Even though this should not affect the speed of nectar removal, it may affect the bee's behavior, so that it is not as efficient in getting all of the nectar present.

Data from 2-4 p.m. for staminate flowers and 1-4 p.m. for pistillate flowers showed late day increases in time spent on the flowers (Table 46). Since sample sizes were small, additional data was taken in 1969 to check on the results (Table 46). Once again there was an increase in values. A possible explanation is that flight activity decreases after 2 p.m. thus providing more time between bee visits and a resultant increase in nectar replacement and the length of bee visits.

Table 46. - Comparison of the time spent on pistillate and staminate cucumber flowers by honey bees.

Time (EST)	Sample size	Avg. time/ pistillate flower	Sample size	Avg. time/ staminate flower
7 - 8 AM	32	16.0 ± 2.3 sec	111	7.1 ± 0.7 sec
8 - 9 AM	41	14.7 ± 2.3 "	144	7.3 ± 0.5 "
9 -10 AM	47	15.4 ± 1.6 "	171	7.0 ± 0.3 "
10 -11 AM	90	12.3 ± 1.0 "	347	6.6 ± 0.2 "
12 - 1 PM	43	9.6 ± 0.8 "	164	6.7 ± 0.3 "
1 - 2 PM	46	7.8 ± 0.8 "	176	5.5 ± 0.2 "
2 - 3 PM	11	9.7 ± 1.9 "	65	5.0 ± 0.4 "
3 - 4 PM	8	15.0 ± 3.9 "	56	5.5 ± 0.4 "
Overall mean		12.6		6.3
1969 values				
2 - 3 PM	98	8.2 ± 0.6 "	135	5.1 ± 0.3 "
3 - 4 PM	42	9.6 ± 2.3 "	65	6.0 ± 0.4 "

CHAPTER IV

THE CHEMICAL COMPOSITION OF CUCUMBER NECTAR

Many researchers have found that nectar is primarily a solution of sugars in varying proportions. The predominant sugars are sucrose and its breakdown products, glucose and fructose. They have been found in most samples of nectar analyzed to date, Wykes (1951b), Caillas (1926), Shuel (1952), Vansell (1929,1944a,1944b,1952) Maurizio (1954,1961), Luttge (1961) and Cotti (1962).

Percival (1961), while analyzing the nectar from 889 plant species in 101 families, found ten common types of nectar. She classified these into three broad groups: (1) nectars with dominant sucrose, (2) balanced nectars with about equal amounts of sucrose, fructose and glucose, and (3) nectars with dominant fructose plus glucose.

Six sugars, other than the three dominant ones, have been isolated in some nectars. These include: (1) xylose, Ifteni (1967), (2) melezitose, Beutler (1953), and Percival (1965), (3) trehalose, in sedges only, Beutler (1953) and Percival (1965), (4) melibiose, (5) raffinose, Wykes (1951a,1952b), Beutler (1953), Percival (1961, 1965), and Feltner and Sackett (1964), (6) maltose, Wykes (1951a, 1952b), Bailey, Fieger and Oertel (1954), Beutler (1953), Ifteni (1967), Furgala, Gochnauer and Holdaway (1958) and Percival (1961,1965).

Percival (1961,1965) found that the sex of the flower in some species of willows affects the nectar composition. The male catkins have a sucrose-dominated nectar, while the female catkins have fructose and glucose predominating. Generally, the age of the flower does not affect nectar composition. Kartashova and Novikova (1964) found a change in nectar composition with age of the flower in only one species out of twelve. Percival (1961,1965) found a change in the nectar of Hibiscus syriaca.

Percival (1961) examined the nectar of two species from the family Cucurbitaceae. These were the staminate and pistillate flowers of Luffa cylindrica (Dish-rag or Loofah Gourd) and staminate flowers of Momordica balsamina. All samples had sucrose dominant nectar with fructose and glucose present. Nectar from Luffa cylindrica contained one unknown. Browne (1908) in analyzing honey from flowers of Cucurbitaceae found that it contained 19.23% water, 72.05% glucose and fructose, 1.89% sucrose, 0.24% ash, 2.55% dextrin and 4.04% of undetermined materials. White et al. (1962) found cantaloupe honey to contain 15.4% water, 37% fructose, 34.51% glucose, 2.89% sucrose, 5.41% maltose and 1.10% higher sugars. Cucumber honey contained 18.7% water, 38.2% fructose, 32.59% glucose, 1.45% sucrose, 5.66% maltose and 0.96% higher sugars. He referred to all reducing disaccharides present as maltose.

Test of Gas Liquid Chromatography for Nectar Analysis

Many researchers have used variations of paper chromatography for qualitative and quantitative analysis of nectar; however, this

method is time consuming. To expedite this phase of research, gas liquid chromatography was used for qualitative and quantitative nectar analysis. Kleinschmidt, Dobrenz, and McMahon (1968), Butler et al. (1972) and Pauratallier (1968) have successfully used gas liquid chromatography in separating sugars that are found in nectar and honey.

Materials and Methods

Nectar was removed from cucumber flowers and placed in one dram glass screw top vials. The vial covers were lined with aluminum foil since the silylating reagent reacted with the inner covering.

Three methods were used to transport the nectar to the laboratory (1) nectar removed, placed in the vial and frozen immediately in dry ice, (2) flowers picked, placed in a wide mouth thermos bottle with nectar removal taking place upon arrival to the laboratory, Shuel (1968) and (3) bringing the vial with the nectar in it to the laboratory (Table 47).

In 1971 all 19 vials of nectar were placed in a freezer until the nectar was frozen. The vials were then placed in a lyophilizer until all visible liquid had evaporated. Next, the samples were placed in the freezer until they were to be analyzed. During September, 1972, an additional 25 samples of nectar were collected and frozen. On August 3, 1973, the vials were removed from the freezer and lyophilized. After 4 hrs. they were removed and refrozen until analysis. When the vials were removed from the freezer, 1 ml of Tri-Sil Z was added. Tri-Sil Z is a commercial silylation reagent produced by the Pierce Chemical Company, Rockford, Illinois. In their "Handbook of Silylation" they reported that Tri-Sil Z is a mixture of N-tri-methylsilylimidazole in

dry pyridine (1.5 meq/m) and is used for derivatizing hydroxy and polyhydroxy compounds in either dry or aqueous solutions. It forms volatile and thermally stable trimethylsilyl derivatives of sugars and related substances, Sweeley et al. (1963). Most silylation procedures have been performed under anhydrous conditions and since nectar is an aqueous solution, Tri-Sil Z was chosen as the reagent. It was also reported that sugars are usually completely silylated when dissolved. It was found that sucrose, fructose and glucose dissolved rapidly and an hour appeared to be sufficient time for the silyation reaction to be completed and stability reached.

Standards used for comparison were made from: (1) d(+) Sucrose, Nutritional Biochemicals Corporation, Cleveland, Ohio, (2) Beta-D-Fructose NRC (levulose)-General Biochemicals, Chagrin Falls, Ohio, and (3) dextrose (anhydrous d-Glucose)-Fisher Scientific Co., Fair Lawn, N. J. Ten milligrams of the sugar plus one milliliter of Tri-Sil Z were used for each standard. The samples were stored in a refrigerator.

Sugar derivatives were separated by using two different glass columns in 1971. Sucrose was separated using a six foot x 1/8 inch glass column of 5% QF-1 on 100/120 mesh Gas Chrom Q at 180^{o} C, N_2 carrier at 120 ml/min and a sensitivity of $1x10^{-9}$ amps full scale. Glucose and fructose were separated by using a six foot x 1/4 inch glass column of 10% D.C. 200 on 60/80 mesh G.C.Z. at 180^{0} C, N_2 carrier at 100 ml/min and a sensitivity of $1x10^{-9}$ amps full scale. Likewise in 1973 two different glass columns were used to separate the sugar derivatives. Sucrose was separated using a six foot x 1/8 inch glass column

Table 47. - Cucumber nectar samples analyzed by gas liquid chromatography.

Vial no.	Date	Time	Cultivar	Sex	Nectar vol. (ul)	% Sugar	Total amt. of sugar (mg)	Mg sugar/ ul	Transportation
7	8/19/71	1:35	9805	F	89.06	51.7	57.16	0.64	Dry ice
8	8/19/71	2:15	9805	F	64.17	39.1	29.46	0.45	Vial
9	8/19/71	2:30	9805	F	110.78	34.6	44.17	0.39	Thermos
11	8/31/71	2:45	35G x 381G	F	30.74	36.6	13.07	0.42	Vial
12	8/26/71	4:00	MSU 35G	F	39.77	29.4	13.17	0.33	Dry ice
14	8/31/71	3:15	Spartan Progress	M	31.96	44.3	17.01	0.53	Vial
16	8/26/71	4:15	Spartan Progress	M	28.30	42.4	14.29	0.50	Dry ice
17	8/26/71	2:15	Piccadilly	M	12.44	45.1	6.76	0.54	Dry ice
18	8/26/71	3:40	Spartan Progress	F	12.64	27.7	3.92	0.31	Dry ice
19	8/26/71	3:00	35G x 381G	F	70.27	37.3	30.54	0.43	Dry ice
1	9/13/72	3:00	SMR 58	F	23.91	34.9	9.62	0.40	Vial
2	9/13/72	3:10	SMR 58	M	60.02	38.0	26.65	0.44	Vial
3	9/13/72	3:20	SMR 58	M	19.03	37.0	8.19	0.43	Vial
4	9/13/72	3:40	MSU 35G	F	36.36	32.2	13.34	0.36	Vial
5	9/13/72	4:00	35G x 381G	F	55.63	37.3	24.17	0.43	Vial
6	9/13/72	4:15	Piccadilly	M	46.60	37.2	20.19	0.43	Vial
7	9/13/72	4:30	Piccadilly	F	37.82	31.7	13.64	0.36	Vial
8	9/14/72	3:00	MSU 35G	F	101.50	43.0	52.13	0.51	Dry ice
9	9/14/72	3:30	SMR 58	M	94.67	41.7	46.88	0.49	Dry ice
10	9/14/72	4:00	Piccadilly	F	46.85	41.1	22.81	0.48	Dry ice
11	9/14/72	4:10	Piccadilly	M	46.85	41.5	23.07	0.49	Dry ice
12	9/14/72	4:20	35G x 381G	F	90.04	45.1	48.95	0.54	Dry ice
13	9/15/72	3:00	MSU 35G	F	47.34	46.7	26.84	0.56	Vial
14	9/15/72	3:25	SMR 58	M	52.70	43.7	27.59	0.52	Vial
15	9/15/72	3:45	Piccadilly	F	32.45	45.6	17.88	0.55	Vial
16	9/15/72	4:00	Piccadilly	M	52.21	43.2	26.96	0.51	Vial
17	9/28/72	1:15	MSU 35G	F	127.12	26.9	38.11	0.29	Dry ice
18	9/28/72	1:45	35G x 381G	F	112.72	28.1	35.48	0.31	Dry ice
19	9/28/72	2:00	Piccadilly	F	103.70	28.3	32.90	0.31	Dry ice
20	9/28/72	2:20	SMR 58	F	62.22	28.2	19.66	0.31	Dry ice
21	9/28/72	2:30	SMR 58	F	84.18	27.4	25.76	0.30	Vial
22	9/28/72	2:45	SMR 58	M	112.24	31.2	39.74	0.35	Dry ice
23	9/28/72	3:00	Piccadilly	M	85.89	30.3	29.42	0.34	Dry ice
24	9/28/72	5:00	MSU 35G	F	136.88	19.5	28.85	0.21	Vial
25	9/28/72	5:15	381 x 35G	F	76.37	20.9	17.35	0.22	Vial

of 1% D.C. 200 on 60/80 mesh Gas Chrom Z at 220^0 C, N_2 carrier at 86 ml/min and a sensitivity of $1x10^{-8}$ amps full scale. Glucose and fructose were separated by using a glass column 6 ft. x 1/4 inch of 3% OV-17 (5 ft) on G.C.Q. 100/120 mesh and 1% OV-17 (1 ft) on G.C.Q. on 60/80 mesh at 160^0 C, N_2 carrier at 26 ml/min and a sensitivity of $1x10^{-9}$ amps full scale. In both cases the type of detector was a hydrogen flame. The peaks were quantitated by peak height ratios. After each injection into the column, of the gas liquid chromatograph, the syringe was cleaned with glass distilled hexane or nanograde acetone. Analysis was done by a 7600 series Packard Gas Chromatograph.

Results

Various approaches were tried, attempting to identify the 3 main sugars of nectar isothermically in 1971. There were changes in the length and diameter of the glass columns, types of liquid phases on different types and sizes of column supports, oven temperatures (135^0C-240^0C), and attenuation ($3x10^{-10}$-$1x10^{-7}$) amps full scale. All were somewhat unsuccessful, therefore, a second approach was taken. It was found that a glass column 6 ft by 1/4 inch of 3% OV-17 (5 ft) on G.C.Q. 100/120 mesh and 1% OV-17 (1 ft) on G.C.Q. mesh would separate the three main sugars of nectar at different temperatures at sensitivities of $1x10^{-8}$ and $1x10^{-9}$ amps full scale. Column temperature was 160^0 C. Fructose came off first at 3 min and 25 sec and glucose at 6 min and 5 sec with the sensitivity at $1x10^{-9}$ amps full scale. After glucose came off, the programmed temperature operation began, being controlled automatically by the digital programmer. The temperature rose from

160° C to 220° C at a rate of 9.9°/min. With the rise in temperature, sucrose came off at approximately 25 min depending on the time that the digital programmer was started. This method was abandoned because of severe tailing on the sucrose peaks.

By using the two different columns, (5% QF-1 and 10% D.C. 200), the three main sugars found in nectar were successfully separated. Sucrose came off at 3 min, 20 sec with the 5% QF-1 column. The 10% D.C. 200 column brought fructose off at 11 min, 50 sec and 18 min 10 sec, whereas glucose came off at 16 min, 5 sec and 23 min, 25 sec.

In 1973 it was found that a six foot x 1/8 inch glass column of 1% D.C. 200 on 60/80 mesh Gas Chrom Z with the oven temperature programmed from 150° - 220° C at a rate of 10-15°/min and the N_2 carrier at 10 or 20 p.s.i. would separate the 3 main sugars found in nectar when using the standard solutions. But the curves of the nectar samples did not coincide with those of the standards. Changes in column length, attenuation, type of column supports and size did not correct the situation. Therefore, I went back to two different columns to separate the sugar derivatives as in 1971.

Sucrose came off at 3 min, 42 sec with 1% D.C. 200 column. The combination column of 1% and 3% OV-17 brought fructose off at 5 min, 45 sec. Glucose came off at 9 min, 53 sec and at 15 min, 7 sec.

The nectar of cucumbers was found to be sucrose dominant, with fructose predominating over glucose in all samples except one (Table 48). Overall, sucrose averaged $60.5 \pm 1.9\%$, fructose $25.1 \pm 1.2\%$, and glucose $14.4 \pm 1.0\%$ of the total sugars present. During 1971 sucrose ranged from

39.7% - 59.3% with a mean of $51.8 \pm 3.0\%$. The values for 1973 were higher, ranging from 43.1% - 78.9%, with a mean of $62.9 \pm 2.1\%$. Glucose ranged from 16.6% - 33.1% with a $21.9 \pm 2.4\%$ average in 1971 and from 7.4% - 19.2% with a mean of $12.4 \pm 0.68\%$ in 1973. Fructose ranged from 21.2% - 31.3%, averaging $26.3 \pm 1.3\%$ for 1971 and $24.7 \pm 1.5\%$ in 1973 ranging from 13.6% - 41.0%.

Nectar from pistillate flowers was slightly higher in sucrose and lower in glucose than from staminate flowers. Fructose was slightly lower in pistillate flowers but the difference was not significant (Table 49). Comparison of the five cultivars that were sampled during the two summers showed that all but one were similar in sugar composition (Table 50). Spartan Progress which was sampled in 1971 was significantly lower in sucrose at the 5% probability level (Student's t test) when compared to its nearest rival.

Once the silylation reagent was added to the nectar sample, the sample was short lived. Within 24 hours a large change had taken place and the chromatograph curves could not be duplicated (Table 51). This was true when the samples were stored at room temperature, in the refrigerator or in the freezer. Since the nectar samples were good only on the day they were silylated, many of our early samples in 1971 became worthless in storage while we were working on methodology as explained in materials and methods. As a result all samples that were transported to the laboratory as flowers stored in a thermos bottle were lost.

Freezing nectar immediately upon removal from the flower with dry ice looks to be the best method by the 1971 data (Table 52).

Table 48. - The composition of cucumber nectar on the day of silylation.

Vial no.	Sex	Fructose curve	Micro-grams of sugar	% Fructose	Glucose curve	Micro-grams of sugar	% Glucose	Sucrose curve	Micro-grams of sugar	% Sucrose	Total sugar (micrograms)
1971											
16	M	206	4.53	31.3	123	2.55	17.7	595	7.35	51.0	14.43
19	F	267	5.88	29.3	260	5.73	28.6	683	8.44	42.1	20.05
11	F	106	2.33	26.3	85	1.76	19.9	386	4.77	53.8	8.86
17	M	59	1.30	21.2	59	1.22	19.9	293	3.62	58.9	6.14
14	M	129	2.84	27.2	167	3.46	33.1	336	4.15	39.7	10.45
18	F	67	1.48	24.7	51	1.06	17.7	279	3.45	57.6	5.99
12	F	119	2.62	24.1	87	1.80	16.6	521	6.44	59.3	10.86
1973											
1	F	330	3.1	27.2	205	1.3	11.4	101	7.0	61.4	11.4
2	M	430	4.0	20.6	263	1.6	8.3	198	13.8	71.1	19.4
3	M	371	3.5	34.0	305	1.9	18.4	70	4.9	47.6	10.3
4	F	273	2.6	18.8	180	1.1	8.0	146	10.1	73.2	13.8
5	F	543	7.9	33.1	268	3.2	13.4	184	12.8	53.5	23.9
6	M	256	4.1	17.3	176	2.6	11.0	172	17.0	71.7	23.7
7	F	210	3.7	18.0	129	1.9	9.2	151	15.0	72.8	20.6
8	F	846	15.0	31.4	373	5.6	11.7	275	27.2	56.9	47.8
9	M	447	4.2	26.2	189	2.8	17.5	64	9.0	56.3	16.0
10	F	630	11.2	33.8	267	3.9	11.8	182	18.0	54.4	33.1
11	M	377	3.5	20.0	374	2.3	13.1	169	11.7	66.9	17.5
12	F	486	8.6	26.7	285	4.2	13.0	196	19.4	60.3	32.2
13	F	329	5.8	15.1	243	3.5	9.1	70	29.2	75.8	38.5
14	M	311	5.5	20.4	282	4.1	15.2	176	17.4	64.4	27.0
15	F	443	7.9	32.0	224	3.3	13.4	136	13.5	54.6	24.7
16	M	349	6.2	28.6	213	3.0	13.8	145	12.5	57.6	21.7
17	F	542	5.0	24.6	235	3.3	16.3	106	12.0	59.1	20.3
18	F	285	5.1	16.3	209	2.9	9.2	271	23.4	74.5	31.4
19	F	394	7.0	30.6	207	2.9	12.7	151	13.0	56.7	22.9
20	F	215	3.8	15.8	171	2.4	9.9	208	17.9	74.3	24.1
21	F	216	3.8	13.6	145	2.1	7.5	223	22.1	78.9	28.0
22	M	661	6.2	35.0	244	3.4	19.2	57	8.1	45.8	17.7
23	M	785	13.9	41.0	369	5.4	15.9	147	14.6	43.1	33.9
24	F	360	6.4	22.3	253	3.5	12.4	212	18.3	64.9	28.2
25	F	195	3.5	16.2	112	1.6	7.4	191	16.5	76.4	21.6
Overall				25.1 ± 1.2			14.4 ± 1.0			60.5 ± 1.9	

Sugar curves expressed as peak height ratio/microliter

Table 49. - Percentages of sugars in nectar from staminate and pistillate cucumber flowers.

Year	Sex	N	% Fructose	% Glucose	% Sucrose
1971	male	3	26.6 ± 2.9	23.6 ± 4.8	49.9 ± 5.6
1973	male	9	27.0 ± 2.7	14.7 ± 1.2	58.3 ± 3.6
Overall		12	26.9 ± 2.1[a]	16.9 ± 1.8	56.2 ± 3.2
1971	Female	4	26.1 ± 1.2	20.7 ± 2.7	53.2 ± 3.9
1973	Female	16	23.5 ± 1.8	11.0 ± 0.6	65.5 ± 2.3
Overall		20	24.0 ± 1.5[a]	13.0 ± 1.1	63.0 ± 2.3

Overall means in each column followed by the same small letter are not significantly different at the 10% probability level (Student t test).

Table 50. - Percentage of sugars in nectar from various cucumber cultivars.

Cultivar	N	% Fructose	% Glucose	% Sucrose
Spartan Progress	3	27.7 ± 1.9	22.8 ± 5.1	49.4 ± 5.2
Piccadilly	9	26.9 ± 2.7	13.4 ± 1.0	59.6 ± 3.1
35G x 381G	6	24.6 ± 2.8	15.2 ± 3.2	60.1 ± 5.4
35G	6	22.7 ± 2.3	12.4 ± 1.4	64.9 ± 3.2
SMR 58	8	24.1 ± 2.8	13.4 ± 1.7	62.5 ± 4.3

Samples that were placed in vials and not frozen had a lower percentage of sucrose with higher amounts of glucose and fructose. However, the 1973 values were the reverse of 1971. Statistical comparison of the overall values for the two methods, showed that they were not significantly different at the 5% probability level (Student's t test). It is possible that some change in the nectar could take place during transit in a warm car from the field to the freezer.

Some atypical peaks came off in 1973 that were not present with the standards. Nine of the 25 samples had two small peaks come off at 2 min, 35 sec and 3 min, 3 sec, just prior to sucrose at 3 min, 42 sec. In looking at the nine samples involved, no definite trends could be found. All four of the cultivars used in 1973 were involved, with five samples coming from pistillate flowers and four from staminate. Therefore, pollen contaminants found in the nectar of staminate flowers could not be the cause. Six of the samples were quick frozen on dry ice and three brought to the laboratory in vials. Testing showed that the unknowns were not maltose since it came off with the 1% D.C. 200 column after sucrose at 4 min, 45 sec.

The same nine samples also acted differently on the column used for separating glucose and fructose. The largest variations were in the second fructose curve of the standard. This curve only showed up with these nine samples and four variations of it were seen. Secondly, an unknown was found between the two glucose curves in all nine of the samples and peaked at 12 min, 24 sec.

Table 51. - Stability of silylated nectar samples and standards.

Vial no.	Sex	Sugar	0	4	7	8	14	21	28
16	M	Fructose	206		109[a]		116		
16	M	Glucose	123		127		119		
16	M	Sucrose	595[a]		311[a]		477*		
19	F	Fructose	267[a]		259[a]		287[a]		
19	F	Glucose	260		240		246*		
19	F	Sucrose	683		480		different curves		
12	F	Sucrose	521				536	383	
12	F	Fructose	119				107	128	127
12	F	Glucose	87				104	116	39
Standard		Sucrose	809	203					
1	F	Sucrose			784*				
2	F	Sucrose			No peaks				
4	F	Sucrose			No peaks				
Standard		Fructose	454			204			
1	F	Fructose			143				
3	F	Fructose				127			
Standard		Glucose	483			330			
3	F	Glucose				165			

Expressed as peak height ratios/ microliter
* = change in base size
a = normally two curves, only one present

Table 52. - Comparison of methods for transporting nectar samples to the laboratory.

Year	Method	N	% Fructose	% Glucose	% Sucrose
1971	Vial	2	26.8 ± 0.4	26.5 ± 6.6	46.8 ± 7.1
	Dry ice	5	26.1 ± 1.8	20.1 ± 2.2	53.8 ± 3.3
1973	Vial	14	22.7 ± 1.9	11.3 ± 0.9	66.0 ± 2.6
	Dry ice	11	27.4 ± 2.4	13.7 ± 1.0	58.9 ± 3.0
Overall	Vial	16	23.2 ± 1.7[a]	13.2 ± 1.6[b]	63.6 ± 2.9[c]
	Dry ice	16	27.0 ± 1.7[a]	15.7 ± 1.2[b]	57.3 ± 2.3[c]

Overall mean values in each column followed by the same small letter are not significantly different at the 5% probability level (Student t test).

Discussion

As was pointed out in the literature, the chemical constituents are sometimes characteristic of the plant family as a whole. Cucumber nectar was found to be sucrose dominant with fructose and glucose present. This is similar to Percival's (1961) analysis of nectar from Luffa cylindrica and Momordica balsamina of the family Cucurbitaceae. Both the pistillate and staminate cucumber flowers produce a quality and quantity of nectar that must be considered relatively attractive to the honey bee based both on chemical analysis and observations of bee activity in the field.

Wykes (1952a) found that sugars which occur in nectar were not equally attractive to bees. Consistent preferences were shown for solutions of sugars in the following decending order: sucrose, glucose, maltose and fructose. The acceptance of both sucrose and glucose relative to fructose was markedly high. Von Frisch (1934) cited by Wykes (1952a) found that glucose and fructose were equally attractive to bees. He agreed that sucrose was the most attractive sugar as did Bailey, Fieger and Oertel (1954). These results indicate that nectars containing high percentages of sucrose might be more attractive to bees than nectars containing relatively low quantities of this sugar. This could explain why cucumber nectar is relatively attractive to bees, since over half of the sugar present was sucrose. Percival (1961) found that sucrose predominated in the nectar of flowers visited by bumble bees, honey bees, butterflies and moths.

Wykes (1952a) found consistent preferences for a mixture of equal proportions of sucrose, glucose and fructose, over solutions of

single sugars, mixtures of two sugars, or the same sugars available in different proportions. Furgala, Gochnauer & Holdaway (1958) noted that white sweet clover has this balance of the three sugars and found that bees preferred this nectar to that of alfalfa, alsike or red clover which are sucrose dominant. Flowers that are highly competitive for bee visits with the cucumber may have nectar containing the preferred balance of sugars. Since Percival (1961) found that nectars containing this preferred balance of sugars are uncommon, only 48 of 889 species sampled, it appears that the ratio of the three sugars may be an important aspect in monitoring the potential attractiveness of a crop to bees.

Von Frisch (1950) found that the honey bee's threshold of acceptance for sugar solutions was a 5% concentration, but varied with feeding conditions. If there are many plants in bloom, the threshold may be as high as 40%. Jamieson and Austin (1956) found that honey bees distinguished differences of 5% in sugar syrup concentrations. Significantly more bees were attracted to 50% sucrose solutions than to 45 and 40% solutions. Bees were unable to distinguish between steps of 50,47.5 and 45% sucrose solutions. Woodrow (1968) showed that bees preferred 40% and 50% sucrose solutions to more concentrated and less concentrated solutions. The discrimination against 60% concentration was distinct. Kropacova and Kropac (1968) found a significant positive correlation between the sugar concentration of chive nectar and bee visitation. They found that visitation was virtually independent of the quantity of nectar present. Butler (1945) concluded that nectar concentration was used by the bees to determine which plant species was preferred and

nectar quantity determines the proportion of the foraging population of the colony which will work those flowers. From these studies it would appear that the sugar concentration of nectar is very critical in determining its attractiveness to the bee. However, Woodrow (1968) suggested that a wide variation in sugar concentration is acceptable to the bee since each bee load is ordinarily a composite accumulation of small quantities of nectar from several individual flowers. He suggested that sugar concentration alone at times may be less influential than other factors in the selection of plants by foraging bees. Along the same line of thought, Pedersen (1956) warned plant breeders that selections based on sugar concentration should be used cautiously because of the very pronounced effect of the environment on sugar concentration. If breeding efforts are made to maintain or improve the attractiveness to bees, of bee-pollinated crops, high sugar concentrations, larger quantities of nectar, preferred balance of sugars and possible modifications in flower structure may have to be considered.

Nectar replacement is a rapid event (Chapter III) and with multiple visits throughout the day there is a large decrease in sugar concentration. Woodrow (1968) found that the selection of the preferred concentration occurred in the first few minutes of a test. That is, the honey bee determines whether the nectar is attractive or not on its initial visits to the flower. Even though the sugar concentration of cucumber nectar in the field may decrease throughout the day, making it less attractive to successive visitors, the bees continue to work the flowers due to their original attraction and foraging constancy.

Another phase of this work has shown that many plants competing with cucumber for bee visits have sugar concentrations higher than cucumber (unpublished) and many have preferred sugar mixtures Percival (1961) and Furgala, Gochnauer & Holdaway (1958). Therefore, the presence of large acreages of such plants within flight range of bees located for cucumber pollination will reduce bee visits to the cucumber field and thus affect the efficient use of bees located for pollination of the crop.

Plant breeders in the past, while developing many new strains of economically important plants, rarely considered nectar secretion when selecting desirable traits. If bee-pollinated crops become unattractive to bees or strains to be hybridized vary in attractiveness, pollination of the crop may become a real problem. Nectar volume can be measured and sugar concentration determined with reasonable accuracy using a hand refractometer, without much training, or expensive equipment. If the plant breeder felt it was desirable to know the composition of nectar, gas liquid chromatography seems to provide a suitable technique. By knowing the nectar production characteristics of a plant, the plant breeder could select progeny, so the cultivars attractiveness would be maintained or improved, thereby improving competitive status of the crop and pollination.

This work has shown that gas liquid chromatography is applicable to nectar research. With refinement of methodology, nectar samples could be run in a short time compared to various forms of paper chromatography, and reliable quantitative as well as qualitative data would

be available. Various avenues should be taken to refine the method used for nectar analysis. More work might turn up a column that would separate the sugars isothermically in a relatively short time. As shown, nectar samples and standards are short lived once the silylating reagent is added whether stored at room temperature, in a refrigerator or freezer. A better understanding is needed of what is taking place in the samples during the first 24 hours in relation to changes in peaks, stability and reliability. Other silylation reagents might be found that would prolong the life of the sample. Literature shows that nectar contains many materials, other than sucrose, fructose and glucose. Columns, silylating reagents and methods could likely be found so complete nectar analysis could be made if desired. Already columns and silylation methods have been developed to analyze amino acids, vitamins, alcohols, proteins, volatile organic oils and organic acids.

Gas liquid chromatography is a practical method since nectar samples would only have to contain 10-15 mg of sugar per sample. This is important since many flowers are structured so that large samples are impossible to obtain. Samples could be collected during the day, quick frozen in dry ice in the field, then frozen and lyophilized in the laboratory for later silylation and analysis.

SUMMARY AND CONCLUSIONS

1. In both staminate and pistillate cucumber flowers, nectar was the primary attractant. Few bees were observed collecting pollen. The pellets of those observed collecting pollen were small in size compared to the pellets from major pollen sources.

2. All cucumber cultivars tested in this study produced a quantity and quality of nectar that was attractive to honey bees. New cultivars may have a higher nectar secretion potential because of the swing to gynoecious F_1 hybrids which have predominantly pistillate flowers.

3. The nectaries of staminate and pistillate flowers differ in both shape and size. The nectary of the pistillate flower is in the form of a cup surrounding the base of the style, whereas the nectary of the staminate flower is a three-lobed button lying on the floor of the receptacle. The nectary of the pistillate flower is 1.6 - 1.9 times as wide as that of the staminate flower and it has approximately twice the secretory surface. Most nectaries of staminate flowers are 2 to 3 mm wide, whereas those of pistillate flowers are 4 to 5 mm.

4. The epidermal layer on the surface of the nectary contains stomate-like pores that appear to open and close as the environment around them changes. The stomate-like pores are found only on the inner surface of the nectary of the pistillate flower but in staminate

flower nectaries they are found on the upper surface and outer edge. The nectary surface is irregular and the area surrounding the stomates appears to be slightly depressed.

5. Typically the nectary of a staminate flower is a three-lobed structure, though on occasion four-lobed nectaries may be observed. Populations of the various cultivars contained from 0.7 to 12.3% four-lobed nectaries and the trait appeared to be environmentally influenced in the greenhouse.

6. Positive correlations were consistently found comparing nectary width with petal diameter, volume of nectar, total weight of sugar present, and ovary length, but not sugar concentration.

7. Basically the cucumber flower has a one day secretory cycle with maximum secretion on the day of anthesis. Flowers secrete no nectar in the bud stage. Less than 1/3 of the second day flowers contained nectar and only about 3% of the third day flowers. Flowers on the day of anthesis produced 1.1 times more nectar than the one day old flowers and 3.8 times that of the two day olds. The actual weight of sugar in the nectar showed even a greater reduction due to large decreases in sugar concentration. Flowers on the day of anthesis contained 2.5 times more sugar than one day olds and 11.6 times that of two day old flowers.

8. The commencement of nectar secretion appeared to be temperature dependent. Below 16° C nectaries were dry on the day of anthesis. At 16° C they began to look moist under the microscope. At 17° C, 1-2 small beads of nectar began to form on the inner surface of the cup

of the pistillate flower and by time the temperature reached 21° C, the first measurable amounts of nectar were collected.

9. Nectar in individual flowers varied under different conditions throughout the day from none to over 30 ul in amount, from 13% - 60% in sugar content and from 0 to 12.33 mg of sugar when bees were excluded from the flowers.

10. Throughout the day, without bee visitation, the average volume of nectar and total weight of sugar increased and sugar concentration decreased.

11. The sugar concentration of nectar was greatly reduced "reabsorbed" during the night but the volume of nectar remained about the same. The nectar of pistillate flowers went from 34.8% to 12.0% sugar and from 41.2% to 18.9% in staminate flowers. Comparable decreases were also found in the actual weight of sugar present.

12. The secretory rhythms of staminate and pistillate flowers were similar but differed in content. Pistillate flowers produced approximately 1.5 - 2.3 times as much nectar as staminate flowers but staminate flower nectar had a higher sugar concentration (45.3% compared to 36.3% in one study). The total weight of sugar for both types of flowers was generally quite close, with pistillate flowers having a slight edge.

13. Honey bees must visit more staminate than pistillate flowers to obtain an equal amount of nectar. Even though this requires a greater energy expenditure, the bee is rewarded about equally by staminate flowers because they have a higher concentration of sugar. This helps to insure that both pistillate and staminate flowers will be visited and pollination result.

14. In the field, bees spent almost twice as long per visit on pistillate flowers as on staminate flowers. When honey bees reach down to the nectary, they automatically come in contact with the anther or stigma, so that pollination results. The length of the visit depends on the amount of nectar present. Since pistillate flowers produce from 1.5-2.3 times more nectar than staminate flowers, it takes the bee almost twice as long to collect it. If the honey bee is not disturbed, it will remove all of the nectar present in one visit.

15. Nectar replacement in a flower is a rapid event. Some nectar is replaced within 5 minutes after removal. Six hourly removals from the same flowers showed that the flower can replace approximately the same volume of nectar that was removed the hour before but the sugar concentration and actual weight of sugar decreased sharply. Multiple visitation or nectar removal did not stimulate nectar production.

16. With bees excluded, the mean sugar concentration of nectar taken from both types of flowers was 40.8%. On the other hand the mean sugar concentration of nectar removed from the honey stomachs of bees gathering from cucumbers in the same field was 24.5%, showing a 40% difference in sugar concentration. The difference is largely explained by reduced concentration due to nectar removal and replacement.

17. To accurately compare nectar secreting characteristics of different cultivars, data for staminate and pistillate flowers had to be considered separately due to their secretion differences. No significant differences were found in the cultivars compared. On a field basis, cultivars that produced predominantly pistillate flowers secreted larger

volumes of nectar with more total sugar than staminate lines which produced nectar with higher average sugar concentrations.

18. There tended to be slight increases in flower size, nectary size and volume of nectar in flowers produced further down the vine from the base.

19. Flowers found on lateral vines tended to produce a larger quantity of nectar containing a higher weight of sugar than those on main vines.

20. Only morning pollinations affected nectar secretion. From the time of pollination in the morning to fertilization the cucumber flower continues to secrete nectar and replenish its supply after each visit. After fertilization nectar secretion appeared to cease. Any nectar remaining in the flower may be changed in water content depending on the relative humidity and be partially reabsorbed during the night.

21. Attempts to identify the three main sugars of nectar isothermically with gas liquid chromatography were unsuccessful. Therefore, the three sugars in the nectar samples were quantified with two different columns.

22. Once the silylation reagent (Tri-Sil Z) was added to nectar, the samples changed quantitatively. Within 24 hours a definite change had taken place and chromatograph curves could not be duplicated. This was found to be true regardless of whether samples were stored at room temperature, in the refrigerator, or in the freezer.

23. The nectar of cucumbers was found to be sucrose dominant, with fructose predominating over glucose. Sucrose averaged 60.5%, fructose 25.1% and glucose 14.4% of the total sugars present.

24. Unknown peaks were found in nine of the nectar samples. Two appeared prior to sucrose at 2 min, 35 sec and 3 min, 3 sec and one between the two glucose curves at 12 min, 24 sec.

25. Since the cucumber flower basically secretes for only one day, factors that prevent bees from flying, essentially prevent pollination of that days flower output. Gaps in flower pollination lessen uniformity of pickle production for machine harvest. However, the sugar supply of unvisited flowers may still be potentially available to the bee at a later time due to reabsorption and resecretion.

26. Both pistillate and staminate cucumber flowers were found to produce a quality and quantity of nectar that must be considered relatively attractive to the honey bee, based both on chemical analysis and observations of bee activity in the field. However, in comparing sugar concentration and total weight of sugar with major nectar sources, cucumbers would rate moderately attractive but because of a relatively small number of flowers per acre, it cannot be rated as an important honey plant.

27. When bee visits and pollination were delayed to flowers on later nodes, flowers gave greater rewards to visiting bees, pollination was more effective and fruit yield was of a higher quality. This could be because the cucumber flower reabsorbs its uncollected sugar supply, so the plant was able to build up larger carbohydrate supplies for nectar production through a longer period of photosynthesis and reabsorption before collection.

28. These studies indicate that important factors of attractiveness of a crop to bees could be readily monitored during a plant breeding program. The volume of nectar and total weight of sugar in the nectar appear to be the best indicators. Nectar volume can be measured and sugar concentration determined with reasonable accuracy using a hand refractometer without a great deal of training, consumption of time, or expensive equipment. These values could also be supplemented with measurements of the nectary and analysis of honey stomach contents from bees working the crop. If maintenance or improvement in the attractiveness to bees of bee-pollinated crops is to be considered in a crop breeding program, higher sugar concentrations, larger quantities of nectar, preferred balance of sugars within the nectar and possible modifications in flower structure appear to be factors of greatest significance which may be reasonably monitored.

29. Any significant increases in quantity and quality of nectar produced, for both staminate and pistillate cultivar lines of cucumbers, would help to lessen the competition that exists between the cucumber and other nectar sources in the area of the field.

30. Average analysis of cucumber nectar:

Water - 59.2%

Sucrose - 24.7%

Fructose - 10.2%

Glucose - 5.9%.

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