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**Optimizing Production of Self
Incompatible Crops Using Cross-Pollination
and Seed Set Models**

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Abstract

Data were collected to construct and validate an almond cross-pollination and nut set prediction model (ALMOPOL). Nut set predictions are based upon weather conditions, honey bee foraging activity, and orchard design (i.e., the number of trees of each cultivar per hectare). Data were collected from five different cultivars on: 1) the progression of bloom as a function of temperature, 2) nectar and pollen rewards per blossom, 3) blossom density, 4) blossom nut set potential throughout bloom and during an individual blossom's life, 5) the methods by which honey bees acquire and transfer compatible pollen among cultivars, and 6) the percentage of blossoms that have been cross-pollinated. An equation that predicts final nut set as a function of initial set was tested for accuracy, and the data needed to run an ALMOPOL simulation were collected so that actual nut set could be compared to ALMOPOL predictions.

We were successful in predicting the progression of bloom in each cultivar using accumulated degree days, even though cultivars differed in their base temperature for degree day accumulation. The estimates of pollen and nectar rewards per blossom and time spent per blossom by a forager provided information on the number of blossoms honey bees might visit per hour. Information on blossom nut set potential over time was entered directly into the ALMOPOL program. Data on the size and distribution of the population of foragers carrying compatible pollen on their bodies and the percentage of cross pollinated blossoms over time confirmed the assumption made during ALMOPOL's construction that honey bees could be acquiring compatible pollen in the hive from nestmate contacts. The equation estimating final nut set from initial nut set generated very accurate predictions in almost all cases. The equation loses its accuracy however, if weather conditions, insects, or disease significantly contribute to nut drop. The ALMOPOL program accurately predicted initial and final nut set in four of the five cultivars in both years that it was tested.

Objectives of the Original Proposal

The overall objective of this proposal was to construct and validate a simulation model to predict initial nut set in almonds. This was accomplished by fulfilling the eight objectives stated below:

- 1) Determine the number of open blossoms per tree for each almond cultivar throughout bloom.

2) Estimate floral rewards available to almond foragers (at time (t)) so that the number of blossoms visited by almond foragers and the time it takes to collect full nectar or pollen loads during a single foraging trip can be estimated.

3) Estimate the foraging population on each almond cultivar as a function of weather (i.e., temperature, wind velocity, and solar radiation) and bloom conditions at time (t).

4) Identify the population of foragers capable of cross-pollinating almond blossoms by determining the types of pollen on foragers' bodies. Predictions will be based upon the percentage of the potential foraging population on each almond cultivar and competitive plants.

5) Determine the percentage of blossoms on each cultivar that have been cross-pollinated at time (t).

6) Determine blossom quality throughout bloom, and predict the probabilities of cross-pollination leading to nut set.

7) Determine the percentage of initial nut set that remains on trees until harvest as a function of the initial percentage of blossoms setting nuts.

8) Determine the accuracy of nut set predictions generated by the model by comparing actual and predicted nut yields.

E. Body of the report written in the form of a scientific paper.

An in-depth description of the experiments conducted to fulfill each objective is provided below. The materials and methods used to fulfill each objective, the results of the experiments, and a discussion of how each objective fills a particular component in the ALMOPOL model also are provided.

Research to fulfil all of the proposals objectives was conducted in commercial almond orchards in the U.S. (Dixon, California) and Israel. Weather conditions (average temperature, wind velocity, solar radiation, and rainfall) were monitored hourly throughout bloom using an automated micrologger.

The U.S. research was conducted in a 12 hectare commercially managed almond orchard in Dixon, California. The orchard has an equilateral planting system where all tree trunks are equidistant (7.9m) from each other. Because of pruning practices though, some trees had branches within

the rows that were much closer than their trunk distances would indicate. The orchard contains five cultivars ('NePlus', 'Nonpareil', 'Price', 'Peerless', and 'Mission') arranged as shown in Figure 1. In 1988, 59 honey bee colonies were placed in the orchard, and in 1989 and 1990, 60 colonies were introduced.

Objective-1 : Determine the number of open blossoms per tree for each almond cultivar throughout bloom.

Introduction

Almonds are a self-incompatible plant that must have pollen transferred between two different cultivars for nut set to occur (Tufts and Philp 1972, Socias i Company et al. 1976). Before nut set can be predicted however, an estimate of the number of open blossoms on trees of each cultivar must be made. This estimate is used to determine the number of bees foraging each cultivar, and the chances that pollen will be transferred between cultivars. The hypothesis that was tested to fulfil this objective is that the rate of bloom progression can be predicted as a function of temperature (i.e., accumulated heat units or degree days (DD) (Baskerville and Emin 1969)), because warm temperatures accelerate bloom, while cooler temperatures retard it.

In the ALMOPOL program bloom progression is predicted as a function of accumulated DD since the beginning of the cultivar's bloom. The bloom phenology of each cultivar is defined mathematically using separate equations for each cultivar. Each cultivar's bloom period is divided into a pre- and post-peak bloom interval, and separate equations are used to define each. Bloom progression data were collected prior to the start of this project and also during the first year. Pre- and post-peak bloom equations were derived for each cultivar from these data. Daily blossom counts along with temperature data were used to test the accuracy of those equations in the second and third year of the study.

Materials and Methods

Five trees of each cultivar ('Neplus', 'Nonpareil', 'Price', 'Peerless', and 'Mission') were selected for daily counts of open blossoms. Sections of branches approximately 1m in length were chosen on the four sides of each tree. Trees were chosen along a diagonal transect across the orchard. Hourly temperature estimates were converted to degree days (DD) using the equation:

$$(T / 24) - Bx = DDx$$

where: T = average hourly temperature
 Bx = base temperature for bloom progression for
 cultivar (x).

Results and Discussion

Correlation coefficients for actual and predicted pre- and post-peak bloom progression are shown in Table 1. The bloom progression equations adequately predicted bloom progression in all instances except for the post-peak bloom interval in 1990. Weather conditions other than temperature can strongly affect the length of time blossoms retain their petals. Heavy rains or strong winds can cause blossoms to prematurely drop their petals especially during the post-peak bloom interval. Conversely, low wind velocities and post-peak bloom intervals that are free from rain can cause blossoms to retain their petals. In 1990 there was no rain and wind velocities were very low. Open blossoms retained their petals for longer periods than predicted by the post-peak bloom equations, thus reducing the accuracy of the predictions of post-peak bloom progression. However, pre-peak bloom equations accurately predicted bloom progression as did the post-peak bloom equations in most instances.

Objective 2: Estimate floral rewards available to almond foragers (at time (t)) so that the number of blossoms visited by almond foragers and the time it takes to collect full nectar or pollen loads during a single foraging trip can be estimated.

Introduction

The size of the pollinator population foraging a plant species is influenced by nectar and pollen availability, and also by the distribution of blossoms containing these resources. Almond blossoms are arranged in clusters and a single tree can bear more than 10000 blossoms. Plants can supply relatively little nectar and pollen per blossom, and still attract bees if many flowers exist in a small space. This enables worker bees to walk from blossom to blossom while foraging. Energetically speaking, walking is far less costly than flying, and having many blossoms within a pollinator's walking distance can add to a plant's attractiveness.

The purpose of this objective is to determine nectar and pollen availability along with blossom density to determine the number of blossoms honey bees must visit to obtain full nectar or pollen loads. In addition, bees were timed on blossoms while they collected nectar or pollen so

that the amount of time required to collect full pollen or nectar loads could be estimated.

Materials and Methods

Trees for blossom density, nectar, and pollen measurements, were chosen along a diagonal transect across the orchard. Open blossoms were counted daily (weather permitting) on the four sides (cardinal points) of five trees of each cultivar. The average number of blossoms per cluster for each cultivar was estimated by counting blossoms in four randomly selected clusters (one cluster on each side of a tree) from 17 trees of each cultivar in 1988 and 10 of each in 1989.

Blossoms were classified into stages depending upon the condition of their petals, anthers, and corolla. The classification system enabled us to sample nectar and pollen from similarly aged blossoms and limit variation within cultivars due to blossom age (Beutler 1953). Blossoms were classified in the A-stage when they first opened and the petals had not fully separated, the anthers had not yet dehisced, and the corolla base was white. In B-stage blossoms the petals were fully separated, but the anthers were not dehisced, and the corolla base was white or light pink. Blossoms were considered in the C-stage when the petals were fully separated, less than 50% of the anthers were dehisced, and the corolla base was pink or red. In the D-stage, the petals were fully separated, more than 50% of the anthers were dehisced, and the corolla base was pink or red. Blossoms in the E-stage had at least one petal that had abscised, all the anthers had dehisced, and the base of the corolla was red.

Nectar samples from each cultivar were taken from an equal number of open blossoms of each stage whenever possible. Due to weather conditions and availability of blossoms, in both years nectar was collected at 1-3 day intervals throughout bloom. Samples were taken from a different area of five trees per cultivar using 1, 3, or 5 μ l Drummond microcaps. The samples were sealed and immediately frozen for later measurements of the amount of nectar. The amount of nectar collected was estimated by measuring the length of the micropipette that was filled with nectar, and converting this to microliters. Separate nectar samples were taken to determine the percentage of total dissolved solids (TDS) using the same sampling procedure described above for estimates of the amount of nectar per blossom. TDS was estimated in the field using a refractometer. Samples were taken from all blooming cultivars simultaneously to minimize variation in the amount of nectar and its TDS among cultivars due to weather conditions. However, because

each cultivar started and ended bloom on different dates, sometimes all five cultivars could not be sampled on the same day.

The amount of pollen per blossom was estimated by removing and then freezing all the anthers from blossoms of each cultivar. In 1988 and 1989 pollen samples were collected on the same days as nectar samples. Pollen samples were taken from a different area of five trees of each cultivar on each date. In all instances an equal number of blossoms in each stage were sampled.

To remove the pollen, anthers were sonicated for 40 sec. in 40 ml of ethanol. The pollen and ethanol mixture was then poured on to previously weighed filter paper (Whatman 40, 9 cm diameter) that had been placed in a Buchner funnel attached to a suctioning apparatus. The filter paper was allowed to dry completely, and was then weighed. The weight of pollen on the filter paper was determined by the difference in the weight of the filter paper before and after the pollen sample was added.

The amount of nectar and pollen per blossom and per m, TDS in the nectar, blossoms per m, and blossoms per cluster were analyzed using a one-way analysis of variance to test for differences among cultivars. A $(\log + 1)$ transformation was performed on the 1989 nectar per m data to stabilize the variance prior to the analysis of variance (Ott 1977). When the analysis of variance indicated rejection of the null hypothesis, a Scheffe's multiple comparison test was conducted to determine which cultivars differed.

Honey bees visiting almond blossoms were observed to determine the amount of time required to collect either nectar or pollen from a single blossom. The bee had to alight on the blossom and either begin collecting pollen from the anthers or probe the nectaries with her mouthparts for the behavior to be scored as a visit. The interval that was timed began when the forager landed on the blossom and ended when she left the blossom. Honey bees were timed on five trees of each cultivar in the AM and PM. As few as six and as many as 20 bees were timed per cultivar (depending upon foraging activity) during each sampling interval.

Results and Discussion

In both years some nectar and pollen samples were lost during the freezing and thawing process, resulting in unequal sample sizes among the cultivars. However samples from all dates are represented in the estimates of the amount of nectar and pollen per blossom for each cultivar.

In 1988 the five cultivars averaged equivalent amounts of nectar per blossom, however in 1989 'Mission' blossoms had substantially more nectar than the other cultivars (Table 2). We could not obtain measurable amounts of nectar from 'Price' blossoms in 1989. The cultivars did not differ in the percentage of TDS in the nectar in either year of this study, although in 1989 the percentages were considerably lower than in 1988.

In 1988 'Neplus,' 'Price,' and 'Mission' had significantly more pollen per blossom than did 'Peerless' (Table 3). 'Nonpareil' had an equivalent amount of pollen per blossom as all other cultivars except 'Neplus' which had significantly more. In 1989 the cultivars did not differ in the average amounts of pollen per blossom.

In 1988 'Mission' had significantly more blossoms per cluster than all other cultivars except 'Nonpareil,' and more blossoms per m than all other cultivars except 'Peerless' (Table 4). The number of blossoms per cluster and per m on 'Neplus,' 'Nonpareil,' 'Price,' and 'Peerless' trees did not differ significantly. In 1989 'Neplus' had significantly more blossoms per cluster and per m than the other cultivars, while 'Price' and 'Mission' had the least.

The average number of blossoms per m was multiplied by the average amount of nectar and pollen per blossom to estimate the potential amount of nectar and pollen available to foragers per m of branch (Table 4). In 1988 'Mission' had significantly more nectar and pollen per m of branch than the other cultivars. 'Peerless' had more nectar per m of branch than did 'Neplus,' 'Nonpareil,' or 'Price' which had equivalent amounts. In 1989 all cultivars from which we could obtain nectar had equivalent amounts of nectar per m of branch. However, in 1989 'Neplus' had significantly more pollen per m than all other cultivars, and 'Price' and 'Mission' had the least.

There was no significant difference among the cultivars in either year in the amount of time spent by honey bees collecting either nectar or pollen from a single blossom (Table 5). However, nectar collectors did spend significantly more time per blossom than did pollen collectors. We pooled the data from all cultivars for both years and estimated that a pollen gathering honey bee spends an average of 6.5 sec. per blossom while a nectar collecting forager spends an average of 10.0 sec. per blossom.

Measurements of nectar and pollen were taken from blossoms whose rewards were both exposed to weather conditions and available to foragers. Thus, the estimates are of the standing crop available at time (t) and are not absolute values of the amount of nectar or pollen produced

by blossoms in the absence of pollinators. The number of blossoms and the amount of nectar and pollen per tree for each cultivar might be dependent on conditions that trees experience in a given year and in the previous year. In 1988 'Mission' and 'Peerless' had more blossoms and nectar per m than the other cultivars, and also attracted the most honey bees. 'NePlus' was among the cultivars with the lowest number of blossoms per m in 1988. In 1989 'Neplus' had the highest number of blossoms per cluster and per m, the greatest amount of nectar and pollen per m, and attracted the most honey bees. 'Mission' had considerably fewer blossoms per m in 1989 than in 1988. These data suggest, at least in these cultivars, that a heavy bloom one year might be followed by a lighter one the following year, which ultimately influences the cultivar's relative attractiveness to pollinators.

Nectar per blossom differed greatly between years in all cultivars in both the amount per blossom and its concentration of TDS. Bloom period weather conditions were very different in 1988 and 1989. In 1988 there was no rainfall during the interval of bloom when nectar was sampled. The average TDS concentration in our samples was similar to that reported by Vansell (1934) who reported that almond nectar is 20-40% sugar. However, in 1989 it rained the day before nectar samples were taken in all cases. The precipitation may have influenced the concentration of TDS on the day of the sample, but the cloudiness on the previous day may have affected the nectar volume. Pelopidas (1928) reported that cloudiness not on the sample day but on the preceding day influences nectar secretion due to the influence on photosynthesis. Temperature during the times of nectar sampling was higher and relative humidity was lower in 1988 compared to 1989 on almost every sampling day, and this too may have affected the amount of nectar secreted and its TDS (Veprikov 1936 in Beutler 1953).

Vansell (1934) stated that the structure of almond blossoms protects the nectar so that it never appears to fall below the level of attractiveness for bees. Our data indicate that almond nectar might be influenced by environmental factors which may reduce the amount of nectar and its sugar concentration. Almond blossoms remain attractive to bees, possibly because their arrangement in clusters enables bees to visit many blossoms while covering a relatively small area. Older blossoms that have lost their petals (E-stage) still secrete some nectar, so that even though blossoms of different stages may exist in a cluster, they are all potentially rewarding.

Pollen per blossom did not differ greatly between years, suggesting that this resource is not influenced as strongly by weather conditions as nectar. Our estimates of available pollen per blossom for each cultivar were compared

with those measured by Hill et al (1985) with the same cultivars in Australia. Methods of pollen collection differed between the two studies. In their study the average amount of 'Mission' pollen per blossom ranged between 0.89 mg (1978) and 1.02 mg (1979) which was comparable to our findings. However, 'NePlus' and 'NonPareil' averaged more pollen per blossom in our study.

The attractiveness of a plant is dependent upon the caloric and nutritional rewards available to its pollinators, and the efficiency with which pollinators can collect them (Heinrich and Raven 1972, Pyke et al. 1977, Pyke 1984). Plants that have many blossoms within a pollinators' walking distance permit them to collect the rewards more efficiently and thus add to the plant's attractiveness (Heinrich and Ravens 1972, Heinrich 1975, Kevan and Baker 1983). This is an illustration of the energy optimization theory that is based on a mathematical model which states that bees achieve maximum caloric intake by visiting flowers in close proximity to each other (Waddington and Holden 1979). This theory is supported by the observations and data collected in our study. Almond blossoms are distributed in clusters, and foragers often were seen walking from blossom to blossom among the clusters until they reached an area of branch without blossoms. At that point the forager either flew to a nearby cluster or left the tree. The most attractive cultivars on a per tree basis were those with the greatest number of blossoms per m of branch, with one exception. In 1989 'Mission' had fewer blossoms per m and per cluster than all other cultivars except 'Price'. However, 'Mission' had three times as much nectar per blossom than all other cultivars which apparently made it as attractive as 'Neplus' which had three times as many blossoms per m as 'Mission'.

For a honey bee to collect a full nectar load it must collect about 30 ul of nectar (Frisch 1967, Ribbands 1953), and for a full almond pollen load about 4.5 mg (DeGrandi-Hoffman unpubl. data). In 1988 a honey bee would have had to visit at least 40 blossoms for a full nectar load (this would have taken about 400 sec. not counting transit time between blossoms) and about six blossoms for a full load of pollen (this would have taken about 39 sec. not counting transit time) on the most reward rich cultivars. In 1989 it took about 59 blossoms for a full nectar load (this would have take about 590 sec. not including transit time), and 4 blossoms for a full pollen load (this would have taken about 26 sec. not including transit time). To achieve full loads, a nectar collecting honey bee would have had to cover a minimum of 1.0 m of branch on 'Peerless' or 'Mission,' the most attractive cultivars in 1988, and 1.5 m of branch on a 'Neplus' or 'Mission' tree in 1989. A pollen collector could have collected a full load from as few as 2 blossom clusters in 1988 and one in 1989. Bees probably visit more

blossoms to achieve full pollen or nectar loads when foraging populations are large and many blossoms already have been visited by other foragers. This could occur when weather conditions are very favorable for flight and large populations of bees exist in a given area. It could also occur early and late in a cultivar's bloom when there are not many blossoms on a tree, and resources can be depleted rather quickly. Still, the first bees visiting a tree could have easily obtained full nectar or pollen loads from a relatively small area of a single tree.

Our estimates of time spent per blossom and the number of blossoms that a forager needs to visit to collect full nectar or pollen loads shed some light on the number of blossoms a forager will visit per hour, but the story is not complete. We do not know how long it takes bees to travel from the hive to their foraging area, how much time is spent in the hive each hour, and how many trips to the field a bee makes per hour. We do know that foragers probably can obtain full loads in less than an hour, and that these loads can be collected in a relatively short period of time. Additional information on the number of trips a forager takes per hour is still needed. Because we do not have a good estimate on the number of blossoms a bee will visit per hour, the ALMOPOL program allows users to vary this number through menus. Our default value assumes that a bee will make at least two foraging trips per hour and will visit 100 blossoms per hour. This default value was obtained through multiple simulations using various numbers for this parameter (that were based upon our field estimates of nectar and pollen per blossom and time spent per blossom by foragers) to determine the value which consistently resulted in the most accurate nut set predictions.

Objective 3. Estimate the foraging population on each almond cultivar as a function of weather (i.e., temperature, wind velocity, and solar radiation) and bloom conditions at time (t).

Introduction

Before nut set can be predicted a method must be developed to predict the foraging population in the orchard, and the number of honey bees per tree on each cultivar. Historically, foraging populations have been estimated as a function of colonies/hectare and the population size of those colonies (Farrar 1931, Filmer 1932, and Waller et al. 1985). However, the foraging population on the target crop may not be solely dependent on colony number or strength because honey bees from colonies other than those introduced into the orchard can be foraging almond trees. The purpose of this objective is to develop a series of foraging response equations that do not use hive parameters. Using these equations, predictions will be made on the size of the

almond foraging population at time (t). The foraging population on almond will be considered a response to weather conditions (i.e., temperature, wind velocity, and solar radiation) and the state of the almond bloom (i.e., open blossoms on each cultivar at time (t)). After the foraging population is predicted, it is distributed on almond trees of each cultivar based upon their relative floral density such that trees with more open blossoms will attract more honey bees.

Methods and Materials

Twice daily (once in the AM and again in the PM) foraging honey bees were counted on five trees of each cultivar. Trees were selected along a diagonal transect across the orchard. Counts were made by two observers stationed on opposite sides of the tree. All the bees seen in a 30 sec. interval were included in the count.

During studies conducted prior to this project, equations were derived to predict honey bee foraging responses to temperature, wind velocity, solar radiation, and state of the almond bloom (expressed as the number of DD that accumulated since the beginning of bloom in the orchard) (DeGrandi-Hoffman et al. 1989). Estimates of honey bees per tree taken early in the bloom were used to predict the potential foraging population (PFP) at the site using the equation:

$$\frac{[(B_i * T_i) + (B_j * T_j) \dots + (B_x * T_x)]}{R_t * R_w * R_s * R_b} = \text{PFP}$$

where :

- B_i = average number of bees per tree on cultivar (i)
- B_j = average number of bees per tree on cultivar (j)
- T_i = the number of trees of cultivar (i) per hectare
- T_j = the number of trees of cultivar (j) per hectare
- R_t = reduction in potential flight activity due to temperature (t)
- R_w = reduction in potential flight activity due to wind velocity (t)
- R_s = reduction in potential flight activity due to solar radiation (t)
- R_b = reduction in potential flight activity due to the state of bloom (t)

PFP is used to predict the almond foraging population each hour using the equation:

$$\text{PFP} * (R_t * R_w * R_s * R_b)$$

The active foraging population is distributed to trees of each cultivar according to the number of each per hectare and their state of bloom at time (t).

Actual counts of honey bees were compared with those predicted by the equations using the weather conditions and bloom state at the time of the bee count.

Results and Discussion

We were unsuccessful in predicting honey bees per tree for the entire bloom period using a PFP from sample counts of honey bees per tree taken early in bloom. We had periods where the bloom response equations predicted honey bees per tree within the 95% confidence interval of our estimates of average honey bees per tree at time (t), but at other times the predictions greatly under- or overestimated honey bees per tree. The resources honey bees choose to forage apparently can shift considerably during the almond bloom period which is not surprising. To further confound predictions, honey bee colonies are being introduced and removed from fruit growing areas early and late in bloom. To address these problems and improve predictions of honey bees per tree, we have made a major change in the PC version of the ALMOPOL program currently under construction. PC-ALMOPOL will enable users to enter new estimates of honey bees per tree at any time during the simulation. To obtain the most accurate nut set predictions, users will be instructed to enter estimates of honey bees per tree at least three times during bloom; once during the pre-peak, peak, and post-peak bloom intervals.

Objective 4. The population of foragers capable of cross-pollinating almond blossoms will be identified by the types of pollen on their bodies, and predicted based upon the percentage of the potential foraging population on each almond cultivar and competitive plants.

Introduction

Almond is a self-incompatible species that will set nuts only when blossoms are cross-pollinated (Tufts and Philp 1922, Socias i Company et al. 1976). There are at least two ways in which honey bees might acquire pollen from different cultivars. They can move from tree-to-tree of different cultivars (Williams 1959, Free 1962, Free and Spencer-Booth 1964), or they can acquire pollen in the hive from contacting nestmates who have foraging areas on different cultivars (Betts 1920, Karmo and Vickery 1954, Lukoshus 1957, Free and Williams 1972, DeGrandi-Hoffman et al. 1984, 1986). Observations of honey bees foraging on orchard trees indicate that most establish foraging areas on a single tree and only occasionally move between trees (Free

1966). Most tree-to-tree movement by honey bees is to the nearest tree usually down a row which is often planted to a single cultivar (Free and Spencer-Booth 1964). Honey bees rarely move across rows of different cultivars, and may exhibit fidelity to a single cultivar in orchards of standard apple trees as long as sufficient numbers of blossoms exist (Free 1966).

If tree-to-tree movement is the primary means by which honey bees acquire cross-pollen, and the probability of this type of movement is low, the sub-population of honey bees carrying pollen from cultivars other than the one on which they are foraging should be a relatively small percentage of the total foraging population. Furthermore, if tree-to-tree movement is the primary means of cross-pollination, then the distribution of nut set on a tree should reflect this. The sides of trees adjacent to compatible pollen sources should have higher percentages of blossoms setting nuts than should the sides adjacent to trees of the same cultivar within a row. Free (1962) and Free and Spencer-Booth (1964) found higher percentages of blossoms setting fruit on limbs of apple, plum, and sweet cherry adjacent to compatible pollen sources compared to those adjacent to the same cultivar, and attributed this to movement of foragers from compatible pollen sources across the row.

Alternatively, if honey bees obtain compatible pollen primarily from nestmate contacts within the hive, the percentage of foraging bees carrying cross-pollen relative to the cultivar they are foraging should be large, especially when conditions are favorable for foraging and several cultivars are in bloom.

The ALMOPOL program was constructed with the assumption that the cross-pollinating population is the result of both tree-to-tree movement and compatible pollen transfer in the hive during contacts among nestmates. The purpose of this objective is to determine the proportion of honey bees that carry compatible pollen while foraging on almond. The means by which honey bees might acquire compatible pollen in almond orchards is discussed in light of the size and distribution of the cross-pollinating population of honey bees.

Materials and Methods

Honey bees foraging on trees of each cultivar were sampled once a day every second or third day of bloom depending upon weather conditions and flight activity. One honey bee was collected from five trees of each cultivar on every sample date. Whether the forager was collecting pollen or nectar was recorded at the time of the sample. Bees were considered nectar collectors if they had empty corbiculae and were probing the nectaries of almond blossoms. Pollen

foragers were identified by their pollen collecting behavior on anthers and by the presence of pollen loads in their corbiculae (Thorp 1978). Forager samples were collected from all cultivars except 'Mission' in 1988, but in 1989 'Mission' also was sampled. In both years honey bees were frozen immediately after collection until the pollen was identified.

Pollen was collected from anthers of each cultivar and frozen for later use as standards for comparison of pollen types on the bodies of almond foragers and blossom stigmas (Objective 5). The blossoms used for these samples were bagged in nylon mesh prior to anthesis. Pollen samples from each cultivar were placed on separate aluminum scanning electron microscope (SEM) stubs, sputter coated with gold for 3-5 minutes, and photographed under an ISI-DS130 SEM operated at 20 kV.

Pollen was removed from the bodies of honey bees collected while foraging on almond blossoms by rolling each of them over a separate aluminum SEM stub pretreated with adhesive (sticky tabs). Pollen from corbicular loads was not included in the sample. The same SEM procedures previously described for the standard pollen samples were used for the samples from honey bees.

Exine patterns of pollen grains from each cultivar were classified by the width of the ridges, and the distance and appearance of pores between ridges. Pollen from the bodies of foragers was classified as self-pollen if it had the same exine pattern as the cultivar at which the bee was foraging when captured. If the exine pattern differed but the shape of the pollen grain and the texture of the exine pattern were characteristic of almond, it was classified as cross-pollen. If the pollen grain was from a species other than almond, it was classified as non-almond pollen. Counts of pollen grains from the bodies of bees were made by identifying all the pollen in 40 SEM fields distributed throughout the SEM stub. An average of 35 pollen grains were identified per sample.

The trees used for sampling foraging honey bees were chosen along a diagonal transect across the length of the orchard. Because the cultivars started and ended their blooming periods at different times, sometimes honey bee samples could not be taken from all cultivars. However, sampling times that represent both pre- and post-full bloom periods were chosen for every cultivar. It was not possible to sample trees of different cultivars in the same state of bloom, therefore analysis of variance was performed within each cultivar to determine if the percentages of self-, cross-, and non-almond pollen on the bodies of foraging honey bees differed. For all the data sets, if the analysis

of variance indicated a rejection of the null hypothesis, a Tukey's W multiple comparison test was conducted (Ott 1977).

Results

In both years some honey bees were damaged during the freezing and thawing process resulting in unequal sample sizes. However, honey bees from all sample dates are represented in the estimates of pollen types on the bodies of honey bees foraging on almond blossoms.

In both years of this study every honey bee we examined had self-pollen on its body, and 90% or more also had cross-pollen (Table 6). In 1988, 60-92% ('Price' and 'Nonpareil' respectively) of the bees had pollen from species other than almond on their bodies, but in 1989, 92-100% ('NePlus' and 'Nonpareil', 'Price', and 'Mission' respectively) did so. These profiles of pollen types on foragers' bodies are in agreement with ALMOPOL predictions. ALMOPOL predicts that every forager can acquire some compatible pollen from nestmate contacts after 4-5 hours of uninterrupted foraging if the weather conditions are conducive for flight, and more than one cultivar has sufficient numbers of blossoms to attract honey bees. Under these conditions bees will also have non-almond pollen on their bodies since not all of a colony's foraging population are gathering resources from almond trees. The proportions of self-, cross-, and non-almond pollen on the bodies of nectar or pollen foragers did not significantly differ within any of the cultivars in either year except for 'Peerless' in 1988 for which the proportion of non-almond pollen on nectar foragers was greater than on pollen foragers (Table 7). Separate analysis of pollen and nectar collectors was not possible for 'Price' in 1988, because all the bees we sampled were pollen foragers.

In 1988 foragers on 'NePlus' and 'Nonpareil' had equivalent proportions of self- and cross-pollen on their bodies. 'Peerless' and 'Price' foragers had significantly greater proportions of self- than cross- or non-almond pollen. In 1989 foragers on all cultivars had predominantly self-pollen on their bodies. Foragers had similar proportions of cross- and non-almond pollen with the exception of those on 'Price' which had significantly greater proportions non-almond pollen.

Discussion

The pollen types identified on the bodies of honey bees foraging on almond blossoms indicate that the cross-pollinating population of honey bees can comprise a majority of the overall honey bee population foraging on almonds. This is in agreement with ALMOPOL predictions. The

distribution of cross-pollinated almond stigmas (see Objective 5) and almond nut set (see Objectives 7 and 8) indicate that the cross-pollinating population is homogeneously distributed on a tree and is not biased by the adjacent pollen source. These results differ from those of Free (1962) and Free and Spencer-Booth (1964) who found significant differences in fruit set depending upon a limb's proximity to a pollinizer.

The percentages of pollen types on the bodies of foragers did not always reflect the percentages on the stigmas (see Objective 5). For example, non-almond pollen was found in much higher percentage on stigmas than on the bodies of almond foragers. Conversely, self-pollen was present in higher percentages on foragers' bodies than on stigmas, particularly in 1989. In 1988 and 1989 cultivars that had the highest percentage of cross-pollen on their foragers also had the most cross-pollen on their stigmas, although the percentages were always lower on the stigmas. As expected, most of the pollen on almond foragers was self-pollen. In many cases cross- and non-almond pollen occurred with similar frequency.

The many types of pollen present on the bodies of almond foragers in our study indicate that either honey bees were foraging on different almond cultivars and plant species throughout the day, or the pollen reflects the division of the foraging population in the colony, assuming that all the pollens entering a colony can be transferred from bee to bee. In other studies honey bees that were marked while foraging at standard sized apple trees remained constant to the cultivar on which they were marked (Mommers 1948 cited in Free 1966). With this in mind, along with a forager's tendency to show fidelity to a single species if it offers sufficient rewards (Free 1963), and since full nectar or pollen loads can be collected from a single almond tree (see Objective 2, or DeGrandi-Hoffman et al. 1991), an argument can be made that the types of pollen on the bodies of foragers reflected those entering the colonies. .

Objective 5. Determine the percentage of blossoms on each cultivar that have been cross-pollinated at time (t).

Introduction

If tree-to-tree movement is the primary means of cross-pollination, then the distribution of cross-pollinated blossoms on a tree should reflect this. The sides of trees adjacent to compatible pollen sources should have higher percentages of cross-pollinated blossoms than should the sides adjacent to trees of the same cultivar within a row. Free (1962) and Free and Spencer-Booth (1964) found higher percentages of blossoms setting fruit on limbs of apple,

plum, and sweet cherry adjacent to compatible pollen sources compared to those adjacent to the same cultivar, and attributed this to movement of foragers from compatible pollen sources across the row. Alternatively, if honey bees obtain compatible pollen primarily from nestmate contacts within the hive, the percentage of cross-pollinated blossoms should be homogeneously distributed on a tree.

The purpose of this objective is to determine the proportion and distribution of cross-pollinated blossoms on almond trees.

Materials and Methods

When the bees' foraging activity ceased for the day, one pistil was collected from a different side of five trees per cultivar. Pistils were collected on the same days that foraging honey bees were sampled (see Objective 4). Pistil samples were collected from all cultivars except 'Mission' in 1988, but in 1989 'Mission' also was sampled. In both years pistils were frozen immediately after collection until the pollen was identified.

Pollen was collected from anthers of each cultivar and frozen for later use as standards for comparison of pollen types on blossom stigmas. The blossoms used for these samples were bagged in nylon mesh prior to anthesis. Pollen samples from each cultivar were placed on separate aluminum SEM stubs, sputter coated with gold for 3-5 minutes, and photographed under an ISI-DS130 SEM operated at 20 kV.

Pollen from stigmas was prepared for identification under the SEM by removing the stigmatic surface and a small piece of the style and mounting this on an SEM stub. The sample was sputter-coated with gold for 3-5 minutes, and the pollen was classified as self-, cross-, or non-almond pollen using the SEM conditions and identification criteria previously described for pollen samples from the bodies of honey bees foraging on almond blossoms (see Objective 4). An average of 31 pollen grains were identified per stigma sample.

The percentages of blossoms setting nuts in each cultivar was determined by counting all the blossoms on 1 m sections of branches on the four sides of five trees per cultivar. Six to eight weeks after bloom and immediately before harvest the developing nuts on these limbs were counted.

The trees used for sampling pistils and for nut set estimates were chosen along a diagonal transect across the length of the orchard. Because the cultivars started and ended their blooming periods at different times, sometimes pistil samples could not be taken from all cultivars on the

same day. However, sampling times that represented both pre- and post-full bloom periods were chosen for every cultivar. It was not possible to sample trees of different cultivars in the same state of bloom, therefore analysis of variance was performed within each cultivar to determine if the percentages of self-, cross-, and non-almond pollen on stigmas differed. In 1989 a separate analysis of variance was conducted for each cultivar to determine if differences existed in the proportion of self-, cross-, or non-almond pollen on stigmas depending upon the side of the tree from which they were sampled. This was not possible in 1988 because we did not record the side of the tree from which the pistil was collected. However, an analysis of variance was conducted on initial and final nut set data from limbs adjacent to trees of the same cultivar within a row, and trees of a different cultivar across the row. The distribution of nuts on a tree can be a good indicator of the distribution of cross-pollinating honey bees and cross-pollinated blossoms. Initial and final nut set data from all cultivars was included in the analysis. For all the data sets, if the analysis of variance indicated a rejection of the null hypothesis, a Tukey's W multiple comparison test was conducted (Ott 1977).

Results

In 1988, 42.1% ('Price') to 81.2% ('NePlus') of the stigmas we examined had self-pollen, while 36.8% ('Price') to 68.7% ('NePlus') had cross-pollen (Table 8). Pollen from species other than almond was found on 43.7% ('NePlus') to 94.7% ('Price') of the stigmas. In 1989 the stigmas did not differ significantly for any of the cultivars with regard to the side of the tree being sampled, so all samples for each cultivar were combined. Sixty percent ('Price') to 100% ('Nonpareil' and 'Peerless') of the stigmas had self-pollen, and 10% ('Price') to 100% ('NePlus') had cross-pollen. The percentage of stigmas with pollen other than almond ranged from 80% ('Nonpareil') to 100% ('NePlus', 'Price', 'Peerless', and 'Mission').

In 1988 pollen from non-almond species was the predominant type found on 'Price' and 'Peerless' stigmas (Table 9). 'NePlus' had significantly more self- than cross-pollen, while 'Nonpareil' had equivalent amounts of cross-, self-, and non-almond pollen. In 1989 'Price' and 'Mission' stigmas had significantly more non-almond pollen than either self- or cross-pollen. 'NePlus', 'Nonpareil', and 'Peerless' had equivalent amounts of self- and non-almond pollen. In some instances we could not identify any of the pollen grains on the stigmas surface because they were embedded in stigmatic fluid, and only a small portion of each grain was visible. We did not include these samples in our analysis.

Initial and final nut set did not differ significantly on limbs that were either adjacent to the same cultivar within a row or adjacent to a different cultivar across the row for any of the cultivars in 1988 (Table 10). 'Peerless' set a significantly lower percentage of blossoms to nuts than the other cultivars which set equivalent percentages. In 1989 'NePlus' had the lowest percentage of blossoms setting nuts followed by 'Nonpareil' and 'Peerless'. 'Price' and 'Mission' had the highest percentage of blossoms setting nuts, and 'Price' had significantly higher nut set on limbs adjacent to the same cultivar compared to those next to a different cultivar.

Discussion

The distribution of cross-pollinated almond stigmas and almond nut set indicate that the cross-pollinating population is homogeneously distributed on a tree and is not biased by the adjacent pollen source. These results differ from those of Free (1962) and Free and Spencer-Booth (1964) who found significant differences in fruit set depending upon a limb's proximity to a pollinizer.

The percentages of pollen types on the bodies of foragers (see Objective 4) did not always reflect the percentages on the stigmas. For example, non-almond pollen was found in much higher percentage on stigmas than on the bodies of almond foragers. Conversely, self-pollen was present in higher percentages on foragers' bodies than on stigmas, particularly in 1989. In 1988 and 1989 cultivars that had the highest percentage of cross-pollen on their foragers also had the most cross-pollen on their stigmas, although the percentages were always lower on the stigmas.

One reason for the differences between the percentages of pollen types on the bodies of foragers and on almond stigmas could be that we sampled pollen from most of the bee's body when rolling it on an SEM stub. Observations of honey bees foraging on almond blossoms indicate that the stigma touches only a small portion of the honey bee during a visit. Furthermore, even though we observed the stigma touching many different areas of a honey bee's body during a visit to an almond blossom, perhaps our method of transferring pollen from the bee to the SEM stub enabled us to obtain pollen from areas that had little chance of touching the stigma (Ish-Am and Eisikowitch 1990). Another factor that may have contributed to the differences in pollen types on bees and stigmas could be that other bee species may also have transferred pollen to the stigmas.

Objective 6. Determine blossom quality throughout the bloom period, and predict the probabilities of cross-pollination leading to nut set.

Introduction

The probabilities that cross-pollination will lead to nut set change throughout the life of a blossom. Consequently, even if cross-pollination rates remain constant throughout bloom, nut set rates will vary because of the dynamic nature of blossom quality. The purpose of this set of experiments was to determine the rate that blossom nut set potential changes with age in five commercial almond cultivars. Data collected from this objective was entered directly into the blossom quality arrays of the ALMOPOL model.

Methods and Materials

Blossoms were cross-pollinated by hand with pollen collected from compatible cultivars just prior to the hand-pollination. Blossoms were categorized into age groups according to the state of their petals, anthers, and corolla prior to the hand-pollination. This enabled us to hand-pollinate blossoms in different standardized age groups. Blossoms were in the AB-stage when they first opened, none of the anthers had dehisced, and the corolla was white or pink. Blossoms in the C-, D-, or E-stage were classified according to the criteria described in the Methods and Materials section of Objective 2.

Blossoms were selected for hand pollinations on the four sides of trees of each cultivar. The blossoms were bagged in nylon mesh prior to anthesis to reduce the chances that they would be visited by pollinators prior to our hand pollination. Nut set from hand-pollinated blossoms was counted six to eight weeks after bloom.

Results and Discussion

The results of the hand-pollinations are shown in Table 11. 'NePlus' and 'Peerless' blossoms had their highest nut set potential in the AB- and C-stages. Nut set potentials were reduced in the D- and E-stages. Nut set potentials were highest in the C-stage for 'Nonpareil', 'Price', and 'Mission' which had lower probabilities of setting nuts if cross-pollinated in the AB- or E-stages.

Comparisons were made at the 0.05 level between 1988 and 1989 data on blossom quality in each age category for each cultivar. In 'Nonpareil' and 'Price' there were no significant differences between 1988 and 1989 blossom quality data for any blossom stage. In 'NePlus' there were

no significant differences between the two years in blossom quality of AB-, C-, or E-stage blossoms. However, blossom quality in the D-stage was significantly higher in 1988 than 1989. Sample sizes for D-stage blossoms were greater in 1988 than 1989 (38 in 1988 versus 11 in 1989), making the 1988 results more credible. In light of the difference in sample sizes between the two years and the fact that there were no significant differences between the two years in blossom of the C- or E-stage, we used 1988 D-stage blossom quality in the ALMOPOL program.

'Peerless' blossom quality estimates did not differ significantly for C- or D-stage blossoms between 1988 and 1989. However, AB-stage blossoms had significantly higher quality in 1989 compared to 1988. Blossom quality estimates for 'Mission' in 1988 and 1989 did not differ significantly for AB- or D-stage blossoms. C-stage blossoms, however, had slightly higher blossom quality in 1989 compared to 1988. In 1988 sample sizes were much larger than in 1989 (78 in 1988 versus 11 in 1989) giving more credibility to 1988 blossom quality estimates for the C-stage.

Objective 7. The percentage of initial nut set that remains on trees until harvest will be estimated as a function of the initial percentage of blossoms setting nuts.

Introduction

ALMOPOL generates initial and final nut set predictions. The initial nut set predictions are based upon weather conditions, orchard parameters, and the size of the foraging population. Final set is predicted as a function of initial set (DeGrandi-Hoffman et al. 1989). The algorithm (hereafter referred to as the nut thinning equation) used to predict final set as a function of initial set was tested for the accuracy of its predictions during each year of this study

Materials and Methods

Five trees of each cultivar selected along a diagonal transect across the orchard were used to test the accuracy of predictions from the nut thinning equation. All the blossoms were counted on limbs from each of the four sides of the five trees. Nut set on the limbs was counted six to eight weeks after bloom (initial set) and immediately before harvest (final set). Nut set was expressed as the percentage of blossoms setting nuts. Initial nut set (I) from each limb was entered into the equation:

$$F = (\exp^{- (I * 0.5)} + 0.057) * I$$

to generate an estimate of final set (F).

Results and Discussion

Predictions on final nut set that were generated from the nut thinning equation were within the 95% confidence interval of average actual final set in all instances except Neplus and Peerless in 1990 (Table 12). In these cases actual nut set was lower than that predicted by the equation. Many factors other than crop load (i.e., insect feeding damage, disease, and water stress) can cause nut abscission. The nut thinning equation does not account for these. In 1990 trees were water stressed throughout the year due to drought conditions in California. This may have influenced nut abscission rates and caused the final nut set predictions to be inaccurate. Still, the nut thinning equation accurately predicted final nut set in all cultivars in 1988 and 1989 and in three of the five cultivars in 1990. From this we conclude that the nut thinning equation adequately predicts final nut set based upon initial set.

Objective 8. Determine the accuracy of nut set predictions generated by the model by comparing actual and predicted nut yields.

Introduction

Data required to run an ALMOPOL simulation were collected to determine the accuracy of ALMOPOL nut set predictions.

Materials and Methods

Five trees of each cultivar selected along a diagonal transect were used for model validation data collection. The height, width, trunk height, and percentage of blossoms setting nuts were estimated for each tree. The average number of blossoms per m of branch was estimated by choosing limbs on the four sides of 10 trees per cultivar and counting all the blossoms. This information along with the weather data collected during bloom were entered into the ALMOPOL program, and nut set predictions were generated.

Results and Discussion

ALMOPOL nut set predictions were within the 95% confidence intervals of the actual average percentage of blossoms setting nuts in four of the five cultivars in both 1989 and 1990. In 1989 ALMOPOL predictions were slightly lower than actual set in Mission while in 1990 they were considerably lower than actual set in Nonpareil. In 1989 nut set predictions for Mission could have been improved if blossom quality during the later stages of bloom was increased. There was no way to improve the predictions for

Nonpareil in 1990 (increasing blossom quality resulted in only minor improvements in nut set predictions). Perhaps an error in our estimates of actual nut set occurred in Nonpareil in 1990.

Description of cooperation

We had excellent cooperation between our laboratory in the U.S. and Dr. Eisikowitch in Israel. We discussed the methods to be used for each objective, standardized our data collection sheets, and were in constant communication via BITNET and FAX systems. In addition, Dr. Robbin Thorp at the University of California at Davis provided invaluable cooperation in data collection, interpretation of results, and manuscript preparation. A free exchange of ideas, experience, and knowledge occurred among all participants in this project which largely accounts for the successful completion of this work.

Evaluation of the research achievements with respect to the aims of the original proposal and emphasizing the benefit to agriculture

During the data collection and analysis, we obtained many insights into the almond cross-pollination and nut set system. We were very successful in predicting the progression of bloom using accumulated degree days. Differences in base temperatures among cultivars causes bloom temperature to have subtle effects on cross-pollination and nut set. Bloom in cultivars with lower base temperatures progresses through time faster than those with higher temperatures. Thus, low temperatures can reduce the period of bloom overlap in cultivars with different base temperatures because there can be times when the ambient temperature exceeds the base for one cultivar (hence bloom is progressing) but not another. This occurred in Neplus which was the first cultivar to bloom. In years with cooler weather Neplus was the only cultivar in bloom for several days before either Nonpareil or Peerless blossoms opened. During that time nut set was not occurring even though Neplus had open blossoms upon which honey bees were foraging. Conversely, in years with warmer weather Neplus bloom was followed within 1-2 days by bloom on the other cultivars. Since nut set occurs only when two or more cultivars are in bloom simultaneously, temperature is influencing nut set in a way other than the effects on honey bee foraging activity.

Our data on honey bee foraging activity on trees have led us to the conclusion that the population of honey bees foraging almond throughout bloom is extremely fluid, responding to stimulæ too diverse to predict. Fortunately, computer programs can be made to be highly interactive enabling users to enter information at any point during the

simulation. This should rectify the problem of accurately predicting honey bees per tree because users will be informed to take counts of honey bees if events such as colony removal or introduction occurs in the vicinity of their orchard.

Fruit trees appear to be an exception to the strategy that plants often employ to force pollinators to move from plant to plant to insure outcrossing. Honey bees collecting either pollen or nectar could become satiated on a very small area of tree especially immediately before, during, and immediately after full bloom when a single tree can have 10000's of blossoms. Intense foraging activity may cause many blossoms to be visited so that foragers find many unrewarding blossoms and move between trees to obtain full resource loads. However, this did not seem to be the case in our test orchard. The blossoms we sampled were available to foragers. This brings into question the importance of tree to tree movement in cross-pollination of fruit trees such as almond particularly in light of the size of the population of honey bees with compatible pollen on their bodies. The combination of findings from Objectives 2, 4, and 5 indicate that individual honey bees must be obtaining pollen from sources other than the ones they are foraging. Pollen transfer in the hive during contacts with nestmates is a probable scenario and explanation for the size of cross pollinating population on almond.

Computer simulation models are widely used for decision making in complex systems. Agroecosystems are incredibly complex having a constant movement of energy through their components which are driven largely by the precarious events of weather. Models are used to predict the best management strategies for the biological and economic facets of a farm operation. They also are used for generating recommendations, because different management strategies couched in different environmental scenarios can be tested in simulation. A basic piece of information that is essential each year for good decision making is an estimate of crop size that takes into account the specific conditions of a given year and orchard site. This is especially important in crops that require honey bee cross pollination for seed/fruit set. Crop load can vary greatly from year to year in these plants depending upon weather conditions, blossom quality, honey bee population sizes, and last year's nut set which can affect this year's bloom. Growers need a tool to estimate crop load that takes into account the orchard and weather conditions in a specific year and site. ALMOPOL fills this need by generating predictions on nut set at petal fall so that estimates of crop value can be estimated early in the season. This crop estimate can then be used as the economic basis on which to make management decisions during the remainder of the growing season.

For ALMOPOL to realize its potential as a tool for growers, extension agents, and researchers it must be in a format that will run on personal computers. We are currently converting the mainframe ALMOPOL into PC-ALMOPOL for IBM compatible PC's.

List of Publications

DeGrandi-Hoffman, G., R. Thorp, G.M. Loper, and D. Eisikowitch, 1990. The comparative attractiveness of five almond cultivars to honey bees (Apis mellifera L.). Proc. Vith Interntl. Pollination Symp. Acta Horticulturae 288: 299-302.

DeGrandi-Hoffman, G., R. Thorp, G.M. Loper, and D. Eisikowitch, 1990. Identification and distribution of cross-pollinating honeybees (Apis mellifera L.) in almond [Prunus dulcis (Mill.) D.A. Webb]. J. Appl. Ecology (in press).

DeGrandi-Hoffman, G., R. Thorp, G.M. Loper, and D. Eisikowitch, 1990. Validation of predictions from the ALMOPOL cross-pollination and almond nut set simulation model. in prep.

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Table 1. Correlation coefficients for actual and predicted bloom progression for five almond cultivars. Bloom progression for each cultivar is defined mathematically by separate pre- and post-peak bloom equations.

Cultivar	Year	Correlation coefficient	
		Pre-peak	Post-peak
Neplus	1988	0.71	0.97
Nonpareil		0.94	0.96
Price		0.86	0.96
Peerless		0.93	0.95
Mission		0.97	0.95
Neplus	1989	0.83	0.92
Nonpareil		0.85	0.87
Price		0.90	0.92
Peerless		0.96	0.95
Mission		0.98	0.94
Neplus	1990	0.89	0.79
Nonpareil		0.97	0.63
Price		0.96	0.77
Peerless		0.99	0.69
Mission		0.98	0.46

Table 2. The average amount of nectar and its percentage of dissolved solids (DS) per blossom in five almond cultivars.

Cultivar	Year	Blossoms sampled (amt. of nectar)	Nectar per blossom (ul)		Blossoms sampled (% DS)	% DS per blossom
'NePlus'	1988	21	0.81 $\pm$ 0.28	a	19	37.2 $\pm$ 3.5
'NonPareil'		29	0.71 $\pm$ 0.33	a	27	38.5 $\pm$ 3.7
'Price'		34	0.53 $\pm$ 0.23	a	22	34.9 $\pm$ 3.9
'Peerless'		26	0.83 $\pm$ 0.41	a	17	37.1 $\pm$ 6.2
'Mission'		12	0.83 $\pm$ 0.32	a	9	35.9 $\pm$ 8.2
'NePlus'	1989	42	0.31 $\pm$ 0.19	a	30	5.9 $\pm$ 2.4
'NonPareil'		30	0.28 $\pm$ 0.17	a	29	6.1 $\pm$ 2.8
'Price'		23	0.00		na	na
'Peerless'		46	0.32 $\pm$ 0.21	a	22	6.1 $\pm$ 3.1
'Mission'		47	1.13 $\pm$ 0.48	b	29	5.8 $\pm$ 2.6

Means followed by the same letter within each year are not significantly different at the 0.05 level as determined by Scheffe's S test.

Table 3. The average amount of pollen per blossom in five cultivars of almond.

Cultivar	Year	Sample size	Pollen per blossom (mg)
'NePlus'	1988	20	1.00 $\pm$ 0.07 a
'NonPareil'		20	0.71 $\pm$ 0.10 bc
'Price'		20	0.85 $\pm$ 0.10 ab
'Peerless'		20	0.55 $\pm$ 0.05 c
'Mission'		20	0.85 $\pm$ 0.10 ab
'NePlus'	1989	33	1.20 $\pm$ 0.28 a
'NonPareil'		28	0.70 $\pm$ 0.22 a
'Price'		15	1.20 $\pm$ 0.43 a
'Peerless'		42	1.10 $\pm$ 0.20 a
'Mission'		39	1.20 $\pm$ 0.27 a

Means followed by the same letter within each year are not significantly different at the 0.05 level as determined by Scheffe's S test.

Table 4. The average number of blossoms, ul of nectar, and mg of pollen per m of branch for five almond cultivars.

Cultivar	Year	Blossoms z per		Nectar per m (ul)	Pollen per m (mg)
		m	cluster		
'NePlus'	1988	13.6 a	2.4 a	11.0 a	13.7 a
'NonPareil'		21.5 ac	2.9 ab	15.3 a	15.5 ab
'Price'		22.8 ac	2.4 a	12.2 a	19.5 b
'Peerless'		32.4 bc	2.6 a	27.0 b	18.0 ab
'Mission'		39.4 b	3.3 b	32.7 c	33.5 c
'NePlus'	1989	59.6 a	6.1 a	18.2 a	71.5 a
'NonPareil'		35.3 b	4.1 b	9.9 a	24.7 b
'Price'		17.1 c	3.0 bc	0.0	20.5 c
'Peerless'		28.8 bc	4.4 b	9.2 a	31.7 b
'Mission'		17.1 c	2.7 c	19.7 a	20.5 c

z The average number of blossoms per m was estimated from a sample size of 40 limbs (1 m sections) for each cultivar. The average number of blossoms per cluster was estimated from a sample size of 136 clusters in 1988 and 40 clusters in 1989 per cultivar.

Means followed by the same letter within each year and column are not significantly different at the 0.05 level as determined by Scheffe's S test.

Table 5. The average amount of time spent by foragers per blossom collecting nectar and pollen from five different cultivars of almond.

Cultivar	Year	Bees observed collecting		Avg. time (sec.) spent per blossom collecting	
		pollen	nectar	pollen	nectar
Neplus	1988	116	314	5.6 a	11.9 b
Nonpareil		106	433	6.7 a	10.4 b
Price		106	370	4.5 a	8.6 b
Peerless		167	414	4.9 a	11.4 b
Mission		201	309	3.9 a	8.6 b
Neplus	1989	49	24	9.2 a	11.7 b
Nonpareil		22	12	8.0 a	15.0 b
Price		24	na	5.6 a	na
Peerless		28	9	7.8 a	9.3 b
Mission		16	8	8.4 a	11.7 b

Means followed by the same letter are not significantly different at the 0.05 level as determined by Fishers LSD.

No significant difference between years in time spent collecting pollen or nectar, but nectar collection took significantly more time per blossom than pollen collection.

Table 6. The percentage of honey bees foraging almond with self-, cross-, and non-almond pollen on their bodies.

Cultivar	Year	Bees Sampled	% of Bees With Pollen Type		
			self $\pm$ SE	cross $\pm$ SE	non- almond $\pm$ SE
'NePlus'	1988	9	100	100	89 $\pm$ 20
'Nonpareil'		10	100	100	92 $\pm$ 20
'Price'		10	100	90 $\pm$ 20	60 $\pm$ 30
'Peerless'		10	100	100	90 $\pm$ 20
'NePlus'	1989	27	100	100	92 $\pm$ 10
'Nonpareil'		21	100	100	100
'Price'		12	100	100	100
'Peerless'		21	100	95 $\pm$ 10	95 $\pm$ 10
'Mission'		18	100	100	100

Table 7. The proportion of self-, cross-, and non-almond pollen on the bodies of either nectar or pollen collecting honey bees foraging on almond cultivars.

Cultivar	Year	PC ^z or NC	N ^y	% of pollen type ± SE		
				self- pollen ± SE	cross- pollen ± SE	non- almond ± SE
Neplus	1988	PC	5	60.6±14.0a	32.5±12.2a	6.9±5.2b
		NC	5	54.2±10.2a	37.8±10.4a	8.0±3.5b
Nonpareil		PC	3	43.2±18.2a	50.2±16.2a	6.7±3.3b
		NC	6	56.2± 7.7a	31.7± 5.1a	12.2±3.5b
Price		PC	10	81.1± 7.5a	15.3± 6.4b	3.6±3.4c
		NC	0	na	na	na
Peerless		PC	7	62.7±3.8a	32.1±3.6b	5.1±1.5c
		NC	3	49.3±10.2a	24.4±1.7b	26.2±8.5b
Neplus	1989	PC	20	71.5±2.3a	16.0±2.4b	12.5±1.7b
		NC	7	72.5±7.0a	13.9±5.0b	13.6±5.5b
Nonpareil		PC	7	52.6±5.3a	29.7±2.7b	17.7±4.6b
		NC	14	45.6±4.5a	25.9±2.4b	28.4±5.0b
Price		PC	6	65.8±3.8a	12.1±1.9b	22.0±2.9c
		NC	6	59.6±5.2a	11.1±3.3b	29.3±3.7c
Peerless		PC	12	54.4±4.0a	26.1±4.0b	19.5±5.2b
		NC	9	47.7±4.0a	23.4±3.9b	28.8±5.8b
Mission		PC	11	54.1±5.2a	20.4±3.0b	25.5±6.0b
		NC	7	52.5±6.4a	29.0±4.6b	18.4±8.7b

^z PC = pollen collecting honey bee and NC = nectar collecting honey bee.

^y N = number of honey bees examined

Means within the same cultivar and year followed by the same letter are not significantly different at the 0.05 level as determined by Fisher's LSD.

Table 8. Percentages of almond blossom pistils from five cultivars with self-, cross-, or non-almond pollen.

Cultivar	Year	Pistils sampled	% with pollen type		
			self $\pm$ SE	cross $\pm$ SE	non- almond $\pm$ SE
'Neplus'	1988	16	81.2 $\pm$ 20	68.7 $\pm$ 20	43.7 $\pm$ 30
'Nonpareil'		15	66.6 $\pm$ 30	53.3 $\pm$ 30	60.0 $\pm$ 30
'Price'		19	42.1 $\pm$ 20	36.8 $\pm$ 20	94.7 $\pm$ 10
'Peerless'		20	55.0 $\pm$ 20	50.0 $\pm$ 20	90.0 $\pm$ 10
'Neplus'	1989	9	88.9 $\pm$ 20	100	100
'Nonpareil'		15	100	86.7 $\pm$ 20	80 $\pm$ 20
'Price'		10	60.0 $\pm$ 30	10.0 $\pm$ 20	100
'Peerless'		10	100	90.0 $\pm$ 20	100
'Mission'		17	76.5 $\pm$ 20	47.0 $\pm$ 30	100

Table 9. Proportions of self-, cross-, and non-almond pollen on the pistils of five different cultivars of almond blossoms.

Cultivar	Year	Pistils examined	% of pollen type		
			self pollen	cross pollen	non- almond
'Neplus'	1988	16	49.8 a	18.3 b	25.6 ab
'Nonpareil'		15	36.5 a	28.5 a	35.0 a
'Price'		19	18.8 a	4.6 a	76.6 b
'Peerless'		20	22.6 a	12.6 a	64.8 b
'Neplus'	1989	9	39.3 a	3.3 b	57.3 a
'Nonpareil'		15	52.2 a	17.3 b	30.4 ab
'Price'		10	8.8 a	0.7 a	90.5 b
'Peerless'		10	45.5 a	8.9 b	45.6 a
'Mission'		17	24.0 a	2.9 a	73.0 b

Means followed by the same letter are not significantly different at the 0.05 level as determined by Scheffe's - S test.

Table 10. Initial and final almond nut set from five cultivars where the adjacent tree is the same cultivar within the row or a different cultivar across the row.

Cultivar	Year	Limbs Counted (same, different CV)	Adjacent tree			
			Same CV		Different CV	
			Initial $\pm$ SE	Final $\pm$ SE	Initial $\pm$ SE	Final $\pm$ SE
'Neplus'	1988	10, 10	49.6 $\pm$ 5.9 ab	40.5 $\pm$ 4.3 ab	52.8 $\pm$ 6.5 ab	43.9 $\pm$ 4.4 ab
'Nonpareil'		10, 7	45.3 $\pm$ 2.3 ab	41.3 $\pm$ 1.7 ab	47.2 $\pm$ 5.1 ab	37.8 $\pm$ 1.0 b
'Price'		7, 7	59.6 $\pm$ 8.0 a	52.4 $\pm$ 8.5 ab	50.0 $\pm$ 5.3 ab	44.8 $\pm$ 3.7 ab
'Peerless'		8, 8	8.8 $\pm$ 1.8 c	6.9 $\pm$ 1.7 c	12.4 $\pm$ 1.6 c	10.7 $\pm$ 1.5 c
'Mission'		9, 9	42.2 $\pm$ 2.8 a	37.1 $\pm$ 1.2 b	40.0 $\pm$ 1.5 a	34.6 $\pm$ 1.2 b
'Neplus'	1989	10, 10	9.5 $\pm$ 2.3 a	8.9 $\pm$ 2.2 a	12.1 $\pm$ 1.8 a	8.9 $\pm$ 1.6 a
'Nonpareil'		10, 10	14.2 $\pm$ 3.2 ac	14.0 $\pm$ 3.3 ac	18.1 $\pm$ 4.1 ac	17.5 $\pm$ 3.9 ac
'Price'		10, 10	33.9 $\pm$ 3.8 b	32.0 $\pm$ 3.3 b	28.5 $\pm$ 5.2 ab	27.8 $\pm$ 4.9 ab
'Peerless'		10, 10	12.5 $\pm$ 1.7 a	11.4 $\pm$ 1.6 a	18.7 $\pm$ 3.9 a	15.7 $\pm$ 3.8 a
'Mission'		10, 10	45.7 $\pm$ 7.1 b	42.5 $\pm$ 6.7 b	33.7 $\pm$ 7.2 b	27.2 $\pm$ 5.5 bc

Means followed by the same letter are not significantly different at the 0.05 level as determined by Tukey's W test.

Table 11. Proportion of hand-pollinated blossoms of different age classes setting nuts.

Cultivar	Year	No. of blossoms pollinated by age class				No. of blossoms setting nuts by age class			
		AB	C	D	E	AB	C	D	E
'Neplus'	1988	7	9	72	62	0.57	0.78	0.72	0.73
'Nonpareil'		27	26	36	na	0.70	0.65	0.97	na
'Price'		26	20	50	na	0.73	0.20	0.68	na
'Peerless'		25	26	55	na	0.32	0.46	0.38	na
'Mission'		78	78	67	na	0.51	0.46	0.45	na
'Neplus'	1989	27	12	11	6	0.67	0.67	0.27	0.33
'Nonpareil'		15	16	9	4	0.47	0.75	0.55	0.25
'Price'		10	9	9	11	0.70	0.89	0.55	0.54
'Peerless'		16	14	13	5	0.81	0.43	0.15	0.40
'Mission'		12	11	12	na	0.50	0.73	0.42	na

Table 12. Actual initial and final percentages of blossoms setting nuts, and the final percentage of blossoms setting nuts as predicted using the initial set in the nut thinning prediction equation from the ALMOPOL model.

Cultivar	Year	Actual Set				Predicted final set
		Initial ± SE		Final ± SE		
Neplus	1988	51.2 ±	4.3	42.2 ±	3.0	42.5
Nonpareil		46.5 ±	3.1	39.3 ±	1.0	39.5
Price		55.7 ±	5.1	49.0 ±	4.9	45.3
Peerless		10.6 ±	1.3	8.8 ±	1.2	10.6
Mission		41.3 ±	1.6	35.9 ±	0.9	35.9
Neplus	1989	10.8 ±	3.0	8.9 ±	2.7	10.8
Nonpareil		16.5 ±	5.2	16.2 ±	5.0	16.1
Price		31.2 ±	6.5	30.3 ±	6.0	28.5
Peerless		15.6 ±	4.5	13.5 ±	4.3	15.3
Mission		39.7 ±	10.4	34.8 ±	9.3	34.8
Neplus	1990	19.7 ±	1.2	15.1 ±	1.2	19.8
Nonpareil		24.6 ±	3.4	21.6 ±	3.2	23.1
Price		20.7 ±	2.4	17.2 ±	1.8	19.8
Peerless		19.6 ±	1.8	14.1 ±	1.7	18.9
Mission		10.6 ±	1.1	9.4 ±	1.2	10.6

The nut thinning equation used to predict final set (F) as a function of initial set (I) is:

$$F = (e^{- (I * 0.5) + 0.057}) * I .$$

Table 13. Actual nut set in five almond cultivars and predicted set using the ALMOPOL nut set prediction model.

Cultivar	Year	Actual Set		Predicted Set	
		Initial ± SE	Final ± SE	Initial set	Final set
NePlus	1989	10.8 ± 3.0	8.9 ± 2.7	14.1	13.8
Nonpareil		16.5 ± 5.2	16.2 ± 5.0	10.0	10.0
Price		31.2 ± 6.5	30.3 ± 6.0	25.5	23.7
Peerless		15.6 ± 4.5	13.5 ± 4.3	15.6	15.2
Mission		39.7 ± 10.4	34.8 ± 9.3	26.5	24.6
Neplus	1990	19.7 ± 1.2	15.1 ± 1.2	19.0	16.8
Nonpareil		24.6 ± 3.4	21.6 ± 3.2	9.4	9.4
Price		20.7 ± 2.4	17.2 ± 1.8	22.8	21.6
Peerless		19.6 ± 1.8	14.1 ± 1.7	18.8	18.2
Mission		10.6 ± 1.1	9.4 ± 1.2	10.2	10.2

Actual set was determined from estimates of the percentage of blossoms setting nuts on four limbs of 10 trees per cultivar.

Figure Captions

Fig. 1. Arrangement of cultivars in the orchard used in this study.

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