

AN ABSTRACT OF THE THESIS OF

Jenny M. Gavilánez-Slone for the degree of Master of Science in Entomology
presented on August 29, 2000. Title: Pollination and Pollinators of Pumpkin and
Squash (*Cucurbita maxima* Duchesne) Grown for Seed Production in the
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D. Michael Burgett

'Golden Delicious' winter squash (GDWS), *Cucurbita maxima* Duchesne, provides significant amounts of pollen (24 mg) and nectar (236 μ l), but with a low reward of 14% nectar sugar. The quantity of nectar produced per GDWS flower differed between sites and floral sex. The GDWS male flowers had 25% higher sugar concentration than female flowers. There was no statistical difference in the percent of nectar sugars per flower between sites, but the interaction between site and floral sex was statistically significant for the amount of nectar and percent of nectar sugars. Pollen production per flower differed significantly between sites with the most productive site producing 27% more, and 45% more than the other sites.

Pollination efficiency of honeybees and bumble bees was assessed with field cages (1.8x1.8x1.8 m). No significant differences were found except for the interaction between the bee treatment and year on number of fruit per cage. This

significant difference reflects the increase in fruit number produced by honey bees in 1997.

The effect of distance from honey bee hives on fruit and seed quality was tested, and found significant only for B- and C-seeds weight, which were both less in the plots farthest from the nearest group of honey bee hives. Placement of honey bee hives in fields of ≤ 120 ha appears not to be critical for adequate pollination of GDWS. Other pollinators (excluding honey bees) were frequent visitors to the squash flowers studied here - for example, *Bombus* spp., Megachilids, Halictids, etc. These other pollinators, mostly bumble bees, accounted for 3.55% of all bee visits.

Honey bees visited proportionately more female flowers in the morning, and progressively switched to the more abundant male flowers in the afternoon. This bias differed by site and year. Bumble bees visited proportionally slightly more male GDWS flowers than did female flowers and did it in a similar rate throughout the day. From 15 minute observations each hour of individual female GDWS flower, we calculated that they received approximately 80 honey bee visits per day.

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**POLLINATION AND POLLINATORS OF PUMPKIN AND SQUASH
(*CUCURBITA MAXIMA* DUCHESNE) GROWN FOR SEED PRODUCTION IN
THE WILLAMETTE VALLEY OF WESTERN OREGON**

by

Jenny M. Gavilánez-Slone

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POLLINATION AND POLLINATORS OF PUMPKIN AND SQUASH (*CUCURBITA MAXIMA* DUCHESNE) GROWN FOR SEED PRODUCTION IN THE WILLAMETTE VALLEY OF WESTERN OREGON

1. INTRODUCTION

The use of honey bees as managed pollinators of pumpkin and squash (*Cucurbita maxima* Duch., *C. mixta* Pang., *C. moschata* Duch. and *C. pepo* L.) in Oregon has yet to be fully exploited. Furthermore, the use of potential pollinators such as bumble bees (*Bombus* spp.) and indigenous wild bee species has not been investigated. Pumpkin and squash are incapable of selfing and require insect pollination for seed production (Free, 1993; McGregor, 1976; Mel'nichenko, 1976). Pumpkin and squash are ranked 43th (by gross dollar sales) among Oregon's leading agricultural commodities, and are currently (1999) grown on approximately 1,335 ha in Oregon with an annual production of 66,865 MT at a value of U.S. \$9,657,000 (Sears, 1999).

In the Willamette Valley of western Oregon, squash and pumpkin are planted between May 1 and June 1, using 3.2 – 5.7 kg of seed per ha, depending on the spacing used. The squash and pumpkin fruit is harvested after the first frost and when the fruit has developed its characteristic bright orange color. Seed yields range from 450 to 1120 kg per ha, representing 35 – 40 % of the total fruit weight harvested (Mansour and Baggett, 1985 and H. Ropp, personal communication).

1.1 GOLDEN DELICIOUS WINTER SQUASH

1.1.1 General characteristics

Squash are fruits of any of five domesticated species of the genus *Cucurbita* in the family Cucurbitaceae, order Violales. These species are *C. maxima* Duchesne, *C. argyrosperma* Huber (= *C. mixta* Pang.), *C. ficifolia* Bouché, *C. moschata* Duchesne ex Poir., and *C. pepo* L. All except *C. ficifolia* are actively cultivated by commercial growers. In the Willamette Valley of Oregon, several varieties of pumpkin and squash are grown commercially, with one of the more important squash varieties for seed and food processing being ‘Golden Delicious’ Winter Squash (GDWS), a variety of *C. maxima* in the Hubbard group. It is prized because of its large, plentiful seeds, thick rind, and orange skin that does not degrade the quality of processed flesh like some green skins do. Its fruits are the giants of the plant kingdom, weighing generally from 1 to 50 kg, with exceptional fruit weighing up to 440 kg. Mature fruits have tens to hundreds of flat seeds each with a coat enclosing a collapsed perisperm, an oily embryo and little or no endosperm (Robinson and Decker-Walters, 1997).

Flowers of GDWS are normally 6 to 12 cm across, opening early in the morning, and lasting ~1 day. GDWS is monoecious, with separate male and female flowers on the same plant. The ratio of male to female flowers is generally 10:1 (Crane and Walker, 1984; Free, 1993; McGregor, 1976b). Male flowers have three anthers that produce ~16,500 large (Nepi and Pacini, 1993; Proctor *et al.*, 1996),

spherical, spiny and sticky pollen grains (~200 μ m, as compared to an average of 30-40 μ m for plants in general). Female flowers have a three lobed stigma and an inferior ovary containing approximately 650 ovules (Crane and Walker, 1984; Free, 1993; McGregor, 1976b).

Floral nectaries are borne inside and at the base of the flower in both male and female flowers. The nectary forms a continuous ring surrounding the base of the style in the female flowers, whereas the nectary and its associated pistil rudiment form a button-shaped mound at the center of the male flower (Robinson and Decker-Walters, 1997).

Though most species of *Cucurbita* are native to Mexico, *C. maxima* originated in South America (confined to temperate zones of Peru, Bolivia, Chile, Argentina and Uruguay), and was introduced to the United States around 1827 (Robinson and Trail, 1978; Whitaker and Cutler, 1965). It is an annual, prostrate vine with long trailing branches. Though more cold tolerant than other species of *Cucurbita*, varieties of *C. maxima* such as GDWS are susceptible to frost kill (Hurd *et al.*, 1971; Robinson and Decker-Walters, 1997; Whitaker, 1977). In spite of this, it is widely cultivated in areas with relatively cool climates, such as the Willamette Valley. The crop in the Willamette Valley is planted in May, and harvested in the fall just after the first frost.

1.1.2 Uses of GDWS

Most squash, including GDWS, are grown for human consumption. The flesh is eaten fresh and processed by canning and freezing. Seeds are dried and

salted, and packaged for snacks, and fried flowers are eaten in South and Central America (Robinson and Decker-Walters, 1997; Whitaker, 1977). Other uses of squash include animal feed (flesh and seeds), cooking and illumination oil extracted from seeds, and makeup products extracted from flowers. Several varieties are also used as ornamentals. People from many cultures extract cucurbitacins, which are very bitter triterpenoid compounds, for their effects on the digestive system. Other potential medicinal compounds include saponins, free amino acids and alkaloids (Robinson and Decker-Walters, 1997). In Oregon, GDWS flesh is processed for canned and frozen food and processed baby food. The seeds are used for dried snack foods, and for wild animal food (squirrel and bird food).

1.2 POLLINATION OF PUMPKIN AND SQUASH

Zoophilous flowers employ animals as pollen vectors, and nectar is generally offered as a primary attractant, with pollen as a secondary attractant. Nectar production is synchronized with anther dehiscence (pollen shedding), to ensure the attraction of pollinators (Faegri and van der Pijil, 1979). Since the role of pollen is to move the gametes from flower to flower, these flower visitors inadvertently pollinate the plants during their visits (Proctor *et al.*, 1996; Westerkamp, 1996). If nectar and pollen rewards are too low for pollinators, they will look elsewhere for their resources, and not pollinate the crop, so pollen and nectar quantity and quality are important considerations in a managed pollination

plan (Aizen and Raffaele, 1996; Byers, 1995; Cane and Schiffhauer, 1997; Corbet *et al.*, 1984).

Though some varieties of squash can set fruit without pollination, GDWS is a monoecious plant, and pollen must be transferred from a male to a female flower, either on the same or a different plant, in order to be fertilized and to set fruit (Free, 1993; Jaycox *et al.*, 1975; McGregor, 1976a). This cultivar, with its large pollen grains, needs to be well pollinated by insects to produce marketable fruit.

Inadequate pollination can cause poor fruit set and misshapen fruits (Robinson and Decker-Walters, 1997). Hayase (1953) found that seed number and fruit weight in squash increased in proportion to the amount of pollen deposited on the stigma.

Melendez-Ramirez *et al.* (1996) reported that the number and weight of *C. pepo* fruit increased in proportion to the amount of deposited pollen.

GDWS fruit and seed set depend on the successful completion of several sequential events, including pollen development, anthesis (blooming phase), pollination, pollen-pistil interaction, and fertilization. Anthesis generally starts in the Willamette Valley at 0600 to 0630 hours, and ends at 1330 to 2100 hours, varying with season, temperature, and rainfall (Nepi and Pacini, 1993). During anthesis, prevailing environmental conditions can affect the viability and vigor of GDWS pollen grains.

On the day of anthesis, insects deposit GDWS pollen grains on the stigma of the female flower (Robinson and Decker-Walters, 1997; Shivanna and Sawhney, 1997). Following successful GDWS pollination, pollen grains germinate on the

stigma, and the pollen tubes grow through the tissues of the stigma and style and then enter the embryo sac. Adequate development of pollen tubes and having enough fertilized ovules play important roles in the fruit quality (size and shape) and the quality and quantity of seeds present (Robinson and Decker-Walters, 1997; Shivanna and Sawhney, 1997). Timing of pollination is crucial. In the case of *C. pepo*, the stigma is said to be receptive for four days (-1 to 2 d after anthesis), but the ovules can be effectively fertilized and produce fruit only if pollination occurs during the first day of the anthesis of the female flower. In addition, the viability of *C. pepo* pollen drops to only 10% the day after male anthesis (Nepi and Pacini, 1993). If the same is true for *C. maxima* it is important to provide enough bees for prompt pollination and subsequent fertilization.

As mentioned previously, for effective GDWS fruit and seed set, pollination is a prerequisite. Cucurbits are cross-pollinated, and their pollination by wild bees is often difficult because of insufficient native bee populations resulting from habitat degradation and extensive use of pesticides. In addition, intensive monoculture cropping systems and a crop grown in regions where natural pollinators are absent decrease the availability of pollinators (Robinson and Decker-Walters, 1997; Shivanna and Sawhney, 1997).

Information is not available on the precise pollination requirements of GDWS, but it is probably similar to that of *C. pepo* or other winter squash types. Although honey bees are relatively poorly adapted pollinators of pumpkin and squash (because of the tubular flower, and the large size and stickiness of the pollen

grains), they are the most available and affordable species of pollinators (Crane and Walker, 1984; Free, 1993; Michelbacher *et al.*, 1964; Stanley and Linskens, 1974). There have been several reports of honey bee activity on cucurbit flowers and increases in yield following the introduction of honey bee hives in cucurbit fields (see summary in Free, 1993). Wolfenbarger (1962) demonstrated in detail the value of honey bees in pollinating squash plants. He found that the yield of caged squash plants (excluding insects) was only 19% of the yield of uncaged plants, which is surprising and may suggest self-fertility. Additionally, he found that the yield of fruit decreased with distance from a group of twenty honey bee colonies put at one end of the field. Finally, he found that there was a positive correlation between the number of honey bee colonies per hectare of field and vegetable yield. Wolfenbarger performed his studies in Florida, and the general results may not be applicable to other areas and growing zones, especially in such a different climate as that of Oregon. Also, the effect of indigenous wild bee species, or the use of commercially available bumble bees (*Bombus* spp.) as pollinators is essentially unknown.

The optimum use of honey bees as managed pollinators of pumpkin and squash in Oregon has yet to be fully determined. In the past, the activity of feral honey bees was adequate for pollination, and so the necessary studies were not done. With the advent of *Varroa* and tracheal mites in the feral honey bee populations, their colonies have been devastated (Stauth, 1997), and are no longer available to pollinate squash fields.

According to Percival (1965), honey and bumble bees visit flowers with a sugar concentration range of 10-74%. GDWS flowers have a nectar sugar concentration of about 14-16% (Chapter 2), so bees should visit pumpkin and squash flowers for nectar and pollen. However, this is a low reward (percentage of sugars) for them, so they will also visit other sources for nectar. Clemson (1985) found that pumpkin flowers do produce sufficient nectar to attract bees and have some value as a source of pollen. He also found that bees visit pumpkin and squash flowers more often when the crop is irrigated, implying that they can sense an increased reward under these conditions. Fortunately for Oregon growers, in the Willamette Valley squash is grown late in the season, and there are not many competing flowers for the bees to visit.

1.2.1 Factors Affecting Pollination

A large population of pollinators is needed for successful pollen transfer in large scale monocultures of cucurbits; otherwise, fruits may be oddly shaped (Robinson and Decker-Walters, 1997). After conducting several studies on inheritance and development of fruit shape in *C. pepo*, Sinnot (1932) found that fruit shape is more or less evident in the shape of the immature ovary, but the final shape is ultimately determined by genetic (endogenous) and environmental (exogenous) factors. Endogenous conditions are, for example, the presence of other developing fruits which retard growth, and an excessive rate of fruit growth, which causes the pollen tubes to not reach the more distant. In addition, if there is insufficient production of pollen or few grains are deposited on the stigma,

generally only the closest ovules are fertilized. In both cases, the blossom end of the fruit is stimulated to grow more than the proximal end, and the fruit is misshapen (Robinson and Decker-Walters, 1997).

Conditions that encourage the buildup of carbohydrates such as low temperature, low nitrogen supply, short photoperiod, and high moisture availability, promote female sex expression. These environmental factors influence the level of endogenous hormones (e.g. ethylene, auxin and gibberelic acid) which affect sex expression (Robinson and Decker-Walters, 1997).

In some gynoecious cultivars male flowers for pollination may be lacking. Therefore, a gynoecious hybrid needs a monoecious cultivar grown nearby to provide pollen. At this time, gynoecious cultivars of GDWS have not been developed, though there have been efforts in that (Robinson and Decker-Walters, 1997).

Temperature affects the timing of anthesis in cucurbits. Pumpkin and squash (*Cucurbita* spp.) pollen grains are released at temperatures as low as 10°C, while cucumber (*Cucumis sativus*), watermelon (*Citrulus lanatus*) and melon (*Cucumis melo*) flowers require higher temperatures for anther dehiscence. During warm summer weather when pumpkin and squash bloom, anthesis occurs early in the morning (~ 0600 hours in western Oregon), and if temperatures reach 30°C or above, pumpkin and squash flowers close (Free, 1993).

1.2.2 Pollinators of Pumpkin and Squash

1.2.2.1 Honey bees

Like most winged insects whose energy requirement is carbohydrates, honey bees need nectar for themselves, but they also need nectar and the protein from pollen to feed their brood and for the colony to survive the winter. In order to maintain and increase the size of the colony, honey bees make many more flower visits than other flower-foraging insects (Proctor *et al.*, 1996). During daylight when the weather is favorable new sources of both pollen and nectar are continually sought by foraging worker bees. For commercial production of cucurbits, honey bees are the only effective pollinator that can be currently provided in sufficient numbers for favorable pollination (McGregor, 1976b). Honey bees are not, however, very effective pollinators on an individual basis. They often actively avoid pollinating the flowers they are feeding from (Westerkamp, 1991), and on GDWS flowers, they will miss the sexual parts unless directly landing on them (personal observation).

1.2.2.2 Other bee species as pollinators

Species of *Cucurbita* are polyphilic, so they can be successfully pollinated by numerous species of insect, such as honey bees, bumble bees, carpenter bees, halictid bees, stingless bees, and bee species that are adapted specially to squash plants (Free, 1993; Hurd, 1966; Hurd *et al.*, 1974; McGregor, 1976a). Bee species of the genera *Peponapis* Robertson and *Xenoglossa* Smith (Hymenoptera:

Anthophoridae) obtain their pollen exclusively from indigenous and domestic cucurbit species, though they may obtain nectar from several other sources. Because of their association with pumpkins, squash, and gourds, they are called “squash bees” (Hurd, 1966). Both *Peponapis* and *Xenoglossa* have features adapted to cucurbit flowers, such as the ability to fly at low temperatures and at low light intensities. Squash bees are also adapted to gather and manipulate the large and sticky pollen grains: both genera have a “pollen basket” formed from an abundant, narrow band of hairs located ventrally on their abdomens where they can store large amounts of this pollen (Hurd, 1966; Stephen *et al.*, 1969). Male squash bees spend most of the day and the night in cucurbit flowers, and they carry pollen when visiting other flowers the next morning. Female squash bees also spend the night in the flowers when they have not yet nested (Free, 1993).

Xenoglossa collects pollen from flowers of *Cucurbita* at dawn, and in the early sunlight hours *Peponapis* harvests from the same flowers (Bohart, 1964; Hurd, 1966). These bees often coexist with honey bees that collect nectar from those same flowers until they close later in the day. *Xenoglossa* is not found in the Northwest (Stephen *et al.*, 1969), though *Peponapis* is. Because of their value in pollinating cucurbits, it has been suggested that species of *Xenoglossa* be introduced, selected for their compatibility to the species of cucurbit grown and the climatic and topographical characteristics of the area (Michelbacher *et al.*, 1968).

1.3 GDWS SEED PRODUCTION AND EXTRACTION

GDWS is planted in May in the Willamette Valley and is harvested in October (S. Gapp, Western Farm Services, personal communication) after the first frost, when the fruits have their characteristic mature color and when the seeds break away readily from the flesh (Mansour and Baggett, 1985). A light frost will not hurt the mature fruits and may facilitate harvesting by killing the vine and exposing the fruit; however, long exposures below 10°C or a hard freeze causes chilling injury. Cucurbit seeds will continue to develop even after the fruit is removed from the vine, and if for any reason (i.e., an impending hard frost) the fruits are harvested before they are fully mature, they can be stored for 1 to 2 months to allow for further maturing before the seeds are extracted.

Pumpkin and squash seeds need to be separated from the placental tissue (wet and adherent flesh residing in the hollow cavity of the fruit), washed and dried before they are packaged. Embedded seeds of pumpkin and squash can be removed by chopping and smashing the fruits and adding water to the mixture. The fleshy debris and poorly developed seeds will sink, and the well developed seeds will float off. For commercial seed extraction, special machinery performs these operations in the field. Other recent inventions include the seed sluice for small plots, the bulk seed extractor and the single-fruit seed extractor (Wehner and Humphries, 1995).

All these extractors function in a similar manner. After ~ 15 min of vigorous stirring, the seeds are free of flesh. The seeds are rinsed and then dried by spreading them out under warm (<35°C), dry conditions. Commercial pumpkin

and squash producers use flat drying beds or large rotary dryers and forced air warmed by propane heaters. Seeds ready for storage must have about 5% moisture content, where they snap instead of bend. Dried seeds of pumpkin and squash remain viable for as many as 10 years if they are kept in dark, airtight containers, at approximately 5°C and 25% RH (Robinson and Decker-Walters, 1997).

Pumpkin and squash seeds for consumption are processed in a similar way. The seeds are sorted by size into large “A” seeds, medium “B” seeds, and small “C” seeds. “A” seeds are the ones held on a seed sorter screen No. 28, “B” seeds pass through this screen but are held on sorter screen No. 22, and “C” seeds pass through both screens. Dried and salted A and B seeds are eaten as snack food, and C seeds are used as wild animal food (H. Ropp, Autumn Seeds Co., personal communication).

In summary, for entomophilous crops such as GDWS, insect pollination is a critical component of seed production (Free, 1993; McGregor, 1976a; Mel'nichenko, 1976). The lack of information about the relative value of honey bee densities and area efficiency and the role of wild bees in pollinating pumpkin and squash for seed, presents an opportunity for a controlled study. This will document the relative efficiency of honey bees and bumble bees and report the wild bee pollinating cohort related to pumpkin and squash seed production in western Oregon.

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2. NECTAR AND POLLEN PRODUCTION IN *CUCURBITA MAXIMA* DUCHESNE (CUCURBITACEAE)

2.1 ABSTRACT

The nectar and pollen production, and the nectar sugar concentration of 'Golden Delicious' winter squash (GDWS), *Cucurbita maxima* Duchesne, were evaluated under field conditions in the Willamette Valley, in western Oregon. Nectar and pollen production were evaluated in separate commercial GDWS fields. The quantity of nectar and pollen produced per GDWS flower differed significantly between sites. Both the amount of nectar and concentration of nectar sugars were also significantly different between male and female GDWS flowers, with females producing 246 μ l of nectar with 12.57% total soluble solids, and males producing 128 μ l of nectar with 15.62% total soluble solids. There was no significant difference in the percent of nectar sugar per GDWS flower between sites. The interaction, however, between site and floral sex was significant for both quantity and quality (% sugars) of nectar per flower. Fresh weight of pollen averaged 24.15 mg per GDWS male flower.

2.2 INTRODUCTION

Cucurbita maxima Duchesne (Cucurbitaceae) is an annual, prostrate vine with long trailing branches that is native to South America. A variety of *C. maxima*, 'Golden Delicious' winter squash (GDWS) is widely cultivated in areas

with relatively cool climates such as the Willamette Valley in Oregon, though it is susceptible to frost kill (Robinson and Decker-Walters, 1997; Whitaker, 1977).

In GDWS, pollen must be transferred from a male to a female flower by insects to fertilize and set fruit. Bees are the main pollinators of GDWS. Honey bees are the only generally available and affordable bee species used commercially for pollination of this crop, and several publications report an increased yield in squash after using honey bees (Crane and Walker, 1984; Free, 1993; McGregor, 1976; Robinson and Decker-Walters, 1997). Melendez-Ramirez *et al.* (1996) reported that the number and weight of fruit increases in proportion to the amount of pollen deposited on the stigmas in *C. pepo*. This closely related species produces ~16,500 large pollen grains and ~93 μl of nectar per male flower, and ~118 μl of nectar per female flower (Nepi and Pacini, 1993).

Knowledge of the amounts of nectar and pollen available in specific monocultures is crucial for apiculturists to calculate the number of honey bee colonies to place for pollination. Once the amount of pollen and nectar, and the loads of pollen per bee are known, we can theoretically calculate the number of hives per hectare of crop. If we know the quantity and quality (percent sugars) of the nectar, we can determine the relative attractiveness of the crop to bees (Corbet, 1978; Percival, 1965). Corbet (1978) documented that the amount and composition of floral nectar can vary from hour to hour and from day to day in *Echium vulgare* (Boraginaceae). This is partially explained by the activities of the nectaries (secretion or reabsorption), equilibration with the humidity of the air (evaporation

or condensation), and removal of nectar by the insects. These aspects can also be species- and cultivar-specific (Bahadur *et al.*, 1986; Cane and Schiffhauer, 1997). According to Bahadur *et al.* (1986), the nectar production varied among four species of *Kalanchoe* (Crassulaceae) in relation to temperature, time of day and plant moisture content. Nectar secretion was greater at 1530 hours when the moisture content and temperature were relatively high. At 0630 hours (blooming time), there was no nectar production. Nothing has been published about factors affecting nectar and pollen production in *C. maxima*. Shaw (1953) found that sugar content in nectar of *C. maxima* ranges from 18-38 % with an average of 30 %.

Pollination requirements of some tropical crops (such as the cucurbit in this study) have not been well studied. We do not know whether inadequate pollination is a significant restriction to their yields (Crane and Walker, 1984), but what little we know about the pollination biology of GDWS indicates that it does require abundant pollinating. Free's discussion (1993) is a general reference for pumpkin and squash pollination.

Faegri and van der Pijil (1979) give very little information about cucurbits, except to mention some examples of relationships between pollinators and cucurbits. Kapil (1986) discusses the pollination of cucurbits in general but says little about *C. maxima*. McGregor (1976) discusses the plant, inflorescence, pollination requirements, pollinators and pollination recommendations and practices for *Cucurbita* spp. This provides a good general view of pollination in pumpkin and squash, but not specifically for *C. maxima*. Real (1983) compiled a

volume with a great number of pollination studies, but little is mentioned about pumpkin and squash.

Mindful of the dearth of specific information available about GDWS pollination, in this study we examine and measure the total secreted nectar and percentage sugars from both male and female flowers of 'Golden Delicious' winter squash, and the total fresh pollen weight from male flowers.

2.3 MATERIALS AND METHODS

2.3.1 Nectar Samples

GDWS nectar production was studied in 1996 in two commercial GDWS fields located in the central Willamette Valley of Oregon. One site (Independence) was located at Independence Rd., Corvallis, Oregon (44°38'16"N-123°11'5"W) and the other site (Riverside-1), at Riverside Dr., Albany, Oregon (44°36'5"N-123°9'35"W). These two fields were ~8 km apart and because of their proximity, weather conditions were assumed to be the same.

The Independence site was planted on May 18 and Riverside-1 on May 21. Both sites were fertilized similarly, and irrigated approximately every 10 days after planting until mid-August (S. Gapp, Western Farm Service, Inc., personal communication). Both sites used sprinkler irrigation, with Independence having wheel lines and Riverside-1 having on-hand lines.

On August 11, 1996, 40 male GDWS flowers and 40 female GDWS flowers that were to have anthesis that day were selected from throughout the Independence

site. On August 1 and again on August 13, the same number of male flowers and female flowers were similarly selected from the Riverside-1 site. At 0600 hours, the selected flowers were covered with brown bags that were stapled closed to exclude insects. This time was chosen because it was before the flowers had opened and before insects could gather the nectar. The flowers were picked at 1500 hours on the same day and transported in a cooler to the laboratory. By then, the flowers had time to fully develop, and produce all the nectar for that day.

In the laboratory, 10, 20 or 100 μ l micropipettes were inserted into the floral nectaries, to withdraw and measure the nectar. The nectar was then deposited into 0.5 ml stoppered microvials and kept refrigerated between 5-10°C. The next day, the concentration of soluble solids (sugars) was measured using an Auto Abbe model 10500 refractometer (Leica Inc.).

2.3.2 Pollen Samples

GDWS pollen production was studied in 1997 in three commercial fields located in the central Willamette Valley in Oregon. One site (Spring Hill) was located at Spring Hill Dr., Corvallis (44°42'10"N-123°8'45"W), another (Riverside-2) at Riverside Dr., Albany (44°36'5"N-123°9'35"W), and the last (Lakeside) at Lakeside Rd., Monroe (44°24'51"N-123°15'15"W). Riverside-2 was the same location as Riverside-1 from the previously described nectar study, though a different field was used.

Spring Hill was planted on May 21, Riverside-2 on May 25 and Lakeside on June 6. These fields were located within 25 km of each other, and as before,

because of their proximity, weather conditions were assumed to be the same.

Fertilization and irrigation procedures were similar to those of the nectar study with all sites using overhead sprinklers. Spring Hill had wheel lines, Riverside-2 had on-hand lines and Lakeside had a center-pivot irrigation system.

On August 19, 1997, 40 male GDWS flowers were selected and bagged at 0600 hours from throughout the Lakeside site, using the same procedure as the nectar study. The next day, the same number of male GDWS flowers were similarly selected from both Spring Hill and Riverside-2 sites. Again, this time was chosen because it was before the flowers had opened and before insects could gather the pollen. The flowers were picked at 1500 hours on the same day and transported in a cooler to the laboratory.

In the laboratory, the pollen was collected from the flowers by carefully removing the petals from each flower, leaving the anthers exposed. Using a fine brush, the pollen was brushed onto a previously tared piece of wax paper. The pollen samples were weighed with a Mettler AC 100 digital-balance with 0.1 mg precision.

2.3.3 Data Analysis

Total amount of nectar, percent of soluble solids, and total fresh pollen weight per flower were analyzed with a fixed-model general linear model analysis of variance (GLM ANOVA, NCSS 7.0 for Windows). When treatment differences were significant ($p \leq 0.05$), Tukey-Kramer's multiple comparison test ($\alpha = 0.05$) was used (Hintze, 1998).

2.4 RESULTS AND DISCUSSION

2.4.1 Nectar Production

The quantity of nectar produced per GDWS flower differed between sites ($p < 0.0001$, GLM ANOVA, Appendix A). The average nectar production per flower at the Independence site (mean \pm 1 SE) of $311 \pm 20 \mu\text{l}$ was nearly double that of the Riverside-1 site ($161 \pm 14 \mu\text{l}$) (Figure 2.1). The amount of nectar was also different between male and female GDWS flowers ($p < 0.0001$, GLM ANOVA) (Figure 2.1). An average female GDWS flower produced $319 \pm 17 \mu\text{l}$ of nectar, which was double than the production of an average male GDWS flower of $153 \pm 17 \mu\text{l}$.

The interaction between site and floral sex was statistically significant for the amount of nectar ($p = 0.00013$, GLM ANOVA, Appendix A). In Independence, female GDWS flowers produced on average 184% more nectar than male flowers (female = $443 \pm 29 \mu\text{l}$ and male = $156 \pm 29 \mu\text{l}$), but in Riverside-1, an average female flower produced only 54% more nectar than an average male flower (female = $195 \pm 20 \mu\text{l}$ and male = $127 \pm 20 \mu\text{l}$) (Figure 2.1, Appendix A). The large nectar production by female flowers at Independence site accounted for most of the site differences in nectar production.

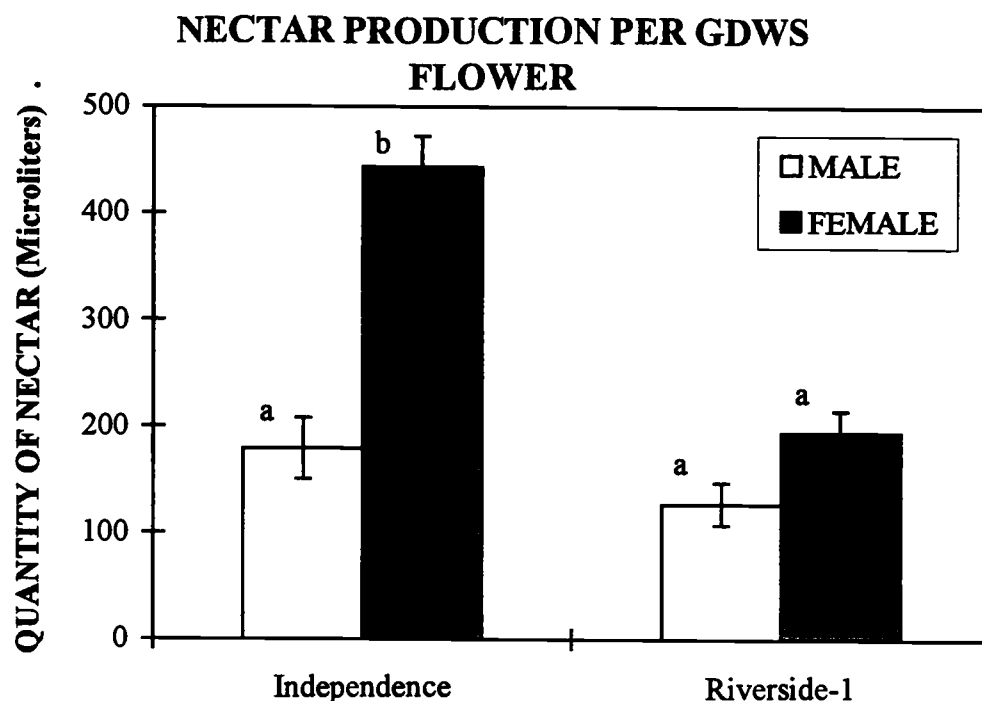


Figure 2.1 Quantity (mean \pm 1 SE μ l) of nectar produced per flower in *Cucurbita maxima* Duchesne var. 'Golden Delicious', 1996. (a is different from b at $\alpha = 0.05$, Tukey-Kramer Multiple-Comparison Test).

2.4.2 Nectar Quality

The concentration of nectar sugars of male and female flowers of GDWS differed ($p < 0.0005$, GLM ANOVA, Appendix A). The average sugar concentration in GDWS male flower was 25% higher than in female flower, with $15.62 \pm 0.61\%$ for male and $12.57 \pm 0.60\%$ for female flower (Figure 2).

There was no difference in the percent of nectar sugars per flower between Independence ($14.38 \pm 0.59\%$) and Riverside-1 sites ($13.81 \pm 0.62\%$) ($p = 0.5063$, GLM ANOVA, Appendix A), but the interaction between site and floral sex was

statistically significant ($p = 0.0319$, GLM ANOVA, Appendix A). At Independence, GDWS male flowers had 41% more nectar sugars than female flowers ($16.83 \pm 0.83\%$ versus $11.93 \pm 0.83\%$ sugars respectively), but at Riverside, GDWS male flowers had only 9% more nectar sugars than female flowers ($14.41 \pm 0.89\%$ versus $13.21 \pm 0.86\%$ sugars respectively) (Figure 2.2).

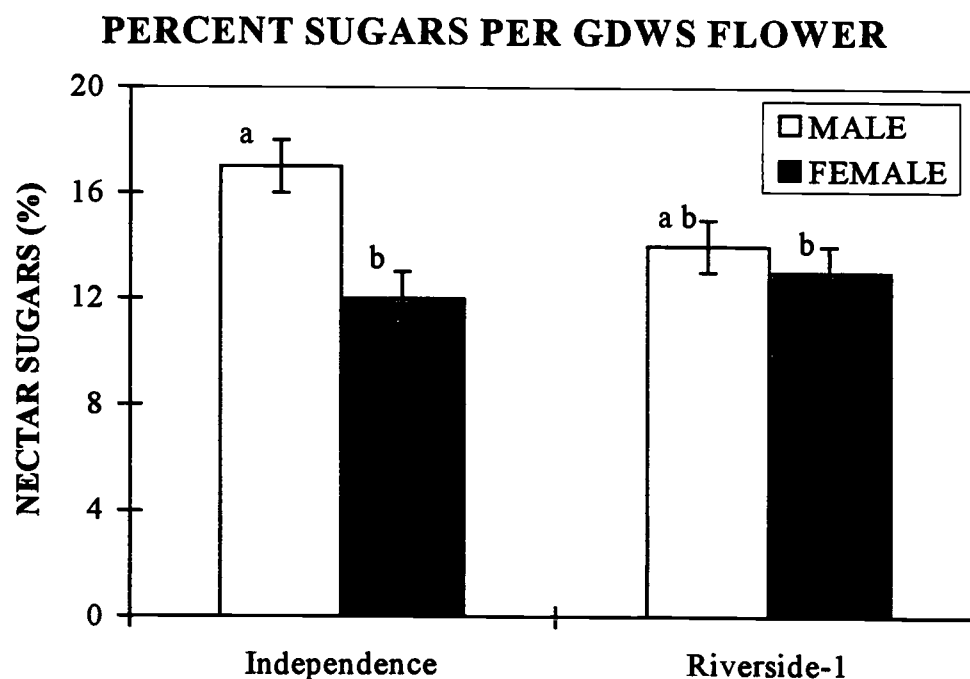


Figure 2.2 Quality (mean \pm 1 SE % sugars) of nectar produced per flower in *Cucurbita maxima* Duchesne var. 'Golden Delicious', 1996. (a is different from b at $\alpha = 0.05$, Tukey-Kramer Multiple-Comparison Test).

2.4.3 Pollen Production

Pollen production averaged 24.15 mg per GDWS male flower. The production of pollen per flower differed between sites ($p = 0.0018$, GLM ANOVA, Appendix A). Spring Hill and Riverside-2 sites were similar in pollen production per flower, 23.00 ± 1.78 mg and 20.21 ± 1.78 mg respectively (Figure 2.3; Appendix A), but in Lakeside GDWS flowers produced 27% more pollen per flower (29.23 ± 1.80 mg) than of Spring Hill, and 45% more than Riverside-2 ($\alpha = 0.05$, Tukey test).

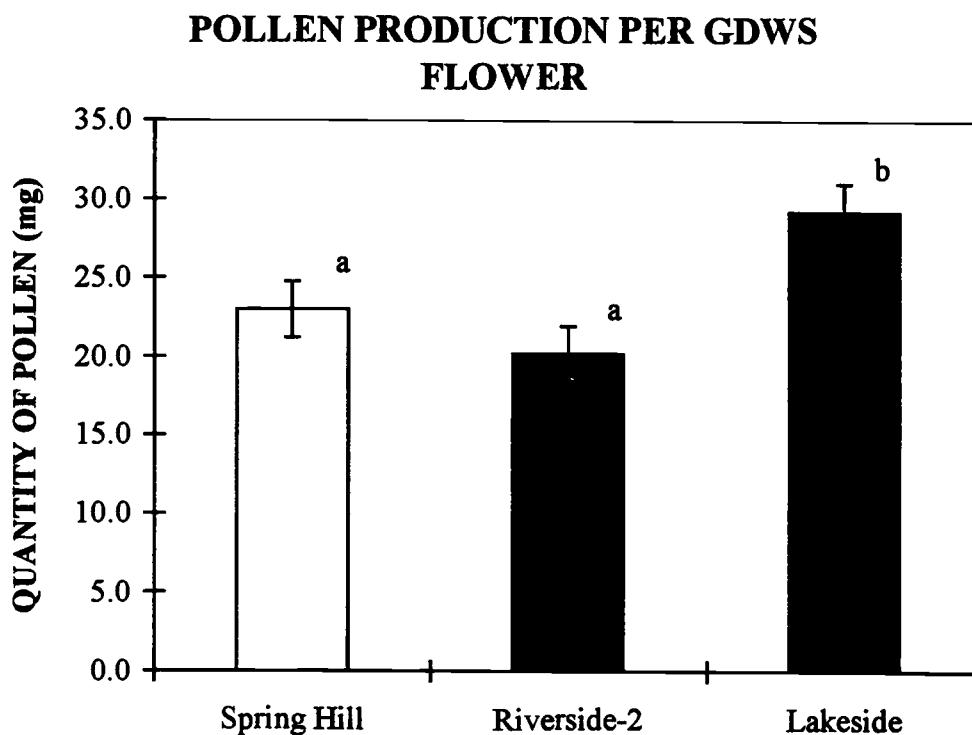


Figure 2.3 Pollen (mean \pm 1 SE mg) produced per male flower in *Cucurbita maxima* Duchesne var. 'Golden Delicious', 1997. (a is different from b at $\alpha = 0.05$, Tukey-Kramer Multiple-Comparison Test).

GDWS provides significant amounts of pollen (24 mg) and nectar (236 μ l), but with a low reward of 14% nectar sugar, according to Percival's (1965) classification. This level of sugars concentration was lower than the 30% found by Shaw (1953) in *C. maxima*. GDWS female flowers produced more nectar (319 μ l) with a lower sugar concentration (13%) than males (153 μ l of nectar and 16% sugars). The amount of nectar produced by each GDWS flower (236 μ l) is more than double that of the amount produced by *C. pepo* (105 μ l, (Nepi and Pacini, 1993), and GDWS had a higher sugar concentration in the male flower than in the female flower, contrary to Nepi and Pacini's 1993 findings on *C. pepo*.

According to Percival (1965), honey and bumble bees are found visiting flower species with a sugar concentration range of 10-74%. Though bees would visit pumpkin and squash flowers for nectar and pollen; they would also visit other sources for nectar because the nectar of pumpkin and squash offers such low rewards. Clemson (1985) mentions that bees visit pumpkin and squash flowers more frequently when they are grown under irrigation than when grown under normal conditions, however he offers no explanation as to why.

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3. SEED PRODUCTION IN *CUCURBITA MAXIMA* DUCH. (CUCURBITACEAE) WHEN POLLINATED BY HONEY BEES AND BUMBLE BEES

3.1 ABSTRACT

The pollination efficiency of 'Golden Delicious' Winter Squash (GDWS), *Cucurbita maxima* Duchesne (Cucurbitaceae) by honey bees (*Apis mellifera* L. (Hymenoptera: Apidae)) and bumble bees (*Bombus occidentalis* Greene (Hymenoptera: Apidae)) was evaluated under field conditions in the Willamette Valley, in western Oregon. In the summer of 1996 and again in 1997, nine 1.8x1.8 m cages were randomly assigned in three blocks of three treatments. These treatments were 1 hive of >2500 honey bees, 1 colony of 50 – 100 bumble bees, and no insects in the first year, and honey bees, bumble bees, and 1500 western spotted cucumber beetles (WSCB) (*Diabrotica undecempunctata undecempunctata* Mannerheim (Coleoptera: Chrysomelidae)), in the second year.

The WSCB and insect exclusion cages produced no fruit, indicating that western spotted cucumber beetles do not pollinate GDWS. After harvesting, GDWS seeds from the honey bee and bumble bee cages were classified in decreasing size as "A", which are seeds held on a seed sorter screen No. 28, "B" seeds which passed through this screen but were held on sorter screen No. 22, and "C" seeds that passed through both screens. A and B seeds are packaged for human consumption, and C seeds are used as wild bird and squirrel feed. Six dependent variables were considered for analysis, considering that growers could

use these to evaluate pollination of GDWS. These variables were number of fruit per cage, weight of fruit, weight of 100 random seeds, weight of A seeds, weight of B seeds, and weight of C seeds.

There is insufficient evidence to state that either honey bees or bumble bees were more efficient in pollinating GDWS. Results suggest that the number of bees contained within each cage was more than sufficient for full pollination. More studies need to be done under field conditions in order to have a better and long-term estimation on GDWS pollination efficiency. More cage experiments with fewer bees per cage would also be helpful to determine the per-bee and per-colony pollinating efficiency of honey bees and bumble bees.

3.2 INTRODUCTION

Golden Delicious Winter Squash (GDWS), a variety of *Cucurbita maxima* Duchesne (Cucurbitaceae), is an annual, prostrate vine with long trailing branches. Though it is native to the warm climates of South America and is susceptible to frost kill (Robinson and Decker-Walters, 1997; Whitaker, 1977), it is widely cultivated in areas with relatively cool climates, such as the Willamette Valley in western Oregon. Flowers of *C. maxima* are 6 to 12 cm across, opening early in the morning, and lasting for one day or less depending on factors such as temperature and relative humidity. The ratio of male to female flowers in *Cucurbita* is generally 10:1 (Free, 1993; McGregor, 1976; Crane & Walker, 1984). Male flowers have three anthers and produce large, spherical, spiny and sticky pollen

grains. Female flowers have a three lobed stigma (Crane and Walker, 1984; Free, 1993; McGregor, 1976).

GDWS is a monoecious plant, and pollen must be transferred from a male to a female flower in order for it to be fertilized and to set fruit and seeds (Crane and Walker, 1984; Free, 1993; Jaycox *et al.*, 1975; McGregor, 1976). Bees are the main pollinators of pumpkin and squash (Crane and Walker, 1984; Robinson and Decker-Walters, 1997). Under greenhouse conditions pollination of these crops is usually done by hand (Bewley, 1963), and in fields either by native or periodically introduced insects such as bumble bees (*Bombus* spp.) or honey bees (Proctor *et al.*, 1996).

Honey bees are relatively poorly adapted pollinators of pumpkin and squash because of the tubular shape of the flower, and the large size and stickiness of the pollen grains (Crane and Walker, 1984; Free, 1993; Stanley and Linskens, 1974), but are the most important commercial pollinators, because they are the most available and affordable species (Crane and Walker, 1984; Free, 1993; Michelbacher *et al.*, 1964; Stanley and Linskens, 1974). Many publications report honey bee activity on cucurbit flowers and a resultant increase in yield after introducing honey bee hives in cucurbit fields (see summary in Free, 1993; also Hurd *et al.*, 1971; Michelbacher *et al.*, 1964; Wolfenbarger, 1962).

Numerous other insects, mostly in the orders of Hymenoptera, Diptera and Coleoptera have been recorded visiting and pollinating cucurbit flowers. Durham (1928) gave some credit to the striped cucumber beetle, *Acalymma vittatum* (F.)

(Coleoptera: Chrysomelidae), as a pollinator of summer squash; Tontz (1944) credited ants; and Fronk and Slater (1956) attributed it to the wild bees, *Peponapis* spp. and *Xenoglossa* spp. (Hymenoptera: Anthophoridae), with a minor role played by spotted cucumber beetles (*Diabrotica* spp.; Coleoptera: Chrysomelidae). Hurd (1966) thought that insects other than honey bees, such as flies, moths, and cucumber, scarab and meloid beetles, are also involved in pollination of *Cucurbita* species, but to a lesser extent.

The economic products of GDWS are seeds and fruit, and low yields are often the result of insufficient pollination. Effective management of pollinating agents is crucial to improving yields. There are several commercial pollinator options now available for the grower, but proper selection requires a thorough knowledge of both the crop and the pollinators (Shivanna and Sawhney, 1997).

Though many studies have been done on the pollination of orchards and other crops grown under field and greenhouse conditions (Kearns and Inouye, 1993; Torchio, 1990), little information is available on the pollination of GDWS. Here, we study yields of GDWS fruit and seeds when pollinated by honey bees, bumble bees and cucumber beetles contained in field cages.

3.3 MATERIALS AND METHODS

GDWS fruit and seed production when pollinated by honey bees (*Apis mellifera* L. (Hymenoptera: Apidae)), bumble bees (*Bombus occidentalis* Greene (Hymenoptera: Apidae)), western spotted cucumber beetles (*Diabrotica undecimpunctata undecimpunctata* Mannerheim (Coleoptera: Chrysomelidae)), or

no insects, was studied during the summers of 1996 and 1997 in two commercial GDWS fields located in the central Willamette Valley of Oregon. These fields (Riverside-1 = 10 ha, and Riverside-2 = 20 ha) were located at Riverside Dr., Albany (44°36'5"N-123°9'35"W). Riverside-1 was planted on May 21, 1996 and Riverside-2 on May 25, 1997.

3.3.1 Field Cages

Three replications in a randomized block experimental design each containing three cages of 1.8x1.8 m were selected each year from within the commercial fields. In 1996 the treatments were (1) no insects, (2) honey bees (1 nucleus colony per cage with at least 2500 adult worker bees), and (3) bumble bees (1 colony per cage with about 50-100 worker bees). In 1997, the treatments were (1) spotted cucumber beetles (about 1500 adults), (2) honey bees, and (3) bumble bees.

Cages of sixteen-mesh nylon, 1.8(L)x1.8(W)x1.5(H) m were used to exclude insects other than those used in treatments, and to contain the treatment insects. On July 10, 1996 the nine cages were placed in the Riverside-1 field, and on July 5, 1997, in the Riverside-2 field, just before the GDWS started to bloom. The honey bees, bumblebees and spotted cucumber beetles were introduced as soon as GDWS started blooming, and were left caged for 35 days. All existing blossoms were removed when the treatments were introduced.

3.3.2 Cage Samples

In October, when the fruits were fully developed, they were cut from the vines and left in the field for one week to fully mature. As per industry practice, this allows more uniform development of the fruits and a more efficient harvest. After the week, each fruit was individually labeled with block number, cage number, and fruit number. They were transported to the Oregon State University Vegetable Research Farm, to process the fruit and seeds.

The GDWS seeds were separated from each fruit and put in a labeled bucket. Enough water to cover the seeds was added and after 15 min of vigorous stirring and rubbing, the seeds were free of spongy placental material. The seeds were rinsed and then dried by spreading them out under warm (~35°C), dry conditions.

Of the seeds collected from each fruit, 100 seeds were randomly selected and weighed on a Mettler PN 1210 digital balance with a 0.01-gram sensitivity. All seeds from each fruit were then separated into “A-” “B-” and “C-seed” classes according to industry practice. An Exact model 628 seed sorter combined with a Tecron model 5530 power supply amplifier were used with size 28 and 22 screens (Appendix C). The larger A-seeds remained on top of the size 28 screen, the medium size B-seeds passed through the 28 screen but remained on the size 22 screen, and all the small seeds that passed through both screens were classed as C seeds. The A, B, and C seeds were weighed separately using the same balance as for the “100 seeds” weight.

To evaluate the pollination efficiency by the different insects, 19 dependent variables were considered (Appendix B). After preliminary examination, the following variables were selected for further evaluation:

- (1) Number (n) of fruit per cage. The fully mature orange fruits in each cage were counted, and all immature green fruits were disregarded.
- (2) Fruit weight (Kg). Total weight of all mature fruits in each cage before the seeds were extracted.
- (3) Weight (g) of 100 seeds. The average weight of 100 dried, cleaned, and fully developed randomly chosen seeds from all the mature fruits in each cage.
- (4) Weight (g) of “A” seeds. The weight of dried, cleaned, and fully developed “A” seeds from all the mature fruits in each cage.
- (5) Weight (g) of “B” seeds. The weight of dried, cleaned, and fully developed “B” seeds from all the mature fruits in each cage.
- (6) Weight (g) of “C” seeds. The weight of dried, cleaned, and fully developed “C” seeds from all the mature fruits in each cage.

3.3.3 Data Analysis

Although data were collected from each fruit separately, the experimental unit was a cage and data of individual fruits from that cage were combined. The latter six variables were analyzed with multiple-analysis of variance after $\log(x+1)$ transformations (MANOVA, NCSS 97 for Windows). When treatment differences were significant ($p \leq 0.05$), the multiple-comparison factor Tukey-Kramer's test ($\alpha = 0.05$) was used (Hintze, 1998).

3.4 RESULTS

The insect exclusion treatment and the western spotted cucumber beetle treatment produced no fruit. These treatments were not included in any further analysis.

In 1996, GDWS pollinated by bumble bees produced 1.78 times more fruits, and 1.87 times more total fruit weight per cage than those pollinated by honey bees (Figures 3.1a & 3.1b, Appendix D), but in 1997, the honey bee treatment produced 1.19 times more fruits and 1.17 times more fruit weight than the bumble bee treatment. The number of GDWS fruit produced by honey bees was 1.84 times higher in 1997 than in 1996, but the number of fruit produced by bumble bees in 1997 was only 0.87 times that of 1996.

The honey bee and bumble bee treatments were analyzed with MANOVA, and no significant differences were found except for the interaction between bee treatment and year on number of fruit per cage ($p = 0.0421$) (Appendix D). This significant difference reflects the increase in fruit number produced by honey bees in 1997.

The mean weight of 100 seeds was more even between treatments, with GDWS pollinated by bumble bees producing 1.08 times more weight per 100 seeds in 1996 than those pollinated by honey bees, and only 1.01 times more in 1997 (Figure 3.1c).

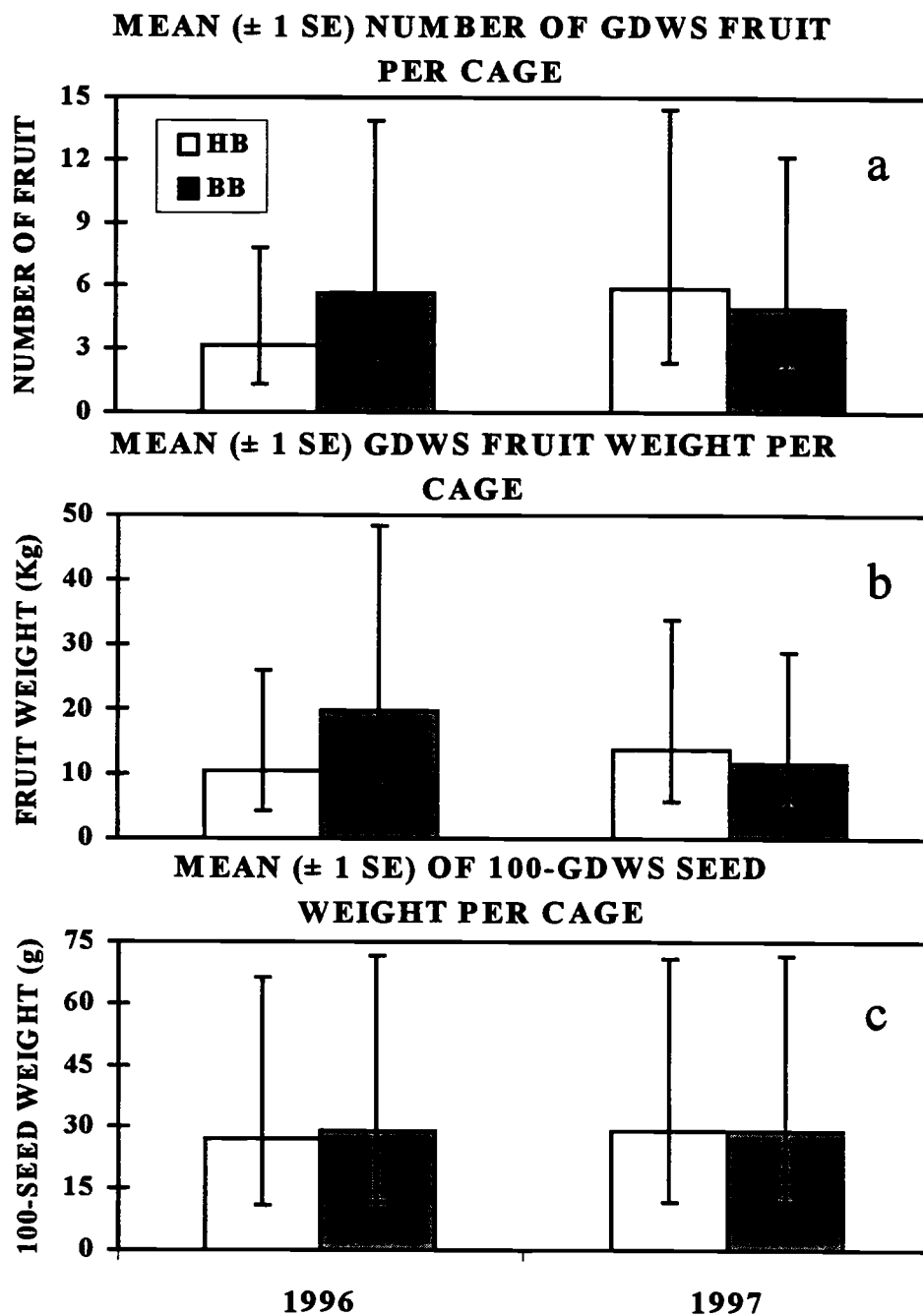


Figure 3.1 Means (\pm 1 SE) of the (a) total number of fruit, (b) total weight (Kg), and (c) total weight (g) of 100 seeds of GDWS, *Cucurbita maxima* Duchesne var. Golden Delicious, within the honey bee and bumble bee treatment cages. Means are from MANOVA, back-transformed from $\log(x+1)$.

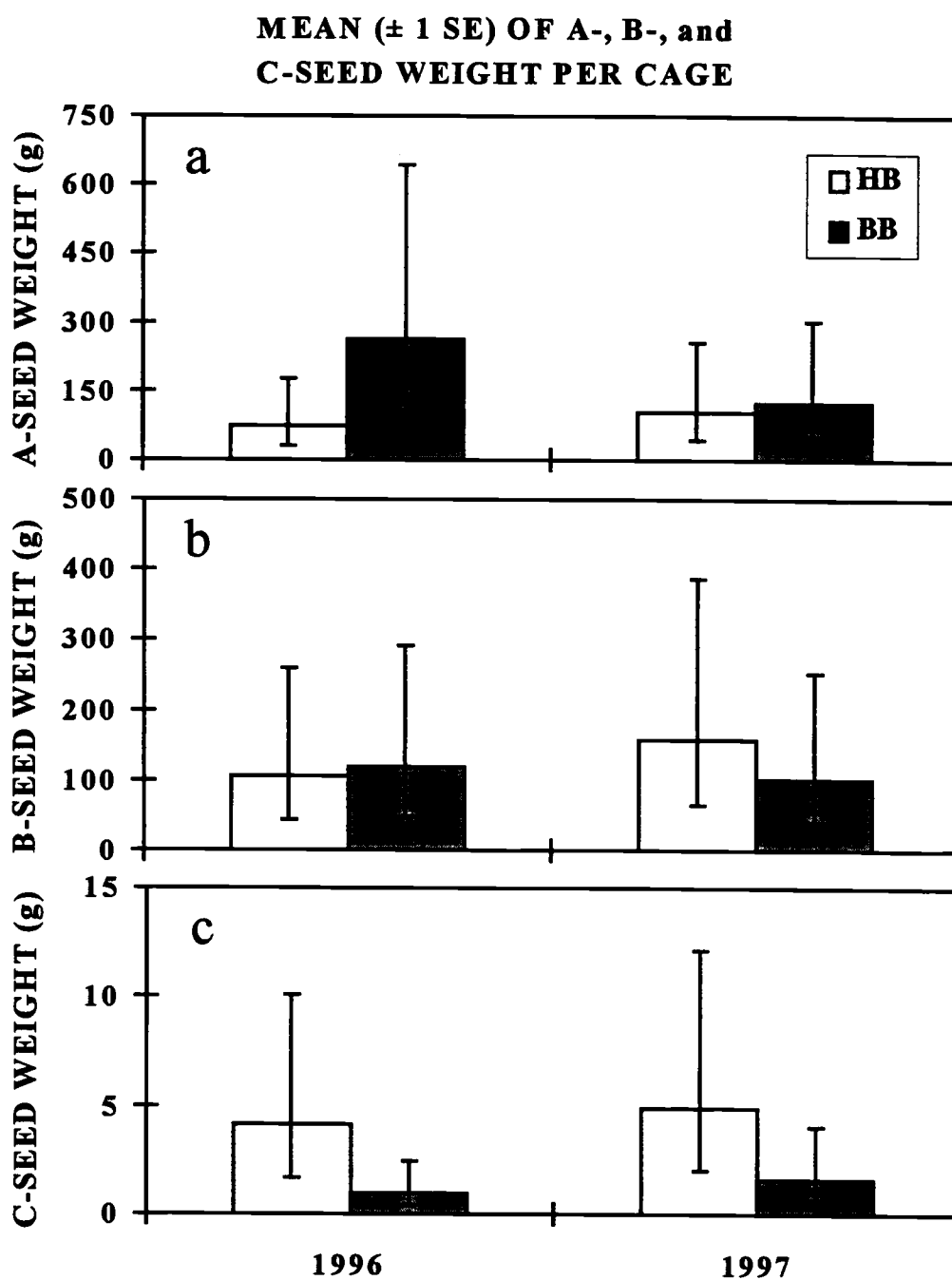


Figure 3.2 Mean (\pm 1 SE) of the total weight (g) of A, B, and C seeds produced by GDWS within the honey bee and bumble bee treatment cages. Means are from MANOVA, back-transformed from $\log(x+1)$.

Bumble bee pollinated GDWS produced more A seeds per cage by weight than did those pollinated by honey bees in both years. In 1996 bumble bees produced 3.66 times more A seeds by weight than did honey bees, and in 1997, 1.18 times more (Figure 3.2a). Conversely, in 1996, bumble bee pollinated GDWS produced 1.12 times more B seeds per cage by weight than did those pollinated by honey bees (Figure 3.2b), but in 1997, honey bees produced 1.54 times more. Honey bee pollinated GDWS produced more C seeds per cage than bumble bee pollinated squash did in each year: 4.10 times more in 1996 and 3.00 times more in 1997 (Figure 3.2c). None of these treatment differences, however, were significant.

3.5 DISCUSSION

It is no surprise that the insect exclusion and WSCB treatments produced no fruit. Durham (1928), Fronk and Salter (1956), and Hurd (1966) all suggested that cucumber beetles pollinate squash, but we felt that this was unlikely, due to their smooth cuticle which does not pick up pollen well, and their low mobility between flowers. That 1500 beetles pollinated no flowers in such a small enclosure introduces doubt that they are capable of pollinating at all, and certainly not on a large scale.

It was more surprising that the honey bee and bumble bee treatments showed no significant differences in any of the variables when viewed from the results of two years. During the treatment time, numerous honey bees were seen clinging to the top of the cage, apparently trying to escape. It appeared that they were not foraging (pollinating) with any great efficiency, while the bumble bees

were seen on the flowers, and generally not on the cage walls and ceiling. For these reasons, we expected to find that bumble bees would be the better pollinators under caged conditions. It is probable, given the large number of honey bees present relative to bumble bees, that they made up with numbers what they lacked in efficacy.

Overall, bumble bee pollinated GDWS produced 1.23 times more fruit, 1.26 times more fruit weight, and 2.08 times more A seeds by weight than those pollinated by honey bees. 100 seeds also weighed 1.04 times more in the bumble bee cages. Honey bee pollinated GDWS produced, on a two year average, 1.17 times more B seeds by weight and 3.51 times more C seeds by weight than those pollinated by bumble bees. It would appear from these results that bumble bees are better pollinators in some ways (Stanghellini *et al.*, 1998), but not in all aspects.

Though no variable showed significant differences, it is interesting that the bumble bee treatment consistently produced more A seeds per cage (bumble bees = 179 g vs. honey bees = 86 g), and the honey bees more C seeds per cage (honey bees = 4.5 g vs. bumble bees = 1.3 g). More testing would be necessary to determine whether this is a chance occurrence, or that bumble bees truly do produce more high-quality seeds in GDWS through more effective pollination.

The size of the experiment may not have had enough power to show a difference between the pollinator species. If another experiment shows this, or another species of bumble bees to be slightly more efficient on a per-colony basis than honey bees, they would still not be a commercially viable solution for GDWS

pollination. The colonies are currently very expensive: approximately 4-5 times the price of honey bee hives used for GDWS (>\$150 vs. approximately \$35 per colony, respectively). If bumble bee colonies are placed in GDWS fields at the same density as honey bee hives (a plausible rate considering the results of this study), they would likely not produce a crop that would pay for the added expense. For the foreseeable future, honey bees will likely remain the only viable commercial pollination option for GDWS.

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4. THE EFFECT OF HONEY BEE HIVE DISTANCE ON POLLINATION AND SEED PRODUCTION IN *CUCURBITA MAXIMA* DUCHESNE (CUCURBITACEAE)

4.1 ABSTRACT

Honey bees have an effective foraging range of 1-3 km from the hive, but does their pollination efficacy drop off significantly before this distance?

Pollination of 'Golden Delicious' winter Squash (GDWS), *Cucurbita maxima* Duchesne, was studied in plots that were located between 15 and 450 m from the closest group of honey bee (*Apis mellifera* L. (Hymenoptera: Apidae)) hives, at commercial GDWS fields in the Willamette Valley in western Oregon. Six variables (number of fruit, total fruit weight, the weight of 100 seeds, and A-, B-, and C-seeds weight) were analyzed to determine the effect of distance on the pollination of GDWS by honey bees.

The six variables were analyzed with multiple regression analysis, which were significant ($p \leq 0.05$) only for the weight of B- and C-seeds (the medium and small sizes, respectively). These were reduced in the plots that were farthest from the nearest group of honey bee hives. The results suggest that positioning of honey bee hives in squash fields of ≤ 120 ha in the Willamette Valley appears not to be critical for adequate pollination.

4.2 INTRODUCTION

Pollination of 'Golden Delicious' winter Squash (GDWS), *Cucurbita maxima* Duchesne (Cucurbitaceae), as with other cucurbits, depends on the mechanical transportation of pollen between flowers. This is because *C. maxima* is monoecious (the male and female organs are borne on different flowers on the same plant), and the pollen is too heavy and sticky to be carried by wind (Crane and Walker, 1984; Free, 1993; Jaycox *et al.*, 1975; McGregor, 1976a).

Many publications report honey bee activity on cucurbit flowers and a resultant increase in yield after the introduction of honey bee hives in cucurbit fields (see summary in Free, 1993; also Hurd *et al.*, 1971; Michelbacher *et al.*, 1964; Wolfenbarger, 1962). Honey bees are relatively poorly adapted pollinators of pumpkin and squash because of the tubular shape of the flower, and the large size and stickiness of the pollen grains (Crane and Walker, 1984; Free, 1993; Stanley and Linskens, 1974). Nevertheless, they are the most important commercial pollinators, because they are the most available and affordable species (Crane and Walker, 1984; Free, 1993; Michelbacher *et al.*, 1964; Stanley and Linskens, 1974).

Commercial squash growers place honey bee hives in their fields when their plants bloom in order to improve fruit and seed production (Robinson and Decker-Walters, 1997). For a pollination program in a pumpkin or squash crop, a stocking rate of 1-3 honey bee hives per ha is recommended by various authorities (Clemson, 1985; Free, 1993; McGregor, 1976a), though others have shown increasing yield in cucurbits with up to seven or more hives per ha (Wolfenbarger,

1962). Bees visit hundreds of flowers to obtain a load of pollen or nectar, and limit their foraging to one species of plant per flight.

Honey bees have an effective foraging range of 1-3 km from the hive, and are capable of flying 8-14 km each way when pollen and nectar sources are scarce (Clemson, 1985). These distances represent maximums, whereas the pollinating range of honey bees can be much less, depending on the crop. In an agricultural crop with rich rewards for the foraging bees, they will forage at (and pollinate) only the closest flowers. As the nearby flowers are pollinated and their reward reduced, the bees may eventually get to the farthest flowers. At harvest, a well-pollinated field exhibits uniformly developed fruits. If parts of the crop are pollinated later than others, there will be variability in the maturity of the crop, with the underdeveloped fruits bringing fewer returns for the grower.

If the effective pollinating distance of honey bees is less than their maximum foraging distance, knowledge of this distance would help growers and beekeepers place honey bee hives more efficiently in GDWS fields. Would honey bees be effective pollinators of GDWS across large fields, or are they limited to closer distances? Is it acceptable to simply place all of the requisite hives in an easily accessible corner of the field, or would it be better (though more tedious) to distribute the hives more evenly? It has been suggested that nearby hives are more effective (McGregor, 1976b; Wolfenbarger, 1962), but would the economic benefits of distributed hives offset the cost and extra work? The answers to these questions are not known for GDWS.

In this study, six variables (number of fruit, total fruit weight, the weight of 100 seeds, and A-, B-, and C-seeds weight) were analyzed to determine the effect of distance from the nearest group of hives on the pollination of GDWS by honey bees.

4.3 MATERIALS AND METHODS

Fruit and seed production of GDWS affected by distance from hives of honey bee (*Apis mellifera* L. (Hymenoptera: Apidae)) was studied in the summers of 1996 and 1997 in five commercial GDWS fields in the central Willamette Valley in western Oregon.

4.3.1 Field Plots

Plots were established in five fields, of which two (Independence and Riverside-1) were planted in 1996, and the other three in 1997. All fields were within 25 km of each other: because of their proximity, weather conditions were assumed to be the same within years.

The Independence site was located at Independence Rd., Corvallis (44°38'16"N-123°11'5"W). Riverside-1 (planted in 1996) and Riverside-2 (planted in 1997) were located at Riverside Dr., Albany (44°36'5"N-123°9'35"W; Riverside-2 was at the same location as Riverside-1, though a different field was used). Spring Hill was located at Spring Hill Dr., Corvallis (44°42'10"N-123°8'45"W), and Lakeside was located at Lakeside Rd., Monroe (44°24'51"N-123°15'15"W).

Fifteen ha were planted on May 18, 1996 at Independence and 10 ha on May 21, 1996 at Riverside-1. Seventy ha were planted on May 21, 1997 at Spring Hill, 20 ha on May 25, 1997 at Riverside-2, and 120 ha on June 6, 1997 at Lakeside. All sites were fertilized similarly, and irrigated approximately every 10 days after planting until mid-August (S. Gapp, Western Farm Service, Inc., personal communication). All sites used above ground sprinklers for irrigation, with Independence and Spring Hill having wheel lines, Riverside-1 and Riverside-2 having on-hand lines, and Lakeside, a center pivot system.

Commercial honey bee hives were rented by each of the growers at a rate of 2.5 hives per ha (1 hive per acre), and located by the contracted beekeeper. In 1996, the hives were all located at a single position in each field, while in 1997, they were more distributed throughout the fields (Fig. 4.1).

4.3.2 Plot Samples

A total of 44, 2x2 m plots were located among the fields. Five plots each were established in Independence, Lakeside, and Riverside-2 before the hives were placed. The rest of the plots were located at the time of harvest, with distances from 15 to 375 m to the closest group of honey bee hives (Fig. 4.1, Appendix E).

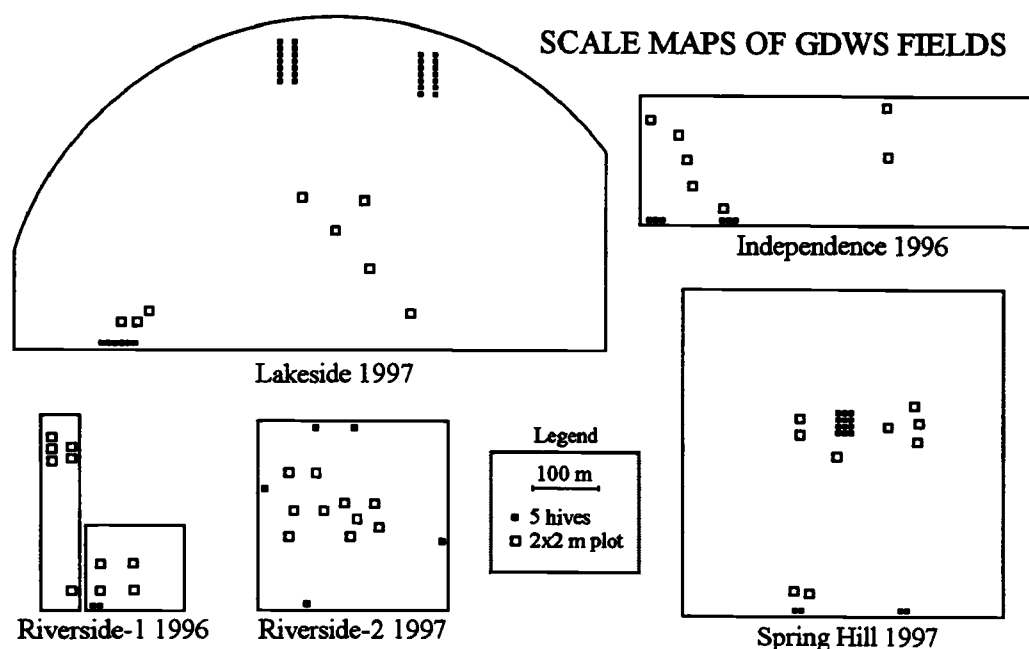


Figure 4.1. Scale maps of *Cucurbita maxima* Duchesne var. 'Golden Delicious' fields used to evaluate the effectiveness of honey bee hives to pollinate squash plants in plots that were at a variable distance from the hives.

At harvest time, the fruits were cut from the vines and left in the field for one week to fully mature. This allows more uniform development of the fruit and improves the harvest. The cut date was Sept. 9, 1996 for Independence and Oct. 8, 1996 for Riverside-1 (114 and 140 days after planting, respectively). In 1997, the cut dates were Sept. 11 for Riverside-2, Sept. 12 for Spring Hill and Sept 26 for Lakeside (109, 114 and 112 days after planting, respectively). After the week in the field, each fruit was gathered and individually labeled with plot number and fruit number. They were transported to the Oregon State University Vegetable Research Farm, for processing the fruit and seeds.

4.3.3 Variable selection and laboratory procedures

After preliminary examination (Appendix B), six variables were recorded for further evaluation:

- (1) **Number (n) of fruit per cage.** The fully mature orange fruits in each cage were counted, and all immature green fruits were disregarded.
- (2) **Fruit weight (Kg).** Total weight of all mature fruits in each cage before the seeds were extracted.
- (3) **Weight (g) of 100 seeds.** The average weight of 100 dried, cleaned, and fully developed randomly chosen seeds from all the mature fruits in each cage.
- (4) **Weight (g) of “A” seeds.** The weight of dried, cleaned, and fully developed “A” seeds from all the mature fruits in each cage.
- (5) **Weight (g) of “B” seeds.** The weight of dried, cleaned, and fully developed “B” seeds from all the mature fruits in each cage.
- (6) **Weight (g) of “C” seeds.** The weight of dried, cleaned, and fully developed “C” seeds from all the mature fruits in each cage.

To record these variables, each mature GDWS fruit was weighed with a commercial spring scale, and the seeds were then separated from each fruit. The empty rind and flesh was then weighed on the same scale and discarded. The seeds and the spongy placental material were placed into a labeled bucket, then stirred and rubbed vigorously in water for 15 min. The seeds were rinsed and then dried by spreading them out under warm (~35°C), dry conditions.

Of the seeds collected from each fruit, 100 seeds were randomly selected and weighed on a Mettler PN 1210 digital balance with a 0.01-gram sensitivity. All seeds from each fruit were then separated into “A-” “B-” and “C-seed” classes according to industry practice. An Exact model 628 seed sorter combined with a Tecron model 5530 power supply amplifier were used with size 28 and 22 screens (Appendix C). The larger A-seeds remained on top of the size 28 screen, the medium size B-seeds passed through the 28 screen but remained on the size 22 screen, and all the small seeds that passed through both screens were classed as C-seeds. The A, B, and C seeds were weighed separately using the same balance as for the “100 seeds” weight.

4.3.4 Data Analysis

It is hypothesized that the effective pollinating ability of a honey bee hive diminishes as distance to the crop increases, so the distance from each plot was measured to the nearest hive group (Figures 4.2 & 4.3, Appendix E). Though data were collected from each fruit separately, the experimental unit was a 4 m² plot, so data from all individual fruits of each plot were combined: the 100-seed weight from each fruit was averaged, and the weights of the whole fruit, and A, B, and C seeds from each fruit were combined into a per plot total. The six variables were analyzed with OLS linear regression after $\log(x+1)$ transformations, the independent variable being distance (Hintze, 1998).

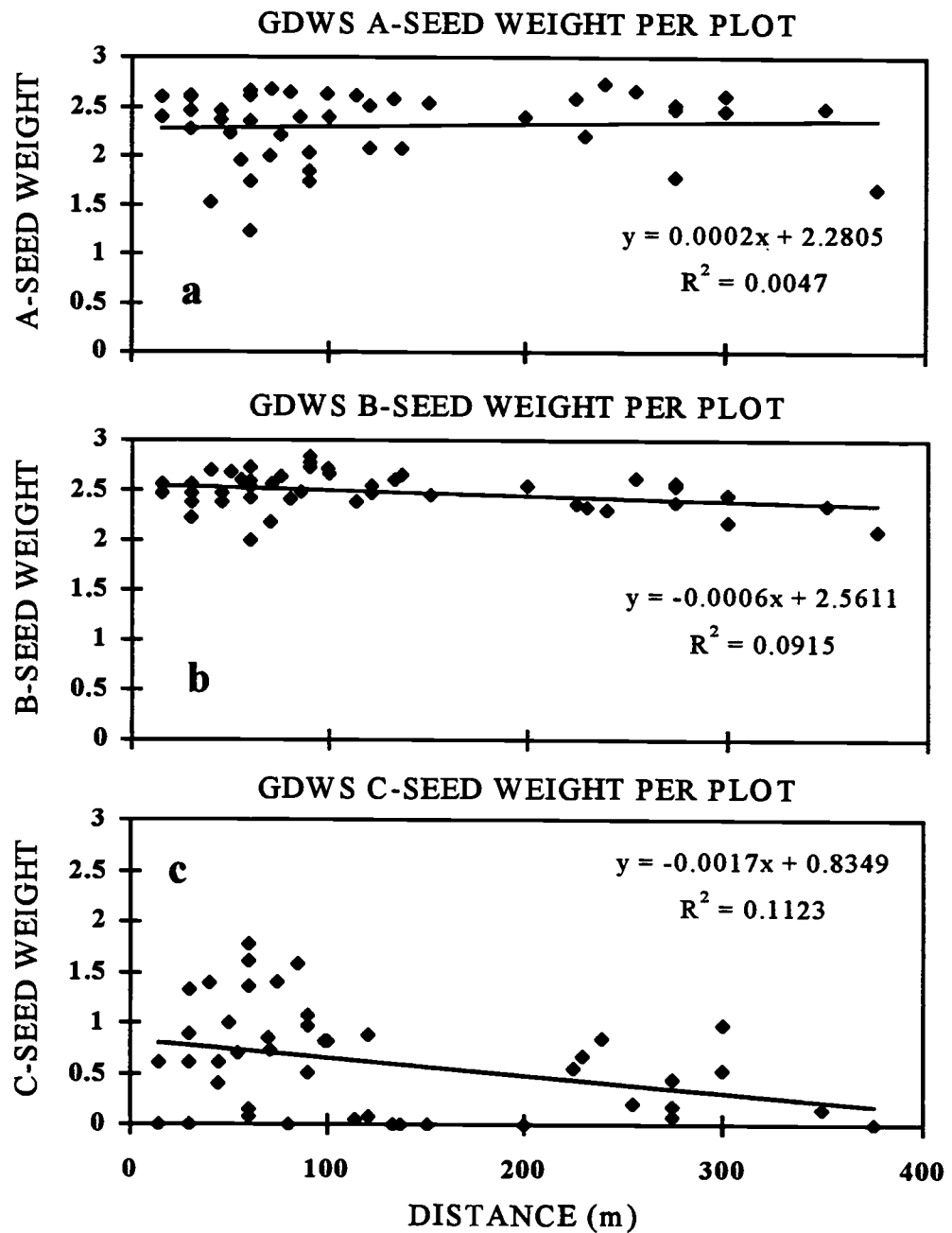


Figure 4.2. Distance effect to the closest honey bee hives on the production of A-seeds (a), B-seeds (b) and C-seeds (c) in *Cucurbita maxima* Duchesne var. 'Golden Delicious'. Log10 transformed dependent variables were used.

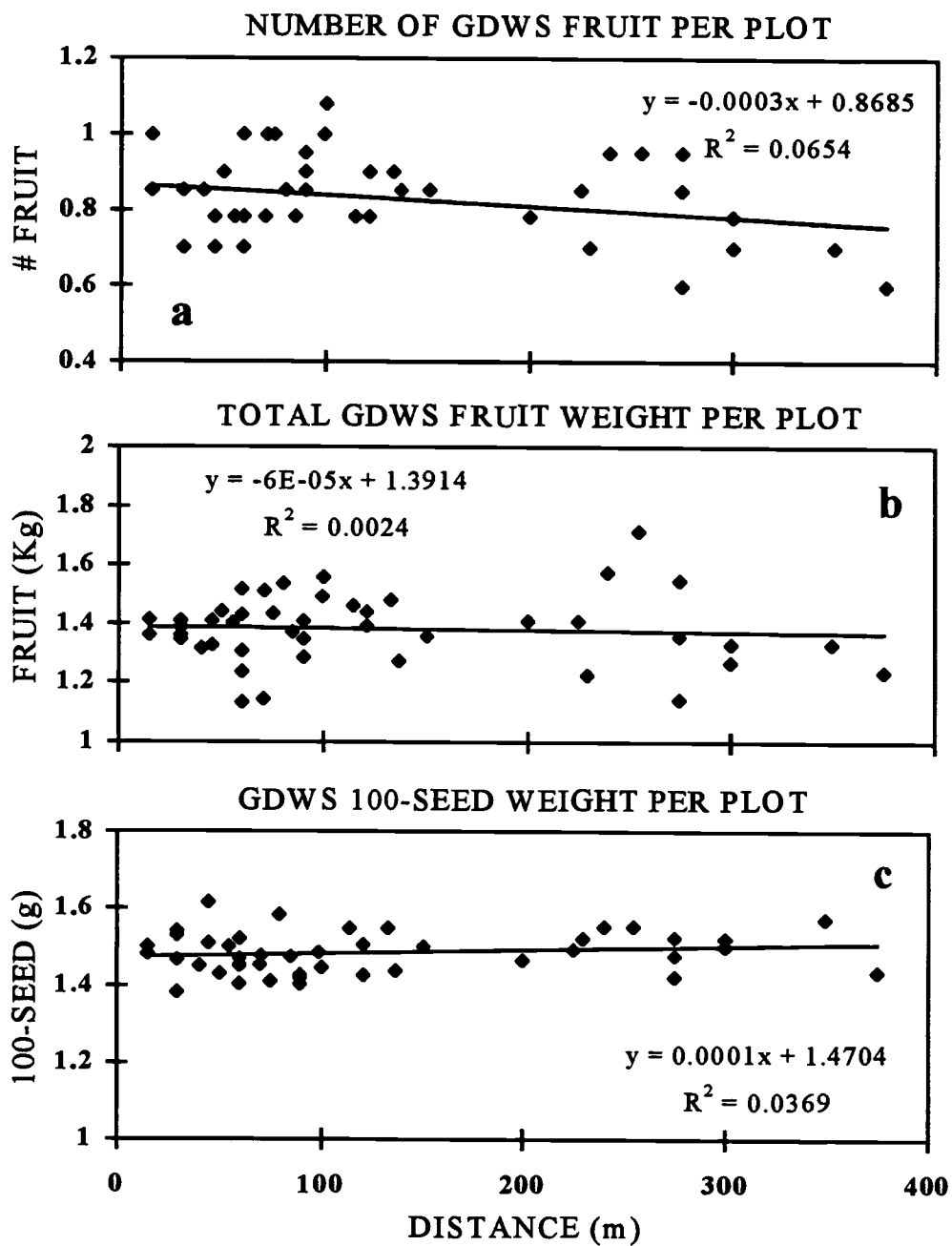


Figure 4.3. Distance effect to the closest honey bee hives on the number of fruit produced (a), fruit weight (b) and 100-seeds weight in *Cucurbita maxima* Duchesne var. 'Golden Delicious'. Log10 transformed dependent variables were used.

4.4 RESULTS AND DISCUSSION

The regression analysis was significant ($p \leq 0.05$) for distance only for the weights of B-seeds and C-seeds, which were reduced in the plots farthest from the nearest group of honey bee hives (Figure 4.2b, c, Appendix F). Placement of honey bee hives in squash fields of ≤ 120 ha appears not to be critical for adequate pollination. The commercial growers used several different patterns of hive placement, from one large group to several small distributed groups. The number of hives were all approximately 2.5 per ha (1 per acre), so any effect of hive clumping or distribution should have made itself evident. The yield among the sites did differ, but the order of the sites did not follow a consistent pattern. For example, Lakeside had the lowest performance for weight of B and C seeds, but was among the highest for weight of 100 seeds. Lakeside had twice the number of pollinator visits (85% of flowers sampled contained honey bees or bumble bees vs. 35-45% at other sites; Chapter 5), which may have some relevance.

The lack of statistical significance in A-seeds weight and other variables, and the weak relationships found in the B- and C-seeds weight related to distance could have been due to the small size of the fields (Steffan-Dewenter and Tschardtke, 1999). Honey bee pollination efficiency will drop off to zero over a long enough distance, since they have a maximum flight range of 8-14 km each way from the hive (Clemson, 1985). More interesting is the distance where the bees no longer provide an economic gain from their pollination services. Unfortunately, we did not find that distance here. A possibility for this is the

ubiquitousness of native pollinators for GDWS, especially bumble bees. Other pollinators were found to be frequent visitors to the squash flowers studied here, for example, *Bombus* spp., megachilids, halictids, etc. (Chapter 5), and may have provided a high enough level of background pollination “noise” that may have masked the effect of distance from honey bee hives. Whether distance out to 400 meters is a significant factor for variables such as fruit weight (Figure 4.3b) could not be determined.

In Chapter 3, we saw that honey bees pollinating in cages produced more C seeds, while bumble bees produced more A seeds. The significantly greater number of the small C seeds from plots nearer to the honey bee hives adds to the evidence that honey bee pollination may result in poor quality seeds compared to native pollinators (mostly bumble bees for the fields here). At plots close to the hives, the effect of honey bees would outweigh that of any native pollinators, resulting in a preponderance of C-seeds, while further from the hives, the native bumble bees produced a relatively greater number of higher quality seeds. These results are puzzling because we are not aware of any physiological mechanisms that can account for differences in seed sizes related to pollinators.

We have observed that bumble bees pollinate GDWS flowers well because of their large size. Honey bees are smaller than bumble bees, and unless they land directly on the stigma, they generally do not touch it while extracting nectar from the female flowers. Bumble bees, on the other hand, generally do touch the stigma while extracting nectar, even when they do not land directly on it. The GDWS

flowers studied here were all equally pollinated whether close or far from the honey bee hives when fruit number or weight is considered, but the plots farthest from the hives had fewer of the lower quality C seeds. Our data does not address whether the native pollinators are responsible for much of the pollination at the farther distances, but they do raise interesting questions that should be tested. If bumble bees are better pollinators of squash flowers as seems likely (Stanghellini *et al.*, 1997; Westerkamp, 1991; Willmer *et al.*, 1994; and chapter 3), then encouraging the growth of their populations around the crop may be an effective way to increase seed quality. Squash growers should look into testing the efficacy of native bumble bees as pollinators of their crop under field conditions.

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5. FLOWER VISITATION RATE OF HONEY BEES AND OTHER POLLINATORS OF 'GOLDEN DELICIOUS' WINTER SQUASH (*CUCURBITA MAXIMA* DUCHENSE) IN THE WILLAMETTE VALLEY OF OREGON

5.1 ABSTRACT

Pollinators of 'Golden Delicious' Winter Squash (GDWS), *Cucurbita maxima* Duchesne (Cucurbitaceae) were studied in the central Willamette Valley of western Oregon. Five commercial GDWS fields near Corvallis, OR were selected, and two related studies were carried out. Two fields were used in 1996, and three in 1997. In the first study a series of 100-flower transects were made through each site, where the sex of each flower in the transect was recorded, and any insect present on or in the flower corolla identified. Alternating with the transects, small groups of flowers were selected and observed for 15 minutes at a time, and the insects visiting or present during that time were recorded, and their visits timed.

We found that honey bees (*Apis mellifera* L. (Hymenoptera: Apidae)) visited proportionally more female flowers in the morning, but then showed a preference for the more abundant male flowers in the afternoon. One site with proportionately more female flowers (15% as opposed to 5% for the other fields) also had honey bees with a more female flower oriented bias. Whether these observations are related is not known. On average, the duration of honey bee visits were 3 times as long as those of bumble bees (*Bombus* spp.(Hymenoptera: Apidae)) (43.3 vs. 14.6 seconds). Yellow jackets (Hymenoptera: Vespidae) spent approximately the same amount of time as honey bees, and cucumber beetles

(Coleoptera: Chrysomelidae) generally stayed on flowers for 900 seconds (the maximum recording time). More research is needed to tie together the number of pollinator visits and the threshold for effective pollination of GDWS.

5.2 INTRODUCTION

‘Golden Delicious’ Winter Squash (GDWS) is an important variety of *Cucurbita maxima* Duchesne (Cucurbitaceae) grown in the Willamette Valley of western Oregon. GDWS is a monoecious plant, and pollen must be transferred from a male to a female flower, either on the same or different plants, in order to be fertilized and to set fruit (Free, 1993; Jaycox *et al.*, 1975; McGregor, 1976). It is considered to be a “low rewards” crop for bees, with an average sugar concentration of 16% for male flowers and 13% for female flowers (Chapter 2). The pollen rewards are rated as only “medium” for bees as well (Clemson, 1985). Considering that honey and bumble bees generally visit flowers with a sugar concentration range of 10-74% (Percival, 1965), and usually can not gain energy from flowers with sugar concentrations of less than 30% (Real, 1983), it would be helpful to know how often commercially obtained honey bees or wild bees such as bumble bees actually visit GDWS flowers, to see if there are sufficient visits per flower for adequate pollination. A range of 6 to 20 visits is required for other cucurbits (Adlerz, 1966; Collison, 1976; Stanghellini *et al.*, 1997; Stanghellini *et al.*, 1998).

Generalist pollinators such as honey or bumble bees visit crops in proportion to the attractiveness of that crop, relative to the competing pollen and

nectar sources nearby. Squash plants bloom late in the summer, and so do not have much competition from other nectar sources for the pollinating services of bees. In the past, feral honey bees and wild bees were generally prevalent enough to ensure adequate pollination of GDWS, but with the advent of *Varroa* and tracheal mites in the feral honey bee populations, habitat degradation, and the use of agricultural pesticides, their numbers have dwindled (Stauth, 1997). With the dearth of other flowering plants at the time of GDWS blooming, we can comfortably expect that commercial honey bees will find the squash flower rewards attractive enough to visit the flowers and provide pollination. We do not know, however, what stocking rate (hives per ha) will provide an adequate visitation rate to ensure adequate pollination. The fields that were studied here apparently did receive adequate pollination, because their fruit yields were within the expected range (S. Gapp, Western Farm Service, Inc., personal communication). Whether they were fully pollinated by honey bees from the 2.5 hives per ha that were used during the blooming season, or how much pollination was augmented by wild bees is not known.

Flower visits by bees depend to some extent on the amount and timing of nectar and pollen availability. Both male and female squash flowers produce nectar, and each flower blooms for only one day. Pollen is available only for a few hours in the morning because of removal by foraging pollinators, and degradation of the remaining pollen grains (Nepi and Pacini, 1993). Nectar, though, is available throughout the day from both floral sexes. This continuing availability of nectar

could be enough to provide an attraction to bees, so the visitation rates could remain high for the period that the bees are active.

Knowledge of the visitation rates of honey bees brought to pollinate GDWS fields would be helpful for apiculturists to calculate the number of honey bee colonies to place. In this study, we look at flower visitation rates by both honey bees stocked at a rate of 2.5 hives per ha, and of various native insects, and discuss their relative importance for the pollination of GDWS. We investigate the relative attractiveness of male and female GDWS flowers, the timing and duration of honey bee and other insect visits, and discuss the implications of these findings on commercial pollination practices for GDWS.

5.3 MATERIALS AND METHODS

5.3.1 Field plots

Two commercial fields of GDWS in the Willamette Valley of Oregon were sampled for flower visitors during August 1996. They were located at Independence Hwy., Corvallis (44°38'16"N-123°11'5"W) (Independence), and Riverside Dr., Albany (44°36'5"N-123°9'35"W) (Riverside-1) and were ~8 km apart. Fifteen ha were planted on May 18, 1996 at Independence and 10 ha on May 21, 1996 at Riverside-1. Both sites were fertilized similarly and irrigated approximately every 10 days after planting (S. Gapp, pers. comm.). The Independence site was irrigated with wheel lines, and Riverside-1 with on-hand

lines. Because of the proximity of the two sites, it is likely weather conditions were the same during the study period.

In August 1997, three GDWS commercial fields were sampled in the Willamette Valley. They were located at Spring Hill Dr., Corvallis (44°42'10"N-123°8'45"W) (Spring Hill); Riverside Dr., Albany (Riverside-2), and Lakeside Dr., Monroe (44°24'51"N-123°15'15"W) (Lakeside). Seventy ha were planted on May 21, 1997 at Spring Hill, 20 ha on May 25, 1997 at Riverside-2, and 120 ha on June 6, 1997 at Lakeside. These fields were located less than 25 km apart, and were in a similar location as the previous year's sites. Riverside-2 was located at the same farm as Riverside-1, but in a different field. Because of the proximity of the three sites, it is likely weather conditions were similar for each field during 1997. As before, all sites were fertilized similarly and irrigated approximately every 10 days after planting. Spring Hill was irrigated with wheel lines, Riverside-2 with on-hand lines, and Lakeside with a center pivot system.

Commercial honey bee hives were rented by each of the growers at a rate of 2.5 hives per ha (1 hive per acre), and located by the contracted beekeeper.

5.3.2 Flower Transects

During the summers of 1996 and 1997, 100 GDWS flowers were sampled at each site using a systematic transect method starting at a random point selected from the approximate center of each field (modified from Andrews and Quezada, 1989). Starting at this point, ten flowers were selected for observation along a straight path in a random direction. Turning to the left or right approximately 30

degrees, a distance of 5m was walked before selecting the next ten flowers closest to the line of travel. This procedure was repeated until 100 flowers were sampled. The total transect length was approximately 60 m. The sex of flowers in the transect was recorded, and any insect present on or in the flower corolla was identified to species. If the species was not known, the insect was captured for later identification.

In 1996, from August 17 to 30, Independence and Riverside-1 were sampled with this procedure every other day, once every hour from 0900 hours until 1600 hours. The procedure in 1997 was similar to the first year, but the sampling dates were different for each site. From July 25 to August 6, Lakeside was sampled on each day except Sundays, and was sampled again on August 14. Riverside-2 was sampled on July 24, August 7, and August 18. Spring Hill was sampled on July 18, August 8, and August 21. In 1997, flowers were observed from 0700 hours until 1100 hours.

Preferences of honey bees for female or male flowers were converted to the z-transformed difference between the proportion of male flowers and the proportion of honey bees found in male flowers per 100-flower transect with the following formula (Hintz, 1998):

$$z = \frac{\frac{X_1}{n_1} - \frac{X_2}{n_2}}{\sqrt{\frac{p(1-p)}{n_1} + \frac{p(1-p)}{n_2}}}$$

Here, X_1 is the number of male flowers found per transect, n_1 is the total number of flowers counted per transect (=100), X_2 is the number of bees found on male flowers during the transect, and n_2 is the total number of honey bees found during the transect, and

$$p = \frac{X_1 + X_2}{n_1 + n_2}.$$

This procedure transforms the proportional data into a distribution resembling the z , or normal distribution. With the transformed data, the normally distributed error allows for further statistical calculation.

5.3.3 Individual Flower Observations

In the same fields as the transects, small groups of flowers were selected and observed for 15 minutes at a time, and the insects visiting or present during that time were recorded. The hours and days of observation were also the same as in the transect study. In this study, each insect that was seen landing on the observation flowers was identified, and its visit was timed. Any insect that was already present when the flowers were put under observation was timed from the beginning of the observation period until it left. Similarly, any insect that remained on the flower after the observation period ended was recorded as having left at that time. Consequently, no insect could have a visit duration of more than 900

seconds. In 1996, the groups consisted of four male and one female flower, and in 1997, the groups had two male and two female flowers.

5.4 RESULTS AND DISCUSSION

The fields studied here were found to produce crops of GDWS of yield and quality consistent with industry expectations (Chapter 4), so the total visitation rates for these fields were high enough for good pollination. Besides honey bees and bumble bees, the squash flowers were visited by a number of other insects, many of them potential pollinators (Table 5.1). We saw that bumble bees are good pollinators of GDWS at densities far less than those of honey bees (Chapter 3), so although their visitation rates were much less (Table 5.2), they may still have contributed significantly to the pollination of the crop.

Table 5.1. List of species found during 1996 and 1997, in the flower transect and flower observation studies combined. No. is the total number of each insect taxon recorded visiting *Cucurbita maxima* Duchesne var. 'Golden Delicious' flowers during both studies.

Insect	Species	No. (%)*	
Honey Bees	<i>Apis mellifera</i>	16523 (96.45)	
Bumble Bees	<i>Bombus vosnesenskii</i>	431 (2.52)	
	<i>B. californicus</i>		
	<i>B. griseocollis</i>		
	<i>B. morrisoni</i>		
	<i>B. mixtus</i>		
	<i>B. fervidus</i>		
	<i>B. occidentalis</i>		
	<i>Bombus spp.</i>		
Other Bees	<i>Halictus rubicundus</i>	176 (1.03)	
	<i>Agapostemon texanus</i>		
	<i>Ceratina namula</i>		
	<i>Megachile sp.</i>		
	<i>Lasioglossum spp.</i>		
	<i>Hylaeus sp.</i>		
Other Hymenoptera	<i>Dolichovespula arenaria</i>	<i>Vespula pensylvanica</i>	28
Diptera	Various		20
Coleoptera	<i>Diabrotica undecempunctata</i>	<i>Acalymma vittata</i>	38604
Hemiptera	Miridae		31

* Percentage of all bees

Table 5.2. Proportional data from the flower transect study. M Prop is the proportion of male flowers found at each site, Flowers is the total number of flowers sampled, HB/F, BB/F, WCB/F, SCB/F, and Other/F are average numbers of honey bees, bumble bees, western cucumber beetles, striped cucumber beetles, and other insects found in each flower corolla of *Cucurbita maxima* Duchesne var. 'Golden Delicious' during the study, respectively.

Site	M Prop.	Flowers	HB/F	BB/F	WCB/F	SCB/F	Other/F
1996							
Independence	0.967	4700	0.354	0.022	1.688	0.287	0.013
Riverside-1	0.957	4300	0.349	0.018	2.324	0.161	0.011
1997							
Spring Hill	0.948	2400	0.411	0.015	1.008	0.089	0.017
Riverside-2	0.940	3000	0.416	0.026	1.020	0.018	0.019
Lakeside	0.852	10800	0.852	0.009	1.165	0.003	0.004
Total	0.911	25200	0.582	0.015	1.428	0.093	0.010

5.4.1 Flower Transects

Honey bees initially visited proportionately more female flowers (Fig. 5.1a), and progressively switched to the more abundant male flowers, which is opposite to the trend reported by Nepi and Pacini (1993) for *C. pepo*. Honey bees at the Lakeside site were biased more toward female flowers than at the other sites (Fig. 5.2a), perhaps because of environmental or physiological factors that made the female flowers at that site more attractive.

All of the 1997 sites had greater female flower visitation rates than did the 1996 sites (Fig. 5.2a), though except for Lakeside, the differences were small. The weather conditions in 1996 were both hotter and wetter than in 1997 (data from Hyslop Experiment Station, Corvallis, OR), and which could account for some of these seasonal differences.

Bumble bees visited proportionally slightly more male GDWS flowers than female flowers and did it in a similar rate throughout the day (Fig. 5.1b). All of the sites during 1996 and 1997 were visited by bumble bees at a similar flower visitation rate (Fig. 5.2b). If honey bees were influenced by the change in temperature between years, bumble bees apparently were not.

Because the viability and amount of pollen available in male flowers decreases throughout the day due to removal by bees and environmental conditions (Nepi and Pacini, 1993), the increase in male flower visitations by honey bees later in the day is probably due to the attraction of nectar remaining in male nectaries. Nectaries in male GDWS flowers are more protected than those in the female

flower, making them more resistant to both evaporation and rapid collection by bees (pers. obs). Both factors would permit more nectar to remain in the male nectaries longer throughout the day, thus making the male flowers progressively more attractive relative to female flowers. Conversely, the easy availability of nectar in female flowers would make them more attractive to honey bees in the morning when there is abundant nectar in their nectaries. On a per-honey bee basis, though, this trend of changing preference is slow, and throughout the day, individual honey bees are visiting both types of flowers on a single trip.

In the case of bumble bees, the overall preference for male flowers could be due to the availability of abundant pollen that male GDWS flowers offer during the morning and nectar in the afternoon. The prevalence of male flowers increases the likelihood of a bee arriving at one or more male flowers before arriving at a female, no matter what the relative attractiveness is.

The honey bee hives placed at the Lakeside site had the largest populations of workers, as determined from hive samples during the study: this may have accounted for some of the increase in bee visits. However, the hives at Lakeside were only ~20% higher in population size than the other sites, which does not seem likely to explain all of a 100% increase in visitations.

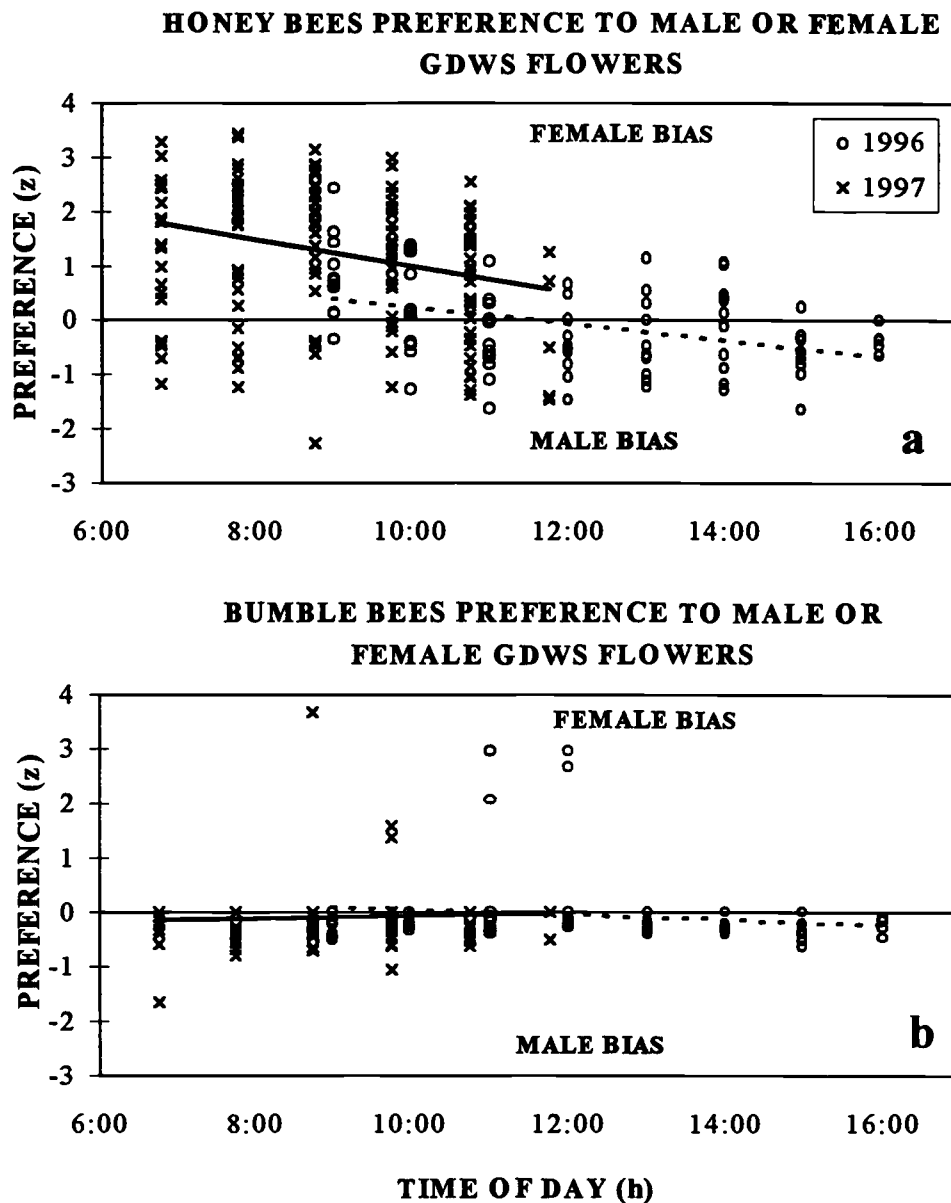


Figure 5.1 Data from all sites in the flowers transect study were combined and analyzed hourly to see the preference of (a) honey bees and (b) bumble bees for male or female flowers of *Cucurbita maxima* Duchesne var. 'Golden Delicious'.

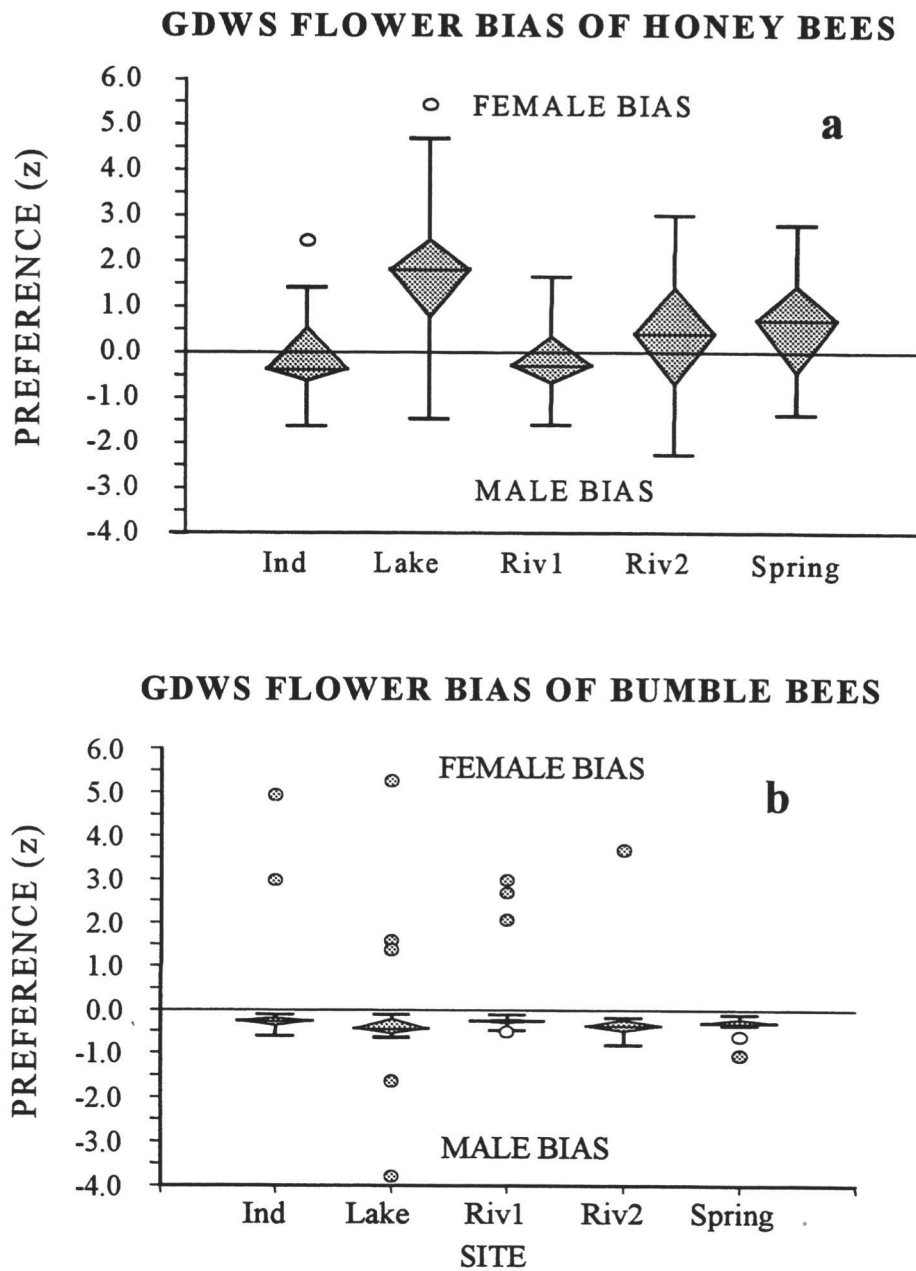


Figure 5.2 Data from all sites in the flowers transect study were analyzed separately to see the preference of (a) honey bees and (b) bumble bees for visiting female flowers of *Cucurbita maxima* Duchesne var. 'Golden Delicious'. The box plot shows three main features about female bias: its center, its spread, and its outliers.

5.4.2 Individual Flower Observations

A wide range of flower visit durations were seen during the 15-minute observations (Fig. 5.3). Honey bees spent approximately 3 times longer per visit than did bumble bees (43.3 vs. 14.6 seconds; back transformed log means), yellow jackets spent approximately the same amount of time as honey bees (46.9 seconds), and both species of cucumber beetles generally stayed on flowers for the full 15-minute observation period. They were usually on the flowers when observation started, and were still there when the observation time was over. Sometimes, it was apparent that the same beetles (such as mating pairs) that were there during one hour were still there during subsequent hours. This, and the skewed nature of their duration distribution (Fig. 5.3) leads us to believe that the actual mean duration time for a beetle visit is much longer than the 15-minute observation time. The presence of beetles on the flowers did not noticeably affect the behavior of honey or bumble bees during their visits (personal observation).

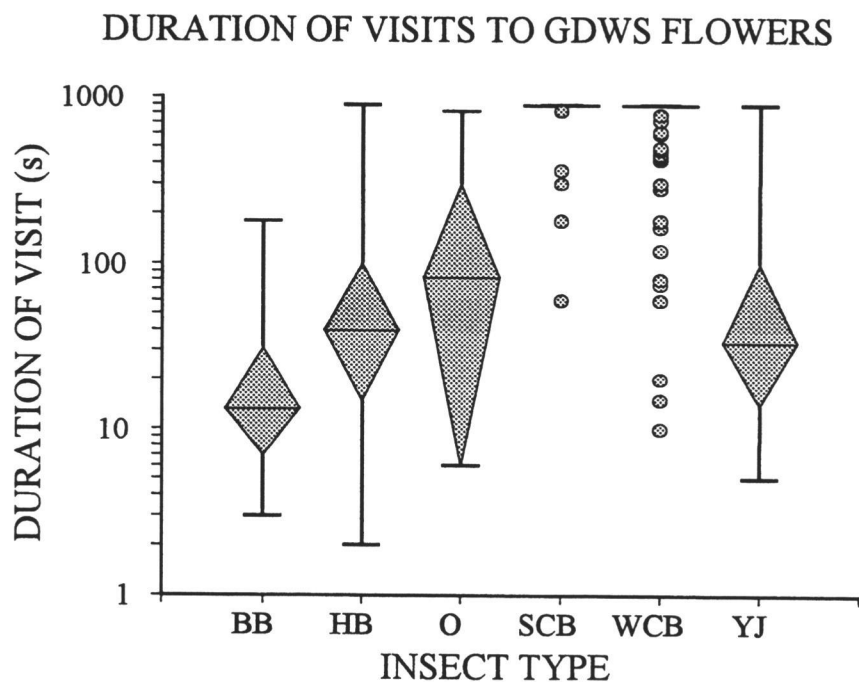


Figure 5.3 Duration of insect visits per insect taxon from the individual flower observation study of *Cucurbita maxima* Duchesne var. ‘Golden Delicious’, all fields combined. These box plots are shown on a log scale to normalize the distributions. The box plot shows three main features about duration of visits: its center, its spread, and its outliers.

We have seen that commercial honey bees, perhaps aided by the native pollinators present in these squash fields, were sufficient to produce squash yields consistent with industry expectations. The rate of pollinator visitation seen here (80 honey bee visits per day), then, can be taken as a baseline for other studies. More research should be undertaken to see whether more or fewer pollinator visits,

both by commercial honey bees and by native bumble bees, results in significantly greater or lesser yield of GDWS fruit and seeds, and which combination is the most economic for growers.

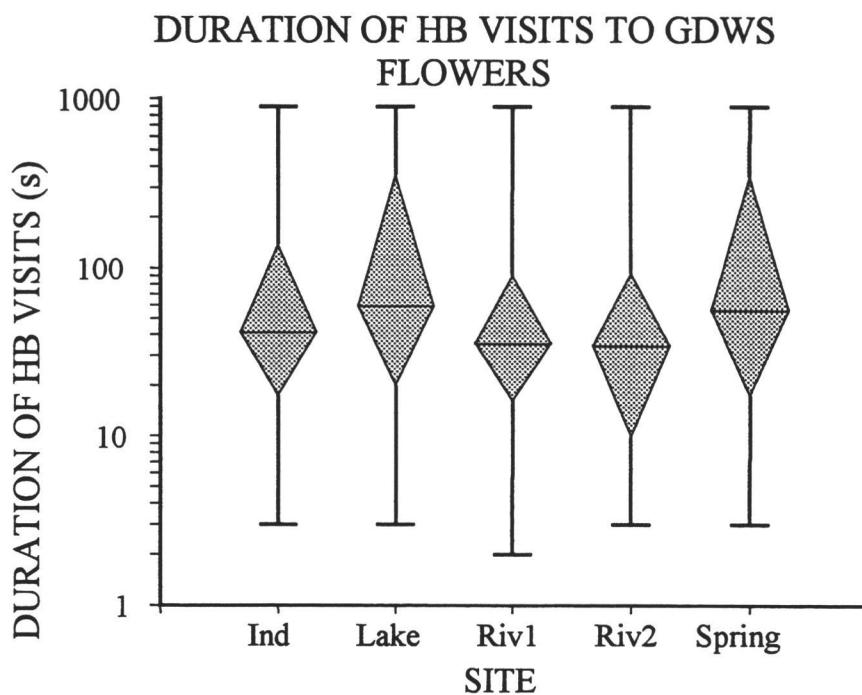


Figure 5.4 Duration of honey bee visits per site from the individual flower observation study. These box plots are shown on a log scale to normalize the distributions. A box plot shows three main features about duration of visits: its center, its spread, and its outliers

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6. CONCLUSIONS

In chapter 2, it was found that GDWS provides significant amounts of pollen (24 mg) and nectar (236 μ l), but with a low reward of 14% nectar sugar. It was also found that the quantity of nectar produced per GDWS flower differed between sites and floral sex. The average nectar production per flower at the Independence site (mean \pm 1 SE) of 311 ± 20 μ l was double that of the Riverside-1 site (161 ± 14 μ l). An average female GDWS flower produced 319 ± 17 μ l of nectar, which was double than the production of an average male GDWS flower of 153 ± 17 μ l.

The concentrations of nectar sugars were different between male ($15.62 \pm 0.61\%$) and female ($12.57 \pm 0.60\%$) flowers of GDWS, where male flowers had 25% higher sugar concentration than female flowers. There was no statistical difference in the percent of nectar sugars per flower between Independence ($14.38 \pm 0.59\%$) and Riverside-1 ($13.81 \pm 0.62\%$) sites.

The interaction between site and floral sex was statistically significant for the amount of nectar and percent of nectar sugars. In Independence, a female GDWS flower produced on average 184% more nectar than a male flower (female = 443 ± 29 μ l and male = 156 ± 29 μ l), but in Riverside-1, an average female flower produced only 54% more nectar than an average male flower (female = 195 ± 20 μ l and male = 127 ± 20 μ l). In Independence, GDWS male flowers had a 41% higher concentration of nectar sugar than female flowers ($16.83 \pm 0.83\%$ versus $11.93 \pm 0.83\%$ sugars respectively), but at Riverside, GDWS male flowers had only

9% more nectar sugars than female flowers ($14.41 \pm 0.89\%$ versus $13.21 \pm 0.86\%$ sugars respectively).

Pollen production averaged 24.15 mg per GDWS male flower. The production of pollen per flower differed significantly between sites. Lakeside GDWS flowers produced 27% more pollen per flower (29.23 ± 1.80 mg) than those of Spring Hill (23.00 ± 1.78 mg), and 45% more than Riverside-2 (20.21 ± 1.78 mg).

In chapter 3, the insect exclusion treatment and the western spotted cucumber beetle treatment produced no fruit. Between the honey bee and bumble bee treatments, no significant differences were found except for the interaction between the bee treatment and year on number of fruit per cage. This significant difference reflects the increase in fruit number produced by honey bees in 1997.

The number of GDWS fruit produced by honey bees was 1.84 times higher in 1997 than in 1996, and the number of fruit produced by bumble bees in 1996 was 1.43 times higher than that of 1997. In 1996, GDWS pollinated by bumble bees produced 1.78 times more fruits, and 1.87 times more total fruit weight per cage than those pollinated by honey bees, but in 1997, the honey bee treatment produced 1.19 times more fruits and 1.17 times more fruit weight than the bumble bee treatment.

The weight of 100 seeds was similar between treatments, with GDWS pollinated by bumble bees producing 1.08 times more weight per 100 seeds in 1996 than those pollinated by honey bees, and 1.01 times more in 1997. Bumble bee

pollinated GDWS produced more A seeds per cage by weight than did those pollinated by honey bees in both years (1996 = 3.66 and 1997 = 1.18 times more).

In 1996, bumble bee pollinated GDWS produced 1.12 times more B seeds per cage by weight than did those pollinated by honey bees, and in 1997, honey bees produced 1.54 times more. Honey bee pollinated GDWS produced more C seeds per cage than bumble bee pollinated squash did in each year: 4.10 times more in 1996 and 3.00 times more in 1997. None of these treatment differences was significant.

In chapter 4, the regression analysis was significant for distance only for the weight of B-seeds and C-seeds, which were both less in the plots farthest from the nearest honey bee hive. Placement of honey bee hives in squash fields of ≤ 120 ha appears not to be critical for adequate pollination. Other pollinators were frequent visitors to the squash flowers studied here - for example, *Bombus* spp., megachilids, halictids, etc. These other pollinators, mostly bumble bees, accounted for 3.55% of all bee visits (Chapter 5).

In chapter 5, it was observed that honey bees were biased toward female flowers, especially in the morning. They initially visited proportionately more female flowers, and progressively switched to the more abundant male flowers. Honey bees at the Lakeside site were biased more toward female flowers than the bees at the other sites. All of the 1997 sites had greater female flower visitation rates than did the 1996 sites.

Bumble bees visited proportionally slightly more male GDWS flowers than female flowers and did it in a similar rate throughout the day. All of the sites during 1996 and 1997 were visited by bumble bees at a similar flower visitation rate.

We observed that on average, a female GDWS flower produced 236 μl of nectar, and was visited by 20 honey bees per day (Chapter 5). These visits were observed during 15 minute observations taken each hour during the day, so we can extrapolate the number of honey bee visits to include the unobserved time, and arrive at an approximate 80 visits per female flower per day. The honey sack of a honey bee can carry 55 μl of nectar, so that flower could be theoretically emptied in only 4.5 visits from the same bee. In reality, bees do not fill their crops from only one flower (Nepi and Pacini, 1993), so the nectaries of GDWS flowers may be producing enough nectar for most of the foragers that arrive.

The number of honey bee visits necessary for optimum pollination has been estimated to be between 6 and 20 for other species of cucurbits (Adlerz, 1966; Collison, 1976; Stanghellini *et al.*, 1997). With the visitation rates experienced at the study sites, it is possible that stocking rates of hives could be reduced by up to 50% (to 1.25 hives per ha). At this point, however, the issue of hive distribution becomes more important, and studies at this stocking rate would have to be performed to ensure even pollination across their field.

Finally, at lower honey bees stocking rates, the issue of poorly developed seeds may become more pronounced. Because these studies were performed with a

(in retrospect) high stocking rate, it is possible that the trend would intensify at lower stocking rates, where honey bees would produce poorer quality fruit. We suggest a directed study of the effects of low rates of honey bee pollination on seed production and fruit quantity and quality to resolve these uncertainties. With netting to exclude native pollinators, this study would show whether honey bees do produce more poorer quality C seeds compared to an open field control.

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APPENDICES

**APPENDIX A. STATISTICAL TABLES FOR CHAPTER 2:
NECTAR AND POLLEN PRODUCTION OF
GDWS, *CUCURBITA MAXIMA* DUCHESNE**

Table A.1 F-statistics for treatment effects from GLM ANOVAs (see Data Analysis) for quantity of nectar and pollen, and quality of nectar produced per flower in *Cucurbita maxima* Duchesne var. 'Golden Delicious'.

Source of Variance	df	SS ⁽¹⁾	F-ratio	Probability
QUANTITY (μl) OF NECTAR				
Site	1	1199700	36.2	0.000000*
Floral Sex	1	1470428	44.37	0.000000*
Site x Sex	1	503431.3	15.19	0.000127*
Error	236	7820645		
QUALITY (% SUGARS) OF NECTAR				
Site	1	12.33543	0.44	0.506335
Floral Sex	1	355.1487	12.78	0.000473*
Site x Floral Sex	1	130.4278	4.69	0.031889*
Error	149	4141.672		
QUANTITY (mg) OF POLLEN				
Site	2	1682.713	6.66	0.001821*
Error	116	14645.62		

⁽¹⁾ Sum of Squares

* Statistically significant at $\alpha = 0.05$

Table A.2 Means, sample sizes (n), standard errors (SE) and 95% confidence intervals (CI) for nectar, μ l, produced by *Cucurbita maxima* Duchesne var. 'Golden Delicious', 1996.

Source of Variance	n	Mean	SE	95% CI	
All	240	236.034	11.75059	212.7976	259.27119
Independence	80	311.025	20.35262	270.7776	351.27230
Riverside-1	160	161.043	14.39147	132.5845	189.50283
Female Flowers	120	319.056	16.61784	286.1944	351.91797
Male Flowers	120	153.012	16.61784	120.1507	185.87427
Females (Independence)	40	442.625	28.78295	385.7067	499.54328
Males (Independence)	40	179.425	28.78295	122.5067	236.34328
Females (Riverside-1)	80	195.487	20.35262	155.2401	235.73480
Males (Riverside-1)	80	126.600	20.35262	86.35269	166.84730

Table A.3 Means, sample sizes (n), standard errors (SE) and 95% confidence intervals (CI) for nectar sugars (%) produced by *Cucurbita maxima* Duchesne var. 'Golden Delicious', 1996

	n	Mean	SE	95% CI	
All	153	14.0926	0.4262	13.2479	14.9372
Independence	80	14.3770	0.5895	13.2089	15.5451
Riverside-1	73	13.8083	0.6171	12.5854	15.0311
Female Flowers	75	12.5668	0.5970	11.3838	13.7498
Male Flowers	78	15.6185	0.6088	14.4120	16.8249
Females (Independence)	40	11.9265	0.8336	10.2746	13.5784
Males (Independence)	40	16.8275	0.8336	15.1756	18.4794
Females (Riverside-1)	35	13.2071	0.8553	11.5122	14.9020
Males (Riverside-1)	38	14.4094	0.8912	12.6434	16.1754

Table A.4 Means, sample sizes (n), standard errors (SE) and 95% confidence intervals (CI) for pollen, mg, produced by *Cucurbita maxima* Duchesne var. 'Golden Delicious', 1997

	n	Mean	SE	95% CI	
All	119	24.1469	1.0300	22.1041	26.1897
Spring Hill	40	23.0025	1.7766	19.4790	26.5260
Riverside-2	40	20.2050	1.7766	16.6815	23.7285
Lakeside	39	29.2333	1.7993	25.6650	32.8017

Table A.5 Weather observations⁽¹⁾ at Hyslop Exp. Station, Corvallis, Oregon.

Day	Temperature (°F)								Prec.	Evapo ration	Wind Run	Growing Degree Days
	Air		Surface		Soil		2 inch	4 inch				
	42 inch	M ⁽²⁾ m ⁽³⁾	M	m	M	m						
August, 1996												
1	84	48	88	48	96	68	88	71	0	.276	46	16
11	100	55	104	54	103	73	94	75	0	.343	30	28
13	86	55	90	55	95	68	87	70	0	.303	65	21
August 1997												
19	79	53	85	53	93	68	85	72	0	.201	46	16
20	87	62	91	62	98	68	88	70	.11	.218	27	25

⁽¹⁾ Observations made daily at 8:00 h by Gerry DeKam, Jim Crane, Jim Fell

⁽²⁾ M = maximum

⁽³⁾ m = minimum

APPENDIX B. VARIABLES CONSIDERED FOR TESTING POLLINATION EFFICIENCY OF HONEY BEES AND BUMBLE BEES IN *CUCURBITA MAXIMA* DUCHESNE VAR. GOLDEN DELICIOUS: LIST AND CORRELATIONS

- (1) Number (n) of fruit per cage. The fully mature fruits in each cage were counted, and all immature fruits were disregarded
- (2) Fruit weight (Kg). Total weight of all fruits in each cage before the seeds were extracted.
- (3) Rind weight (Kg). Weight of all fruits (rind+flesh) in each cage after the seeds were extracted.
- (4) Fresh Seeds weight (Kg). The difference between total fruit weight and fruit weight per cage.
- (5) Weight (g) of 100 seeds. The weight of 100 dried, cleaned, and fully developed randomly chosen seeds from all the fruits in each cage.
- (6) Weight (g) of total seeds. The weight and quantity of the total dried, cleaned and fully developed seeds per cage.
- (7) Weight (g) of “A” seeds. The weight of dried, cleaned, and fully developed “A” seeds from all the fruits in each cage.
- (8) Weight (g) of “B” seeds. The weight of dried, cleaned, and fully developed “B” seeds from all the fruits in each cage.
- (9) Weight (g) of “C” seeds. The weight of dried, cleaned, and fully developed “C” seeds from all the fruits in each cage.

- (10) Number (n) of seeds. The quantity of dried, cleaned and fully developed seeds from all the fruits in each cage.
- (11) Number (n) of “A” seeds. The quantity of dried, cleaned, and fully developed “A” seeds from all the fruits in each cage.
- (12) Number (n) of “B” seeds. The quantity of dried, cleaned, and fully developed “B” seeds from all the fruits in each cage.
- (13) Number (n) of “C” seeds. The quantity of dried, cleaned, and fully developed “C” seeds from all the fruits in each cage.
- (14) Ratio of “A” seeds by weight (g/g). Ratio of the “Weight (g) of “A” seeds” and “Weight (g) of total seeds”.
- (15) Ratio of “B” seeds by weight (g/g). Ratio of the “Weight (g) of “B” seeds” and “Weight (g) of total seeds”.
- (16) Ratio of “C” seeds by weight (g/g). Ratio of the “Weight (g) of “C” seeds” and “Weight (g) of total seeds”.
- (17) Ratio of “A” seeds by number (n/n). Ratio of the “Number (n) of “A” seeds” and “Number (n) of total seeds”.
- (18) Ratio of “B” seeds by number (n/n). Ratio of the “Number (n) of “B” seeds” and “Number (n) of total seeds”.
- (19) Ratio of “C” seeds by number (n/n). Ratio of the “Number (n) of “C” seeds” and “Number (n) of total seeds”.

Table B.1 Pearson correlation coefficients, significance level, and number of observations for 19 variables associated with seed production in pumpkin and squash

			Average weight per fruit									Average No. of seeds per fruit				Average ratio of seeds per fruit					
			No. of fruit	Total	Meat	Seeds & flesh	100-seeds	Total seeds	"A" Seeds	"B" Seeds	"C" Seeds	Total	"A"	"B"	"C"	"A"	"B"	"C"	"A"	"B"	"C"
			n	Kg			g			n				g/g			n/n				
A v e r a g e w e i g h t p e r f r u i t	No. of fruit	1	-0.055	-0.034	-0.189	-0.119	-0.021	-0.099	-0.213	0.124	0.016	-0.128	-0.154	0.261	0.06	-0.148	0.007	0.041	-0.145	0.084	
		0	0.865	0.917	0.557	0.712	0.947	0.760	0.507	0.701	0.961	0.692	0.633	0.412	0.83	0.646	0.982	0.900	0.654	0.796	
		12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
	Total	Kg	-0.055	1	0.998	0.938	-0.445	0.738	0.623	0.407	0.012	0.641	0.585	0.257	-0.096	0.32	-0.386	0.104	0.360	-0.384	0.041
			0.865	0	0	6E-06	0.147	0.006	0.031	0.189	0.971	0.025	0.046	0.421	0.766	0.29	0.215	0.747	0.250	0.217	0.900
			12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
	Meat	Kg	-0.034	0.998	1	0.917	-0.429	0.728	0.618	0.388	0.015	0.622	0.577	0.228	-0.094	0.33	-0.395	0.107	0.368	-0.397	0.045
			0.917	0	0	3E-05	0.164	0.007	0.032	0.212	0.963	0.031	0.050	0.476	0.771	0.28	0.204	0.741	0.240	0.201	0.890
			12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
	Seeds & flesh	Kg	-0.189	0.938	0.917	1	-0.566	0.655	0.543	0.468	-0.011	0.610	0.530	0.372	-0.113	0.23	-0.256	0.084	0.259	-0.241	0.017
			0.557	6E-06	3E-05	0	0.055	0.021	0.068	0.125	0.974	0.035	0.076	0.234	0.726	0.46	0.422	0.795	0.417	0.451	0.957
			12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
	100-seeds	g	-0.119	-0.445	-0.429	-0.566	1	0.021	-0.096	0.178	-0.076	0.027	-0.130	0.183	0.028	-0.12	0.218	-0.184	-0.155	0.217	-0.139
			0.712	0.147	0.164	0.055	0	0.949	0.766	0.580	0.814	0.934	0.686	0.570	0.930	0.70	0.496	0.567	0.631	0.498	0.666
			12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
	Total seeds	g	-0.021	0.738	0.728	0.655	0.021	1	0.736	0.423	0.003	0.973	0.691	0.327	-0.026	0.40	-0.508	0.035	0.425	-0.516	0.003
			0.947	0.006	0.007	0.021	0.949	0	0.006	0.170	0.992	0	0.013	0.299	0.935	0.18	0.092	0.915	0.169	0.086	0.993
			12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
	"A" seeds	g	-0.099	0.623	0.618	0.543	-0.096	0.736	1	-0.127	-0.485	0.663	0.995	-0.204	-0.540	0.89	-0.856	-0.392	0.887	-0.827	-0.477
			0.760	0.031	0.032	0.068	0.766	0.006	0	0.695	0.110	0.019	0	0.526	0.070	1E-0	4E-04	0.208	1E-04	0.001	0.117
			12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
	"B" seeds	g	-0.213	0.407	0.388	0.468	0.178	0.423	-0.127	1	0.358	0.463	-0.169	0.955	0.376	-0.53	0.543	0.297	-0.524	0.536	0.324
			0.507	0.189	0.212	0.125	0.580	0.170	0.695	0	0.253	0.130	0.600	1E-06	0.228	0.07	0.068	0.348	0.081	0.072	0.305
			12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
"C" seeds	g	0.124	0.012	0.015	-0.011	-0.076	0.003	-0.485	0.358	1	0.032	-0.519	0.362	0.965	-0.67	0.369	0.975	-0.663	0.356	0.990	
		0.701	0.971	0.963	0.974	0.814	0.992	0.110	0.253	0	0.921	0.084	0.248	0	0.01	0.238	0	0.019	0.256	0	
		12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12

Table B.1 (cont.)

		Average weight per fruit								Average No. of seeds per fruit				Average ratio of seeds per fruit									
		No. of fruit	Total	Meat	Seeds & flesh	100-seeds	Total seeds	"A" Seeds	"B" Seeds	"C" Seeds	Total	"A"	"B"	"C"	"A"	"B"	"C"	"A"	"B"	"C"			
		n	Kg			g					n				g/g			n/n					
Average seed ratio per No. of fruit	Total seeds	n	0.016	0.641	0.622	0.610	0.027	0.973	0.663	0.463	0.032	1	0.627	0.426	0.030	0.333	-0.430	0.043	0.334	-0.425	0.024		
			0.961	0.025	0.031	0.035	0.934	0	0.019	0.130	0.921	0	0.029	0.167	0.927	0.291	0.163	0.894	0.289	0.169	0.942		
			12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	
			-0.128	0.585	0.577	0.530	-0.130	0.691	0.995	-0.169	-0.519	0.627	1	-0.232	-0.574	0.904	-0.857	-0.421	0.900	-0.825	-0.510		
	0.692		0.046	0.050	0.076	0.686	0.013	0	0.600	0.084	0.029	0	0.469	0.051	6E-05	4E-04	0.173	7E-05	0.001	0.090			
	12		12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12		
	-0.154		0.257	0.228	0.372	0.183	0.327	-0.204	0.955	0.362	0.426	-0.232	1	0.402	-0.574	0.595	0.288	-0.598	0.624	0.321			
	0.633		0.421	0.476	0.234	0.570	0.299	0.526	1E-06	0.248	0.167	0.469	0	0.195	0.051	0.041	0.364	0.040	0.030	0.310			
	12		12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12		
	0.261		-0.096	-0.094	-0.113	0.028	-0.026	-0.540	0.376	0.965	0.030	-0.574	0.402	1	-0.702	0.431	0.884	-0.698	0.412	0.927			
	0.412		0.766	0.771	0.726	0.930	0.935	0.070	0.228	0	0.927	0.051	0.195	0	0.011	0.162	1E-04	0.012	0.183	2E-05			
	12		12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12		
Average seed ratio per No. of fruit	"A" seeds	g/g	0.067	0.328	0.333	0.231	-0.121	0.408	0.890	-0.530	-0.674	0.333	0.904	-0.574	-0.702	1	-0.924	-0.589	0.992	-0.899	-0.659		
			0.836	0.298	0.289	0.469	0.708	0.188	1E-04	0.076	0.016	0.291	6E-05	0.051	0.011	0	2E-05	0.044	0	7E-05	0.020		
			12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12		
			-0.148	-0.386	-0.395	-0.256	0.218	-0.508	-0.856	0.543	0.369	-0.430	-0.857	0.595	0.431	-0.924	1	0.266	-0.927	0.984	0.339		
	0.646		0.215	0.204	0.422	0.496	0.092	4E-04	0.068	0.238	0.163	4E-04	0.041	0.162	2E-05	0	0.404	1E-05	0	0.282			
	12		12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12		
	0.007		0.104	0.107	0.084	-0.184	0.035	-0.392	0.297	0.975	0.043	-0.421	0.288	0.884	-0.589	0.266	1	-0.574	0.260	0.990			
	0.982		0.747	0.741	0.795	0.567	0.915	0.208	0.348	0	0.894	0.173	0.364	1E-04	0.044	0.404	0	0.051	0.414	0			
	12		12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12		
	Average seed ratio per No. of fruit		"A" seeds	n/n	0.041	0.360	0.368	0.259	-0.155	0.425	0.887	-0.524	-0.663	0.334	0.900	-0.598	-0.698	0.992	-0.927	-0.574	1	-0.922	-0.642
					0.900	0.250	0.240	0.417	0.631	0.169	1E-04	0.081	0.019	0.289	7E-05	0.040	0.012	0	1E-05	0.051	0	2E-05	0.024
					12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
-0.145		-0.384			-0.397	-0.241	0.217	-0.516	-0.827	0.536	0.356	-0.425	-0.825	0.624	0.412	-0.899	0.984	0.260	-0.922	1	0.323		
0.654	0.217	0.201	0.451		0.498	0.086	0.001	0.072	0.256	0.169	0.001	0.030	0.183	7E-05	0	0.414	2E-05	0	0.306				
12	12	12	12		12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12			
Average seed ratio per No. of fruit	"C" seeds	n/n	0.084		0.041	0.045	0.017	-0.139	0.003	-0.477	0.324	0.990	0.024	-0.510	0.321	0.927	-0.659	0.339	0.990	-0.642	0.323	1	
			0.796		0.900	0.890	0.957	0.666	0.993	0.117	0.305	0	0.942	0.090	0.310	2E-05	0.020	0.282	0	0.024	0.306	0	
			12		12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
			0.084		0.041	0.045	0.017	-0.139	0.003	-0.477	0.324	0.990	0.024	-0.510	0.321	0.927	-0.659	0.339	0.990	-0.642	0.323	1	

APPENDIX C. SEED CLEANING EQUIPMENT: SCREEN NUMBERING SYSTEM
(excerpted from Harmond *et al.*, 1961)

Screens are manufactured with many sizes and shapes of openings. The size of a round-hole screen is indicated by the diameter of its perforations. Perforations larger than size $5\frac{1}{2}$ are measured in 64ths of an inch. Therefore, a 1-inch round-hole screen is called a No. 64; a $\frac{1}{2}$ -inch screen is a No. 32, etc. Screens smaller than $5\frac{1}{2}/64$ are measured in fractions of an inch. The next size smaller than $5\frac{1}{2}$ is a $\frac{1}{12}$ th; then, in descending order, $\frac{1}{13}$ th, $\frac{1}{14}$ th, etc.

Oblong-hole screens are measured in the same manner as round-hole screens except that two dimensions must be given. In large oblong-hole or slotted screens the hole width is indicated in 64ths of an inch; for example, $11 \times \frac{3}{4}$ means an opening $\frac{11}{64}$ ths of an inch wide and $\frac{3}{4}$ ths of an inch long. In slotted screens smaller than $5\frac{1}{2}/64 \times \frac{3}{4}$ width is generally indicated in fractions of an inch; for example, $\frac{1}{12}$ and $\frac{1}{2}$. There are some exceptions to this latter designation in that such sizes as $\frac{5}{64} \times \frac{3}{4}$, $\frac{4^7}{8}/64 \times \frac{3}{4}$, $\frac{3}{64} \times \frac{5}{16}$, and others, use the large-screen numbering system with hole widths indicated in 64ths of an inch. In all cases, the final number is the length of slot.

Wire-mesh screens are designated according to the number of openings per inch in each direction. A 10 x 10 screen has ten openings per inch across, and ten openings per inch down the screen. The size 6 x 22 has twenty-two openings per inch across the screen, and six openings per inch down the screen. Such screens as 6 x 22 have openings which are rectangular in shape, and are the wire-mesh

equivalents of oblong-perforated or slotted screens. Table C.1 shows manufacturers' screens in sizes and shapes commonly stocked.

Table C.1 Sizes and shapes of screens commonly stocked by manufacturers

PERFORATED METAL SHEET										WIRE CLOTH			
Round holes			Oblong holes		Tri-angles	Oblong cross slot	Round hole half sizes	Oblong half sizes	Square openings	Oblong openings			
Fractions	64ths		Fractions	64ths	64ths	Finished screen made only in "9" and "8" model widths. Sheet sizes 26"x 41½" and 26"x 53½"			3 x 3	2 x 8	4 x 15	6 x 14	
									4 x 4	2 x 9	4 x 16	6 x 15	
									5 x 5	2 x 10	4 x 18	6 x 16	
1/25	6	24	1/24 x 1/2	4 7/8 x 3/4	5	6 x 3/4	5 1/2	7 1/2 x 3/4	7 x 7	2 x 11	4 x 19	6 x 18	
1/24	7	25	1/22 x 1/2	5 x 3/4	8	7 x 3/4	6 1/2	8 1/2 x 3/4	8 x 8	2 x 12	4 x 20	6 x 19	
1/23	8	26	3/64 x 5/16	5 1/2 x 3/4	9	8 x 3/4	7 1/4	9 1/2 x 3/4	9 x 9	3 x 14	4 x 22	6 x 20	
1/22	9	27	1/20 x 1/2	6 x 3/4	10	9 x 3/4	7 1/2	10 1/2 x 3/4	10 x 10	3 x 16	4 x 24	6 x 21	
1/21	10	28	1/18 x 1/4	6 1/2 x 3/4	11	10 x 3/4	8 1/2	11 1/2 x 3/4	12 x 12	3 x 16sp.	4 x 24sp.	6 x 22	
1/20	11	29	1/18 x 1/2	7 x 3/4		11 x 3/4	9 1/2	12 1/2 x 3/4	14 x 14	3 x 17sp.	4 x 26	6 x 23	
1/19	12	30	1/18 x 3/4	8 x 3/4-D		12 x 3/4	10 1/2	13 1/2 x 3/4	15 x 15	3 x 20	4 x 28	6 x 24	
1/18	13	31	1/16 x 1/4-A	9 x 3/4		13 x 3/4	11 1/2	14 1/2 x 3/4	16 x 16	3 x 21	4 x 30	6 x 25	
1/17	14	32	1/16 x 1/2	10 x 3/4-E		14 x 3/4	12 1/2		17 x 17		4 x 32	6 x 26	
1/16	15	34	1/15 x 1/2	11 x 3/4-F		15 x 3/4	13 1/2		18 x 18		4 x 34	6 x 28	
1/15	16	36	1/14 x 1/4-B	12 x 3/4-G		16 x 3/4	14 1/2		20 x 20		4 x 36	6 x 30	
1/14	17	38	1/14 x 1/2	13 x 3/4-H		18 x 3/4	15 1/2		22 x 22			6 x 32	
1/13	18	40	1/13 x 1/2	14 x 3/4-I		10 1/2 x 3/4	16 1/2		24 x 24			6 x 34	
1/12	19	42	1/12 x 1/2-C	15 x 3/4-J		11 1/2 x 3/4	17 1/2		26 x 26			6 x 36	
	20	44	1/22 x 1/2diag.	16 x 3/4-K		12 1/2 x 3/4	18 1/2		28 x 28			6 x 38	
	21	48		17 x 3/4			19 1/2		30 x 30			6 x 40	
	22	56		18 x 3/4			20 1/2		32 x 32			6 x 42	
	23	64		19 x 3/4			21 1/2		34 x 34			6 x 50	
		72		20 x 3/4			22 1/2		36 x 36			6 x 60	
		80		21 x 3/4					38 x 38			18 x 20	
				22 x 3/4					40 x 40			20 x 22	
				24 x 3/4-L					45 x 45				
				32 x 3/4					50 x 50				
									60 x 60				

Source: Harmond *et al.*, 1961.

Triangular screens may be measured in two ways. The system most commonly used in the seed industry indicates length of each side of the triangle in 64ths of an inch. The sides of the hole in a No. 11 triangular screen are $\frac{11}{64}$ ths of an inch long. Another system used by perforators is to designate the triangle as the diameter of the largest circle that can be inscribed in the triangle.

APPENDIX D. SEED PRODUCTION IN *CUCURBITA MAXIMA* DUCHESNE(CUCURBITACEAE) WHEN POLLINATED BY HONEY BEES AND BUMBLE BEES

Table D.1 F-statistics for treatment effects from MANOVA (see Data Analysis) for the variables number of fruit, total weight (Kg), and weight (g) of 100, A, B and C seeds in *Cucurbita maxima* Duchesne var. 'Golden Delicious'.

Term(DF) Test Statistic	Test Value	DF1	DF2	F-Ratio	Prob Level
A(1):YEAR					
Wilks' Lambda	0.186384	6	3	2.18	0.278542
Hotelling-Lawley Trace	4.365280	6	3	2.18	0.278542
Pillai's Trace	0.813616	6	3	2.18	0.278542
Roy's Largest Root	4.365280	6	3	2.18	0.278542
Log # Fruit	0.032012	1	8	2.37	0.162027
Log Total Weight (Kg)	0.008616	1	8	0.14	0.717027
Log 100-Seeds Weight (g)	0.000632	1	8	0.16	0.700580
Log "A" Seeds Weight (g)	0.021220	1	8	0.09	0.774045
Log "B" Seeds Weight (g)	0.009020	1	8	0.10	0.763716
Log "C" Seeds Weight (g)	0.064523	1	8	0.14	0.717288
B(1):Bee Treatment					
Wilks' Lambda	0.292036	6	3	1.21	0.473724
Hotelling-Lawley Trace	2.424232	6	3	1.21	0.473724
Pillai's Trace	0.707964	6	3	1.21	0.473724
Roy's Largest Root	2.424232	6	3	1.21	0.473724
Log # Fruit	0.023256	1	8	1.72	0.225606
Log Total Weight (Kg)	0.030705	1	8	0.50	0.498521
Log 100-Seeds Weight (g)	0.001050	1	8	0.26	0.621339
Log "A" Seeds Weight (g)	0.304188	1	8	1.26	0.293434
Log "B" Seeds Weight (g)	0.013965	1	8	0.15	0.708831
Log "C" Seeds Weight (g)	0.891470	1	8	1.94	0.200671
AB(1)					
Wilks' Lambda	0.225925	6	3	1.71	0.352718
Hotelling-Lawley Trace	3.426251	6	3	1.71	0.352718
Pillai's Trace	0.774075	6	3	1.71	0.352718
Roy's Largest Root	3.426251	6	3	1.71	0.352718
Log # Fruit	0.078727	1	8	5.84	0.042131*
Log Total Weight (Kg)	0.087771	1	8	1.44	0.264997
Log 100-Seeds Weight (g)	0.000717	1	8	0.18	0.682371
Log "A" Seeds Weight (g)	0.180409	1	8	0.75	0.411735
Log "B" Seeds Weight (g)	0.042174	1	8	0.45	0.520164
Log "C" Seeds Weight (g)	0.013802	1	8	0.03	0.866555

Note: MANOVA performed on log10 transformed data

Table D.2 Analysis of variance tables for log # fruit, log total weight (kg), log of 100-, A-, B-, and C-seeds weight (g) per cage of *Cucurbita maxima* Duchesne var. 'Golden Delicious', when pollinated by honey bees or bumblebees, 1996-1997.

Source Term	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power ($\alpha=0.05$)
Log # Fruit						
A: YEAR	1	3.201151E-02	3.201151E-02	2.37	0.162027	0.236844
B: Bee Treatment	1	0.0232561	0.0232561	1.72	0.225606	0.185061
AB	1	7.872735E-02	7.872735E-02	5.84	0.042131*	0.491792
S	8	0.1079256	0.0134907			
Total (Adjusted)	11	0.2419205				
Log Total Weight (Kg)						
A: YEAR	1	8.616406E-03	8.616406E-03	0.14	0.717027	0.060636
B: Bee Treatment	1	3.070452E-02	3.070452E-02	0.50	0.498521	0.088377
AB	1	8.777097E-02	8.777097E-02	1.44	0.264997	0.162104
S	8	0.4887902	6.109878E-02			
Total (Adjusted)	11	0.6158822				
Log 100-Seeds Weight (g)						
A: YEAR	1	6.323046E-04	6.323046E-04	0.16	0.700580	0.061993
B: Bee Treatment	1	1.04998E-03	1.04998E-03	0.26	0.621339	0.069993
AB	1	7.170459E-04	7.170459E-04	0.18	0.682371	0.063612
S	8	3.182986E-02	3.978732E-03			
Total (Adjusted)	11	3.422919E-02				
Log "A" Seeds Weight (g)						
A: YEAR	1	2.121963E-02	2.121963E-02	0.09	0.774045	0.056638
B: Bee Treatment	1	0.3041885	0.3041885	1.26	0.293434	0.148376
AB	1	0.1804092	0.1804092	0.75	0.411735	0.107675
S	8	1.924714	0.2405892			
Total (Adjusted)	11	2.430531				
Log "B" Seeds Weight (g)						
A: YEAR	1	9.020038E-03	9.020038E-03	0.10	0.763716	0.057284
B: Bee Treatment	1	1.396475E-02	1.396475E-02	0.15	0.708831	0.061300
AB	1	4.217408E-02	4.217408E-02	0.45	0.520164	0.084491
S	8	0.7458429	9.323036E-02			
Total (Adjusted)	11	0.8110018				
Log "C" Seeds Weight (g)						
A: YEAR	1	6.452329E-02	6.452329E-02	0.14	0.717288	0.060615
B: Bee Treatment	1	0.8914698	0.8914698	1.94	0.200671	0.202708
AB	1	1.380231E-02	1.380231E-02	0.03	0.866555	0.052261
S	8	3.667405	0.4584256			
Total (Adjusted)	11	4.6372				

* Term significant at $\alpha = 0.05$

Table D.3 Within correlations\covariances for log # fruit, log total weight (kg), and log of 100-, A-, B-, and C-seeds weight (g) per cage of *Cucurbita maxima* Duchesne var. 'Golden Delicious', when pollinated by honey bees or bumblebees, 1996-1997.

	Log # Fruit	Log Total Weight (Kg)	Log 100Seeds Weight (g)	Log "A" Seeds Weight (g)	Log "B" Seeds Weight (g)	Log "C" Seeds Weight (g)
Log # Fruit	0.0134907	2.351113E-02	-1.855245E-03	9.22682E-03	2.504878E-02	5.041667E-02
Log T. W. (Kg)	0.8189173	6.109878E-02	2.864115E-03	7.202911E-02	5.413621E-02	5.297968E-02
Log 100-Seeds (g)	-0.253228	0.1836969	3.978732E-03	2.096115E-02	2.862572E-04	-1.734186E-02
Log "A" Seeds (g)	0.1619559	0.594092	0.6774927	0.2405892	1.315494E-02	-0.1037178
Log "B" Seeds (g)	0.7063023	0.7172869	1.486296E-02	0.0878359	9.323036E-02	0.1152011
Log "C" Seeds (g)	0.6410952	0.3165619	-0.4060587	-0.3123064	0.5572416	0.4584256

Table D.4 Within-cell correlations analysis for log # fruit, log total weight (kg), and log of 100-, A-, B-, and C-seeds weight (g) per cage of *Cucurbita maxima* Duchesne var. 'Golden Delicious', when pollinated by honey bees or bumblebees, 1996-1997.

Variable	R-Squared Other Y's	Canonical Variate	Eigenvalue	Percent of Total	Cumulative Total
Log # Fruit	0.896424	1	2.956152	49.27	49.27
Log Total Weight (Kg)	0.939533	2	2.076166	34.60	83.87
Log 100-Seeds Weight (g)	0.688847	3	0.511204	8.52	92.39
Log "A" Seeds Weight (g)	0.857732	4	0.319555	5.33	97.72
Log "B" Seeds Weight (g)	0.778314	5	0.101018	1.68	99.40
Log "C" Seeds Weight (g)	0.630846	6	0.035906	0.60	100.00

Table D.5 Sample sizes (n), means, standar errors (SE), means \pm 1SE, and 95% confidence intervals (CI) for number of fruit, total weight (kg), and weight of 100, A, B, and C seeds per cage of *Cucurbita maxima* Duchesne var. 'Golden Delicious', when pollinated by honey bees or bumblebees, 1996-1997.

Term	Count	Mean ⁽¹⁾	Standard Error ⁽¹⁾	Mean ⁽²⁾	Min. ⁽²⁾ (Mean-1SE)	Max. ⁽²⁾ (Mean+1SE)	-SE ⁽²⁾	+SE ⁽²⁾	95% Confidence Interval	
Number of Fruit										
All	12	0.6783862		4.7685485						
A: YEAR										
1996	6	0.6267371	0.2764132	4.2338659	2.2403914	8.0011111	1.9934745	3.7672452	1.0431617	17.183932
1997	6	0.7300352	0.2764132	5.3707533	2.8419864	10.149588	2.5287668	4.7788344	1.3232739	21.798201
B: Bee Treatment										
BB	6	0.722409	0.2764132	5.2772662	2.7925168	9.9729169	2.4847493	4.6956507	1.3002401	21.418766
HB	6	0.6343634	0.2764132	4.3088701	2.2800806	8.1428531	2.0287895	3.833983	1.0616416	17.488351
AB: YEAR,Bee Treatment										
1996,BB	3	0.7517575	0.3909073	5.6462162	2.2953568	13.888802	3.3508594	8.2425863	0.7787006	40.939682
1996,HB	3	0.5017167	0.3909073	3.1748024	1.2906527	7.8095139	1.8841497	4.6347115	0.4378544	23.019912
1997,BB	3	0.6930604	0.3909073	4.932424	2.0051788	12.132986	2.9272452	7.2005621	0.6802576	35.764105
1997,HB	3	0.76701	0.3909073	5.8480355	2.3774024	14.385246	3.4706331	8.5372107	0.8065347	42.403037
Total Weight (Kg)										
All	12	1.131025		13.521504						
A: YEAR										
1996	6	1.157821	0.2764132	14.382057	7.6104055	27.179045	6.7716513	12.796989	3.5435254	58.372253
1997	6	1.104229	0.2764132	12.712442	6.7269128	24.023827	5.9855296	11.311385	3.1321572	51.595812
B: Bee Treatment										
BB	6	1.181609	0.2764132	15.191792	8.0388847	28.709273	7.1529071	13.517482	3.7430321	61.658713
HB	6	1.080442	0.2764132	12.034887	6.3683775	22.74339	5.666509	10.708504	2.9652174	48.845825
AB: YEAR,Bee Treatment										
1996,BB	3	1.293929	0.3909073	19.675646	7.9987422	48.39899	11.676904	28.723344	2.7135763	142.66452
1996,HB	3	1.021714	0.3909073	10.512693	4.2737262	25.85957	6.2389672	15.346877	1.4498632	76.22562
1997,BB	3	1.069289	0.3909073	11.729757	4.768499	28.853354	6.9612575	17.123597	1.6177151	85.050323
1997,HB	3	1.139169	0.3909073	13.777455	5.6009501	33.890369	8.1765049	20.112914	1.9001244	99.89781

⁽¹⁾ Log 10 transformed data

⁽²⁾ Back-transformed data (antilog)

Table D.5 (cont.)

Term	Count	Mean ⁽¹⁾	Standard Error ⁽¹⁾	Mean ⁽²⁾	Min. ⁽²⁾ (Mean-1SE)	Max. ⁽²⁾ (Mean+1SE)	-SE ⁽²⁾	+SE ⁽²⁾	95% Confidence Interval	
100-Seeds Weight (g)										
All	12	1.45491		28.504275						
A: YEAR										
1996	6	1.447651	0.2764132	28.031801	14.833301	52.974175	13.1985	24.942374	6.9066198	113.77228
1997	6	1.462169	0.2764132	28.984713	15.337543	54.774977	13.647169	25.790264	7.1414031	117.63985
B: Bee Treatment										
BB	6	1.464264	0.2764132	29.12487	15.411709	55.039845	13.713161	25.914974	7.1759358	118.2087
HB	6	1.445556	0.2764132	27.896903	14.761918	52.719247	13.134985	24.822344	6.873383	113.22477
AB: YEAR,Bee Treatment										
1996,BB	3	1.464736	0.3909073	29.156541	11.853011	71.720499	17.30353	42.563958	4.0211385	211.40875
1996,HB	3	1.430567	0.3909073	26.950511	10.956194	66.294012	15.994317	39.343501	3.7168928	195.41323
1997,BB	3	1.463793	0.3909073	29.093301	11.827302	71.564938	17.265999	42.471637	4.0124167	210.95021
1997,HB	3	1.460545	0.3909073	28.87653	11.739178	71.031715	17.137351	42.155185	3.9825206	209.37844
A-Seeds Weight (g)										
All	12	2.093945		124.14951						
A: YEAR										
1996	6	2.135996	0.2764132	136.77162	72.374037	258.46944	64.397586	121.69782	33.698498	555.11307
1997	6	2.051894	0.2764132	112.69224	59.632196	212.96449	53.060041	100.27226	27.765695	457.3824
B: Bee Treatment										
BB	6	2.253159	0.2764132	179.12615	94.78635	338.51054	84.339803	159.38439	44.134026	727.01681
HB	6	1.934731	0.2764132	86.046062	45.532112	162.60886	40.51395	76.562796	21.200473	349.23395
AB: YEAR,Bee Treatment										
1996,BB	3	2.417824	0.3909073	261.71222	106.39389	643.77084	155.31833	382.05862	36.094168	1897.6275
1996,HB	3	1.854169	0.3909073	71.477442	29.057731	175.82325	42.419711	104.34581	9.8578461	518.26988
1997,BB	3	2.088494	0.3909073	122.601	49.840995	301.57914	72.760002	178.97814	16.908576	888.95744
1997,HB	3	2.015294	0.3909073	103.58432	42.110141	254.8011	61.474174	151.21679	14.285881	751.07095

⁽¹⁾ Log 10 transformed data

⁽²⁾ Back-transformed data (antilog)

Table D.5 (cont.)

Term	Count	Mean ⁽¹⁾	Standard Error ⁽¹⁾	Mean ⁽²⁾	Min. ⁽²⁾ (Mean-1SE)	Max. ⁽²⁾ (Mean+1SE)	-SE ⁽²⁾	+SE ⁽²⁾	95% Confidence Interval	
B-Seeds Weight (g)										
All	12	2.077411		119.51186						
A: YEAR										
1996	6	2.049994	0.2764132	112.2003	59.37188	212.03483	52.828415	99.834532	27.644488	455.38577
1997	6	2.104827	0.2764132	127.29959	67.361818	240.5693	59.937771	113.26971	31.36473	516.66906
B: Bee Treatment										
BB	6	2.043297	0.2764132	110.48339	58.463364	208.79024	52.020028	98.306851	27.221468	448.4174
HB	6	2.111524	0.2764132	129.27781	68.408615	244.30773	60.869199	115.02991	31.852135	524.69805
AB: YEAR,Bee Treatment										
1996,BB	3	2.075164	0.3909073	118.89511	48.334441	292.46325	70.560671	173.56814	16.397477	862.08674
1996,HB	3	2.024824	0.3909073	105.88245	43.044404	260.45416	62.83805	154.57171	14.60283	767.73434
1997,BB	3	2.011431	0.3909073	102.66703	41.737237	252.54472	60.929793	149.87769	14.159373	744.41989
1997,HB	3	2.198224	0.3909073	157.84252	64.167734	388.26773	93.674784	230.42522	21.768927	1144.4873
C-Seeds Weight (g)										
All	12	0.3798025		2.3977423						
A: YEAR										
1996	6	0.3064748	0.2764132	2.0252321	1.0716713	3.8272603	0.9535608	1.8020282	0.4989871	8.2197811
1997	6	0.4531301	0.2764132	2.8387693	1.5021624	5.3646736	1.3366069	2.5259043	0.6994306	11.521673
B: Bee Treatment										
BB	6	0.1072421	0.2764132	1.2800947	0.6773746	2.4191082	0.6027201	1.1390135	0.3153963	5.1955024
HB	6	0.6523628	0.2764132	4.4912042	2.3765645	8.487426	2.1146397	3.9962218	1.1065661	18.228388
AB: YEAR,Bee Treatment										
1996,BB	3	-6.94E-18	0.3909073	1	0.4065301	2.4598425	0.5934699	1.4598425	0.1379155	7.2508174
1996,HB	3	0.6129497	0.3909073	4.101566	1.66741	10.089206	2.434156	5.9876403	0.5656695	29.739706
1997,BB	3	0.2144842	0.3909073	1.6386424	0.6661575	4.0308023	0.972485	2.3921599	0.2259942	11.881497
1997,HB	3	0.691776	0.3909073	4.9178582	1.9992573	12.097157	2.9186008	7.1792984	0.6782488	35.658492

⁽¹⁾ Log 10 transformed data

⁽²⁾ Back-transformed data (antilog)

APPENDIX E. DISTANCES FOR THE DISTANCE EFFECT STUDY ON PRODUCTION OF GDWS, *CUCURBITA MAXIMA* DUCHESNE (CHAPTER 4)

Table E.1 Distance from each plot to the closest group of hives in each site

Site	Distance (m)	Site	Distance (m)	Site	Distance (m)	Site	Distance (m)
Ind	15	Lake	275	Riv1	240	Riv2	121
Ind	71	Lake	300	Riv1	255	Riv2	133
Ind	99	Lake	349	Riv1	275	Spring	30
Ind	137	Lake	375	Riv2	40	Spring	30
Ind	151	Riv1	15	Riv2	50	Spring	30
Ind	200	Riv1	45	Riv2	70	Spring	60
Ind	300	Riv1	55	Riv2	75	Spring	60
Lake	30	Riv1	60	Riv2	85	Spring	60
Lake	45	Riv1	80	Riv2	100	Spring	90
Lake	60	Riv1	225	Riv2	114	Spring	90
Lake	275	Riv1	230	Riv2	121	Spring	90

Table E.2 Number of plots at each distance (26 distances and 44 plots)

Distance (m)	No. Plots	Distance (m)	No. Plots	Distance (m)	No. Plots	Distance (m)	No. Plots
15	2	70	2	120	2	240	1
30	4	75	1	135	2	255	1
40	1	80	1	150	1	275	3
45	2	85	1	200	1	300	2
50	1	90	3	225	1	350	1
55	1	100	2	230	1	375	1
60	5	115	1				

**APPENDIX F. MULTIPLE REGRESSION REPORT FOR
CHAPTER 4: DISTANCE EFFECT ON
PRODUCTION OF GDWS, *CUCURBITA
MAXIMA* DUCHESNE**

DEPENDENT VARIABLE: LOG # FRUIT

Descriptive Statistics Section

Variable	Count	Mean	Standard Deviation	Minimum	Maximum
Nearest Hive (m)	44	127.5227	99.76425	15	375
Log # Fruit	44	0.8303837	0.1141322	0.60206	1.079181

Correlation Matrix Section

	Nearest Hive (m)	Log # Fruit
Nearest Hive (m)	1.000000	-0.247868
Log # Fruit	-0.247868	1.000000

Regression Equation Section

Independent Variable	Regression Coefficient	Standard Error	T-Value (Ho: B=0)	Prob Level	Decision (5%)	Power (5%)
Intercept	0.8665448	2.756974E-02	31.4310	0.000000	Reject Ho	1.000000
Nearest Hive (m)	-2.835657E-04	1.710173E-04	-1.6581	0.104746	Accept Ho	0.367197
R-Squared	0.061439					

Model .8665448-2.835657E-04*Nearest Hive (m)

Regression Coefficient Section

Independent Variable	Regression Coefficient	Standard Error	Lower 95% C.L.	Upper 95% C.L.	Standardized Coefficient
Intercept	0.8665448	2.756974E-02	0.8109068	0.9221828	0.0000
Nearest Hive (m)	-2.835657E-04	1.710173E-04	-6.286924E-04	6.156112E-05	-0.2479
T-Critical	2.018082				

Analysis of Variance Section

Source	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (5%)
Intercept	1	30.33963	30.33963			
Model	1	3.441325E-02	3.441325E-02	2.7493	0.104746	0.367197
Error	42	0.5257115	1.251694E-02			
Total(Adjusted)	43	0.5601248	1.302616E-02			

Root Mean Square Error	0.1118791	R-Squared	0.0614
Mean of Dependent	0.8303837	Adj R-Squared	0.0391
Coefficient of Variation	0.1347319	Press Value	0.5831164
Sum Press Residuals	4.19455	Press R-Squared	-0.0410

DEPENDENT VARIABLE: LOG TOTAL WEIGHT (Kg)**Descriptive Statistics Section**

Variable	Count	Mean	Standard Deviation	Minimum	Maximum
Nearest Hive (m)	44	127.5227	99.76425	15	375
Log Total Weight (Kg)	44	1.384036	0.1191661	1.135299	1.716247

Correlation Matrix Section

	Nearest Hive (m)	Log Total Weight (Kg)
Nearest Hive (m)	1.000000	-0.048552
Log Total Weight (Kg)	-0.048552	1.000000

Regression Equation Section

Independent Variable	Regression Coefficient	Standard Error	T-Value (Ho: B=0)	Prob Level	Decision (5%)	Power (5%)
Intercept	1.391432	2.967791E-02	46.8844	0.000000	Reject Ho	1.000000
Nearest Hive (m)	-5.79947E-05	1.840944E-04	-0.3150	0.754301	Accept Ho	0.060929
R-Squared	0.002357					

Model 1.391432-5.79947E-05*Nearest Hive (m)

Regression Coefficient Section

Independent Variable	Regression Coefficient	Standard Error	Lower 95% C.L.	Upper 95% C.L.	Standardized Coefficient
Intercept	1.391432	2.967791E-02	1.331539	1.451324	0.0000
Nearest Hive (m)	-5.79947E-05	1.840944E-04	-4.295123E-04	3.135229E-04	-0.0486
T-Critical	2.018082				

Analysis of Variance Section

Source	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (5%)
Intercept	1	84.28444	84.28444			
Model	1	1.439445E-03	1.439445E-03	0.0992	0.754301	0.060929
Error	42	0.6091846	0.0145044			
Total(Adjusted)	43	0.6106241	1.420056E-02			

Root Mean Square Error	0.1204342	R-Squared	0.0024
Mean of Dependent	1.384036	Adj R-Squared	0.0000
Coefficient of Variation	8.701667E-02	Press Value	0.6762096
Sum Press Residuals	4.11488	Press R-Squared	-0.1074

DEPENDENT VARIABLE: LOG 100 SEEDS WEIGHT (g)**Descriptive Statistics Section**

Variable	Count	Mean	Standard Deviation	Minimum	Maximum
Nearest Hive (m)	44	127.5227	99.76425	15	375
Log 100Seeds Weight (g)	44	1.483692	5.403376E-02	1.382017	1.61595

Correlation Matrix Section

	Nearest Hive (m)	Log 100Seeds Weight (g)
Nearest Hive (m)	1.000000	0.191974
Log 100Seeds Weight (g)	0.191974	1.000000

Regression Equation Section

Independent Variable	Regression Coefficient	Standard Error	T-Value (Ho: B=0)	Prob Level	Decision (5%)	Power (5%)
Intercept	1.470432	1.322222E-02	111.2092	0.000000	Reject Ho	1.000000
Nearest Hive (m)	1.039761E-04	8.201847E-05	1.2677	0.211883	Accept Ho	0.236104
R-Squared	0.036854					

Model 1.470432+ 1.039761E-04*Nearest Hive (m)

Regression Coefficient Section

Independent Variable	Regression Coefficient	Standard Error	Lower 95% C.L.	Upper 95% C.L.	Standardize Coefficient
Intercept	1.470432	1.322222E-02	1.443749	1.497116	0.0000
Nearest Hive (m)	1.039761E-04	8.201847E-05	-6.154384E-05	2.694961E-04	0.1920
T-Critical	2.018082				

Analysis of Variance Section

Source	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (5%)
Intercept	1	96.85899	96.85899			
Model	1	4.626852E-03	4.626852E-03	1.6071	0.211883	0.236104
Error	42	0.120918	0.002879			
Total(Adjusted)	43	0.1255448	2.919647E-03			
Root Mean Square Error		5.365631E-02	R-Squared		0.0369	
Mean of Dependent		1.483692	Adj R-Squared		0.0139	
Coefficient of Variation		3.616406E-02	Press Value		0.1338461	
Sum Press Residuals		1.970109	Press R-Squared		-0.0661	

DEPENDENT VARIABLE: LOG "A" SEEDS WEIGHT (g)**Descriptive Statistics Section**

Variable	Count	Mean	Standard Deviation	Minimum	Maximum
Nearest Hive (m)	44	127.5227	99.76425	15	375
Log "A" Seeds Weight (g)	44	2.311939	0.3597128	1.238046	2.745777

Correlation Matrix Section

	Nearest Hive (m)	Log "A" Seeds Weight (g)
Nearest Hive (m)	1.000000	0.068283
Log "A" Seeds Weight (g)	0.068283	1.000000

Regression Equation Section

Independent Variable	Regression Coefficient	Standard Error	T-Value (Ho: B=0)	Prob Level	Decision (5%)	Power (5%)
Intercept	2.280543	0.0894817	25.4861	0.000000	Reject Ho	1.000000
Nearest Hive (m)	2.462043E-04	5.55062E-04	0.4436	0.659636	Accept Ho	0.071793
R-Squared	0.004663					

Model 2.280543+ 2.462043E-04*Nearest Hive (m)

Regression Coefficient Section

Independent Variable	Regression Coefficient	Standard Error	Lower 95% C.L.	Upper 95% C.L.	Standardize Coefficient
Intercept	2.280543	0.0894817	2.099962	2.461124	0.0000
Nearest Hive (m)	2.462043E-04	5.55062E-04	-8.739562E-04	1.366365E-03	0.0683
T-Critical	2.018082				

Analysis of Variance Section

Source	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (5%)
Intercept	1	235.1828	235.1828			
Model	1	2.594237E-02	2.594237E-02	0.1967	0.659636	0.071793
Error	42	5.537971	0.1318565			
Total(Adjusted)	43	5.563913	0.1293933			
Root Mean Square Error		0.3631204	R-Squared		0.0047	
Mean of Dependent		2.311939	Adj R-Squared		0.0000	
Coefficient of Variation		0.1570631	Press Value		6.174148	
Sum [Press Residuals]		13.3327	Press R-Squared		-0.1097	

DEPENDENT VARIABLE: LOG "B" SEEDS WEIGHT (g)**Descriptive Statistics Section**

Variable	Count	Mean	Standard Deviation	Minimum	Maximum
Nearest Hive (m)	44	127.5227	99.76425	15	375
Log "B" Seeds Weight (g)	44	2.49062	0.1822427	1.994757	2.834993

Correlation Matrix Section

	Nearest Hive (m)	Log "B" Seeds Weight (g)
Nearest Hive (m)	1.000000	-0.302450
Log "B" Seeds Weight (g)	-0.302450	1.000000

Regression Equation Section

Independent Variable	Regression Coefficient	Standard Error	T-Value (Ho: B=0)	Prob Level	Decision (5%)	Power (5%)
Intercept	2.561076	4.331231E-02	59.1304	0.000000	Reject Ho	1.000000
Nearest Hive (m)	-5.524964E-04	2.686697E-04	-2.0564	0.045990	Reject Ho	0.519704
R-Squared	0.091476					

Model 2.561076-5.524964E-04*Nearest Hive (m)

Regression Coefficient Section

Independent Variable	Regression Coefficient	Standard Error	Lower 95% C.L.	Upper 95% C.L.	Standardize Coefficient
Intercept	2.561076	4.331231E-02	2.473669	2.648484	0.0000
Nearest Hive (m)	-5.524964E-04	2.686697E-04	-1.094694E-03	-1.029902E-05	-0.3025
T-Critical	2.018082				

Analysis of Variance Section

Source	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (5%)
Intercept	1	272.9404	272.9404			
Model	1	0.1306403	0.1306403	4.2288	0.045990	0.519704
Error	42	1.297493	3.089269E-02			
Total(Adjusted)	43	1.428133	0.0332124			
Root Mean Square Error		0.1757632	R-Squared		0.0915	
Mean of Dependent		2.49062	Adj R-Squared		0.0698	
Coefficient of Variation		7.057003E-02	Press Value		1.42634	
Sum [Press Residuals]		6.257375	Press R-Squared		0.0013	

DEPENDENT VARIABLE: LOG "C" SEEDS WEIGHT (g)**Descriptive Statistics Section**

Variable	Count	Mean	Standard Deviation	Minimum	Maximum
Nearest Hive (m)	44	127.5227	99.76425	15	375
Log "C" Seeds Weight (g)	44	0.6119583	0.5202793	0	1.775246

Correlation Matrix Section

	Nearest Hive (m)	Log "C" Seeds Weight (g)
Nearest Hive (m)	1.000000	-0.335159
Log "C" Seeds Weight (g)	-0.335159	1.000000

Regression Equation Section

Independent Variable	Regression Coefficient	Standard Error	T-Value (Ho: B=0)	Prob Level	Decision (5%)	Power (5%)
Intercept	0.834853	0.1222236	6.8305	0.000000	Reject Ho	0.999999
Nearest Hive (m)	-1.747882E-03	7.581626E-04	-2.3054	0.026152	Reject Ho	0.615067
R-Squared	0.112331					

Model .834853-1.747882E-03*Nearest Hive (m)

Regression Coefficient Section

Independent Variable	Regression Coefficient	Standard Error	Lower 95% C.L.	Upper 95% C.L.	Standardized Coefficient
Intercept	0.834853	0.1222236	0.5881958	1.08151	0.0000
Nearest Hive (m)	-1.747882E-03	7.581626E-04	-3.277916E-03	-2.178481E-04	-0.3352
T-Critical	2.018082				

Analysis of Variance Section

Source	DF	Sum of Squares	Mean Square	F-Ratio	Prob Level	Power (5%)
Intercept	1	16.47769	16.47769			
Model	1	1.307503	1.307503	5.3150	0.026152	0.615067
Error	42	10.33219	0.2460045			
Total(Adjusted)	43	11.63969	0.2706905			

Root Mean Square Error	0.4959884	R-Squared	0.1123
Mean of Dependent	0.6119583	Adj R-Squared	0.0912
Coefficient of Variation	0.8104938	Press Value	11.16565
Sum Press Residuals	18.52798	Press R-Squared	0.0407