Mobility between the trees and cross-pollination efficiency. Most honey bees collect nectar and pollen within a limited area of 1 to 3 trees. They often perform cross pollination only between neighboring trees that carry opposite-stage flowers and are at a distance of not more than two rows. A small percentage of the foraging honey bees (2 - 4%) move farther between rows and fields, and may carry avocado pollen for hundreds of yards away from its source. These are the scout bees, which, for the sake of information gathering, move among different locations and flowering species throughout the food collecting flight. The efficiency of cross pollination between neighboring trees is similar to the efficiency of close pollination, but it drops dramatically with increasing distance from the pollen source (Table 2).

Does pollination limit avocado productivity?

One may assume that, in the case of the avocado, pollination cannot play a role as a limiting factor to yield. A medium-sized mature avocado tree produces about 1 million flowers during a 30 - 60 day flowering season, or approximately 10,000 to 40,000 new female flowers per day. Out of this, a total of only 400 to 600 flowers need to be successfully pollinated and fertilized to produce a reasonable crop. Theoretically, this can be accomplished by 2 - 3 honey bees in just 1 day, during the 1 hr of the male and female flowers' self-overlap, if the bees devote only half of their visits to the female flowers. However, field observations show that a measurable initial fruit set requires the activity of 5 - 10 honey bees per tree for the entire female blooming period. At least one week of this level of visitation is needed to achieve a fair crop, and much more is needed for a good one. This paradox can be explained by the need for more than 20 pollen grains per stigma for efficient fertilization and the low average number of pollen grains that is deposited on the stigma by the bee during a visit. It may also stem from the heavy selective initial-fruit drop (where mostly cross-pollinated fruits remain on the tree) and the inability of the honey bees to perform as efficient cross pollinators.

To summarize, pollination may be a limiting factor for avocado productivity where one or two of the following conditions exist:

1. The activity of the pollinators, which in most cases is the honey bee, is low, due to a low population of pollinators in the vicinity, or to the presence of more attractive competing bloom.
2. Cross-pollination efficiency is low, due to both the low mobility of the pollinator insect, as in the case of the honey bee, and the typical tree's relatively large distance from the pollinizer.
3. For situations in which efficient self-fertilization within the male-stage flower does occur, and self-pollination may be efficiently carried out by wind and/or gravity, pollination cannot be a limiting factor to yield. There are cultivars, however, in which the male flower's inner stamens are tightly closed around the stigma. In such cases, self pollination may still require the involvement of a pollinator.

What can be done to improve pollination?

Many worthwhile actions can be taken:

Introduce honey bee hives to the orchard and keep them there throughout the blooming season. Do not assume that 1 hive per acre is sufficient. To achieve good pollination, you need at least 5 - 10 honey bees per medium tree, and the presence of more bees is better. Observe your trees twice a week during bloom! If bee density on the flowering trees is lower than 5 - 10, you should add more hives. Only rarely is 1 hive per acre sufficient, and in many cases 4 strong hives per acre are required!

Add pollinizers to the orchard. Most avocado cultivars need cross pollination to achieve their yield potentials. Cross pollination is efficiently performed only between adjacent trees, and generally not between trees separated by more than two rows (about 40 ft). Therefore, the minimum density of pollen-donor trees should be set to every 4th row. Not all cultivars are efficient pollen donors. Consult your extension adviser, and find out which pollinizers you should use, based on the orchard cultivar composition.

Keep the orchard open. Direct sunlight should reach the lower branches of each tree. This can be accomplished by pruning your trees. Improved light penetration into the grove enables the lower branches to carry more bloom, encourages a higher honey bee density in the orchard, and increases the potential for cross pollination.

Alternative insect pollinators should be considered. In Israel, a local species of bumblebee (*Bombus terrestris*) has been studied as an avocado pollinator. In environments with low honey bee activity, and also when pollinizers are spaced at a distance greater than 40 ft, bumblebees significantly enhanced yield. In Mexico, about 8 local species of stingless bees (Apidae, Meliponinae) have been observed extensively visiting all types of avocado bloom, which appears to be more attractive to them than to honey bees. These species, which are likely to be the original pollinators of avocado, should be evaluated, especially within Mexico, for their potential superior pollination efficiency in avocado orchards.

A Review of Avocado Pollination and the Role of Pollinizers

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I. Introduction

Avocado (*Persea americana* Mill.) is an understory tree native to the tropical and subtropical regions of Central and South America. Cultivars (varieties) of Guatemalan, Mexican, and West Indian origin have spread and become important crops in many regions around the world (Bergh, 1986; Davenport, 1986). In Israel (IS), avocado is a major export crop, with exports averaging over $35 million annually (Dag and Regev, 1999). In the US, avocado sales total $392 million, with California (CA) accounting for 95.7% of the net worth and Florida (FL) 4.2% (Anon, 2000). We have initiated a cooperative research project to examine some of the many unanswered questions pertaining to avocado floral biology, pollination, and the role of the European honey bee in avocado fruit production under California and Israeli conditions. We present a review of what is known in general terms about avocado pollination, the role of the honey bee, and some preliminary data that we have collected during the last season on honey bee race-specific visitation to avocado, and pollinizer effects on fruit yield.

The avocado flower is considered to have open form, with exposed nectar and pollen. This is characteristic of plants that have not evolved with specialized pollinators, but rather are visited by a range of insects. A plethora of insect species visits avocado in its native environment, and many of them provide efficient pollination (Ish-Am et al., 1999a). European honey bees (*Apis mellifera* L.), introduced to the New World in modern times, are anatomically suited as efficient pollinators of avocado and are used for this purpose worldwide (Davenport, 1986; 1998; Ish-Am and Eisikowitch, 1993; Ish-Am et al., 1999a; Vithanage, 1990). Bumblebees may also be efficient pollinators of avocado (Ish-Am et al., 1999b) but are prohibitively expensive for most commercial uses.

1. Avocado flowering and pollination

Nirody (1921) was the first to report on the flowering behavior (synchronous dichogamy) of avocado in FL. Individual flowers open first as functionally female, and then close and later reopen functionally male to reveal pollen. Cultivars can be classified into two complementary flowering types. "A" flower cultivars have flowers that open as female in the *morning* of the first day, and then reopen as male on the *afternoon* of the following day. "B" cultivars have flowers that open as female in the afternoon of the first day and reopen as male the morning of the following day. The opening and closing times of the flowers tend to be synchronized within a tree as well as among trees of like cultivar within an orchard. This means that type A or B pollen is released in the orchard at the same time that type B or A flowers of the complementary cultivar are in the female stage, respectively. For this reason, it is common for growers to facilitate cross pollination by introducing honey bees and pollinizers into orchards.

Cultivars vary considerably in the seasonal timing of their flowering as well as other floral attributes, such as flower size. Avocado cultivars are typically separated into early- and late-blooming groups (Ish-Am and Eisikowitch, 1998a). About 85% of the cultivars in IS are early-blooming types, including 'Ettinger', 'Hass', 'Pinkerton', and 'Fuerte', which are generally characterized by low fruit productivity. These cultivars flower at the same time as wildflowers and citrus, which in general seem to be very attractive food sources for honey bees. Honey bees often prefer the competing flowers and abandon the avocado bloom (Clark, 1923; Eisikowitch and Melamud, 1982; Ish-Am and Eisikowitch, 1998a; Vithanage, 1990). Late-blooming cultivars include 'Nabal' and 'Reed', which typically provide good fruit yields. These cultivars bloom when there is little competition from other crops or natural vegetation, and are therefore more likely to be visited by honey bees.

Honey bee visitation rates to avocado correlate positively with fruit set and yield (Eisikowitch and Melamud, 1982; Ish-Am, 1994; Ish-Am and Eisikowitch, 1992; 1998a; Robbertse et al., 1998; Vithanage, 1990). This finding was further supported in the spring of 1999 in IS, wh[...] the wildflower bloom was weak and delayed due to a dry winter. Consequently, large honey bee numbers were observed working the early avocado flowers, and fruit yields were exceptionally high. Thus, if a honey bee line could be developed that preferred avocado over alternative vegetation, yields could potentially be greatly increased.

Although grower experience and research data suggest the benefits of outcrossing, the importance of placing honey bees and pollinizers in avocado groves to promote outcrossing has been a subject of dispute for nearly a century (Stout, 1923; Gustafson and Bergh, 1966; Kobayashi et al., 2000). Indeed, the mere requirement for cross-pollination between cultivars has come into question in light of reports that temperature fluctuations can cause overlap of the male and female phases within a canopy (Sedgley and Grant, 1982). This enables "close" pollination (a type of selfing) to occur between flowers of the same tree or cultivar. In addition, given appropriate conditions, such as high humidity, self-pollination within a flower during the male phase

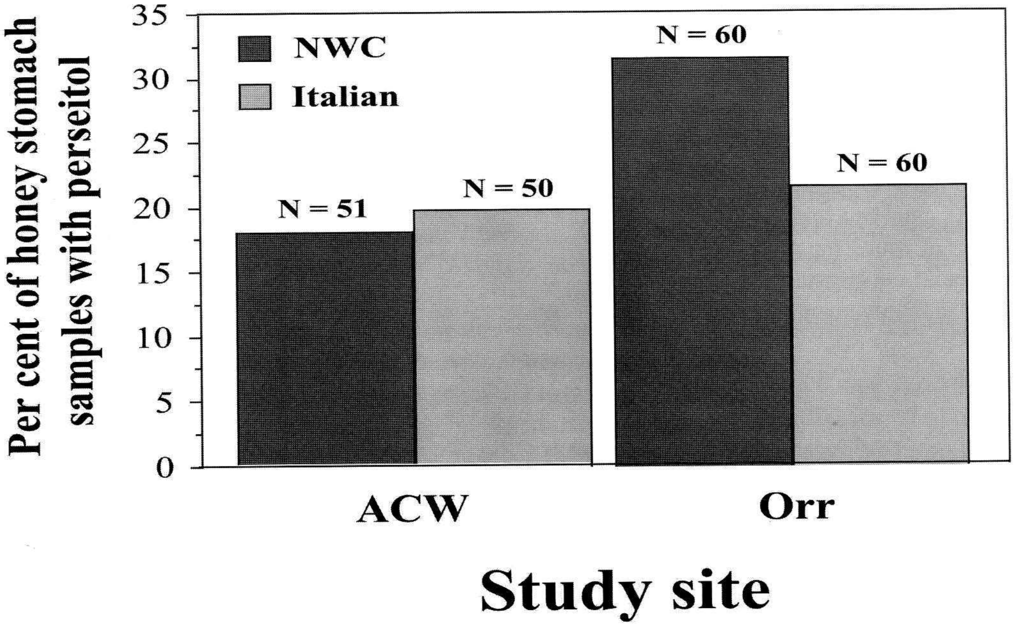

Figure 1. The percentage of honey bees, returning to their hives, whose honey stomachs contained perseitol, indicating that they had been foraging at avocado flowers. Data were collected at the ACW Farm in Fallbrook, CA and the Orr Farm in Somis, CA. Differences between the races are non-significant at both sites, and the difference between sites in the percentage of avocado foragers is also non-significant (*P* > 0.15 in all cases).

can take place, provided the stigma (the female portion of the flower on which the pollen is deposited) has not yet senesced (Davenport et al., 1994). For most growing regions, however, it has been assumed that selfing should not be relied upon as the sole means of ovule fertilization (Peterson, 1955). Accounts of single-cultivar groves producing high yields in the apparent absence of complementary cultivars have been cited as evidence that pollinizer interplantings to facilitate pollination are not necessary (Hodgson, 1947; Gustafson and Bergh, 1966). More recent work by Vrecenar-Gadus and Ellstrand (1985), however, showed that single-cultivar groves can receive substantial amounts of pollen from distant pollinizers in other groves. This means that high yields in single-cultivar orchards cannot necessarily be interpreted as strictly the result of self-fertilization.

Recent observations of avocado floral behavior and pollination in southern FL, however, have prompted a reexamination of the tendency of avocado to self-pollinate. Research showed that cross-pollination occurred in only about 1% of avocado flowers, despite the presence of honey bees and other pollinating insects in orchards. Self-pollination within flowers, without the aid of insects, occurred in more than 95% of the pollinated flowers of most cultivars grown in southern FL (Davenport, 1989; Davenport et al., 1994). This is because, contrary to previous assumptions, a substantial proportion of stigmas remain receptive until the close of the male stage (Davenport, 1986). Moreover, pollen typically disperses within thirty minutes after dehiscence (Davenport, 1998) and may, therefore, be efficiently transferred by wind or gravity within flowers to receptive, white stigmas in the male phase, giving rise to self-pollination rates proportional to the number of receptive stigmas present.

Previous Australian research indicated that pollen tubes stop growing sometime within 24 hrs after pollen is deposited on the stigmas of flowers that are in their male-phase (Sedgley, 1977a; 1977b). This finding supported the argument that fertilization cannot occur during the male phase. T. Davenport recently examined pollen-tube growth in male-phase pollinated flowers that still bore receptive stigmas (which are still white, as opposed to brown and desiccated). He observed pistils at 24 and 48 hrs after pollen deposition in the male phase and found that, regardless of the pollen source, each cultivar displayed a substantial proportion of flowers in which ovules were penetrated by a pollen tube within 48 hrs of pollination (Table 1). These data support the contention that a substantial portion (~25% to ~85%) of the male-phase pollinated flowers are successfully fertilized and that fertilization generally occurs between 24 and 48 hrs after pollination. In addition, outcross pollen from the complementary cultivars tested appeared to have no benefit over (self) pollen from the same cultivar, in terms of pollen-tube growth.

Selfing is clearly the primary mode of avocado pollination in FL, and results in successful fertilization, but is it universally effective in the production of a crop? Researchers in IS found that 'Hass' fruit derived from flowers pollinated by 'Ettinger' (Goldring et al., 1987; Degani et al., 1989) and 'Ardith' (Degani et al., 1997) were preferentially retained on the plant all the way to fruit maturity, relative to fruit derived from self-pollinated flowers. Some pollinizers, however, have not shown this effect when tested. Degani and Gazit (1984) observed that the proportion of self-pollinated progeny ranged from 8 to 93% in caged pairs of several cultivars. Likewise, studies of three cultivars ('Simmonds', 'Tonnage', and 'Choquette') in FL indicate that over 85% of the mature fruit are derived from self-pollinated flowers (Davenport, unpublished data). Recent research examined the rate of outcrossing of 'Hass' from coastal and inland orchards of CA (Kobayashi et al., 2000). Most of the 'Hass' yield resulted from self pollination (about 60 to 80%), although outcrossing was found to explain roughly 10% of the variance in yield. It is unclear, however, whether honey bees were available to serve as pollinators in this study, since the presence or absence of honey bees was not monitored (M. Clegg, L. Francis, personal communication). Several workers have also examined the relationship between distance from a pollinizer and outcrossing, as well as yield. Although results from these studies vary in their magnitude and in their statistical significance, general findings indicate that outcrossing (Degani et al., 1997), as well as yield (Ellstrand, 1992), correlate negatively with distance from a pollinizer.

The key to understanding the importance of cross vs. self-pollination appears to be the proportion of viable female organs that persist into the male phase. Dry, Mediterranean climates may promote high cross vs. self-pollination ratios because of excessive desiccation of stigmas in the male phase. Conversely, more humid conditions may promote high rates of self pollination due to the increased number of receptive stigmas in the male phase. Hence honey bees may increase fruit yield in dry climates by increasing the number of pollinated female phase flowers if sufficient hives are deployed to saturate both the avocado orchard and the more attractive neighboring flowering plants, whereas honey bees may have little impact in conditions where self pollination predominates.

2. *Honey bee behavioral genetics*

Behaviors of honey bees vary among individuals, among genetic lines, and among races. Variation at all these levels has an important genetic component (Frumhoff and Baker, 1988; Robinson and Page, 1988). Various behaviors that have been genetically selected have direct consequences for foraging performance. These include aspects of

Table 1. Proportion (% of total) of flowers in which the pollen tube penetrated the ovule within 48 hr after hand cross pollination (HCP) from adjacent complementary cultivar, hand close pollination (HSP) from same cultivar, and natural self pollination (NSP) within the male phase avocado flowers.

Cultivar	Race	Floral Type	HCP	HSP	NSP
Booth 7	G/W	B	77.41	69.14	73.44
Brooks Late	G/W	A	82.88	50.12	57.28
Choquette	G/W	A	59.94	70.01	75.84
Monroe	G/W	B	25.00	23.58	30.16
Simmonds	W	A	63.77	58.19	64.68
Tonnage	G/W	B	39.77	57.27	56.46
Tower 2	W	B	64.91	73.68	76.76

Race: G/W is Guatemalan and West Indian race hybrid; W is West Indian race.

learning and memory (Benatar et al., 1995; Brandes and Menzel, 1990; Brandes et al., 1998), flight range (Gary and Witherell, 1977), and the tendency to collect nectar or pollen (Hellmich et al., 1985; Calderone and Page, 1988; Gordon et al., 1995; Page, 1999), as well as actual preferences for certain crops over others (Nye and Mackenson, 1968, 1970). Through artificial selection, lines with significantly better performance in desired traits can be created within a few generations.

One of the most successful breeding programs in the U.S. is that of the New World Carniolan honey bee (NWC) (Cobey, 1999), a race that is now used extensively. It was observed at ACW Farm in southern CA that NWC bees were very active on avocado, even though competing vegetation was in bloom in the surrounding area. Such levels of activity were not observed on nearby farms where Italian (IT) honey bees were commonly employed (R. Hofshi, personal communication). These observations raised the hypothesis that NWC bees have a greater genetic predisposition to avocado visitation than IT honey bees.

II. Preliminary results from experiments in Israel and California

1. Honey bee race-specific visitation to avocado

Colonies of NWC and IT honey bees were placed in equal numbers in two avocado orchards each in IS and CA. Various techniques were employed to look for race-specific differences in the bees' visitation to avocado. Avocado nectar is unusual in that it contains a 7-carbon (7C) sugar, perseitol (PSL), and its 7C precursor, D-mannoheptulose. These are the major transport sugars in the avocado tree (Liu et al., 1995, 1999). PSL has been found in the nectar of all avocado cultivars tested to date, and has not been found in the main flora competing with avocado, such as citrus or wild mustard flowers (Ish-Am, 1994). Therefore, PSL offers a tool for measuring honey bee nectar foraging activity on avocado bloom. For each honey bee race, foragers were caught upon their return to the hive. Honey-stomach contents were then collected from each bee and analyzed for the presence of PSL using High Performance Liquid Chromatography. In California, 21.6% (overall) of bees returning to hives had PSL in their honey stomachs, meaning that an average of 22% of nectar-foraging trips from a given hive were to avocado. There was a non-significant trend toward more visitation to avocado by NWC bees as compared to IT bees at the Orr Farm in Somis. Differences between the races, however, were negligible at ACW (Fig. 1). In IS, honey was extracted from each hive separately at the end of the season and PSL concentration was determined for each honey sample. The honey yield from NWC bees was significantly greater than that of IT bees. Additionally, at one of the sites, the honey collected from the NWC hives had significantly more PSL and tended to be darker. Color is another indicator of visitation to avocado, as avocado honey has a molasses-like color. The results of the honey data support the hypothesis that NWC honey bees are more attracted to avocado than IT honey bees. They also suggest that the strength with which honey bees are attracted to avocado is influenced by competing forage, because differences between the races were more pronounced at some sites than others.

2. Effect of pollinizing cultivar on 'Hass' yield

M. L. Arpaia and B. Faber set up a pollinizer (B-flower type cultivar) trial in Oxnard, CA in 1998. The goal of the trial is to quantify potential differences in 'Hass' yield in relation to nearest pollinizer type and the distance from the pollinizer. The 'Hass' cultivar is of the A-flow type. The trial grove contains 6 blocks of 'Hass' with rows of different pollinizers interplanted with every 6th row of 'Hass'. The following B-flower types are included as pollinizers: 'Bacon', 'Ettinger', 'Zutano', 'Fuerte', 'Marvel', 'Nobel', and 'SirPrize'. 'Harvest', an A-flower type, is also included. The latter four cultivars are new selections from the UC Riverside Avocado Breeding Program, whereas the first 4 cultivars are long-used standards. Fruit yield data were collected from a subset of 'Hass' and pollinizers in 3 experimental blocks during March 2001. The preliminary harvest results, which have not yet been statistically analyzed, are presented in Figure 2. The data corroborates the fruitlet count data that was presented both at the Fall 2000 Avocado Research Symposium and at recent avocado grower meetings. This data strongly suggests that there can be a distance effect on 'Hass' yield as related to the distance from the pollinizer. The data also suggests that there may be pollinizer varietal effects on 'Hass' yield. The data from this first year shows that the highest fruit counts were obtained when 'Zutano' was the pollinizer variety followed by 'Ettinger' and then 'Bacon'. Of the 2 unreleased "B" flower

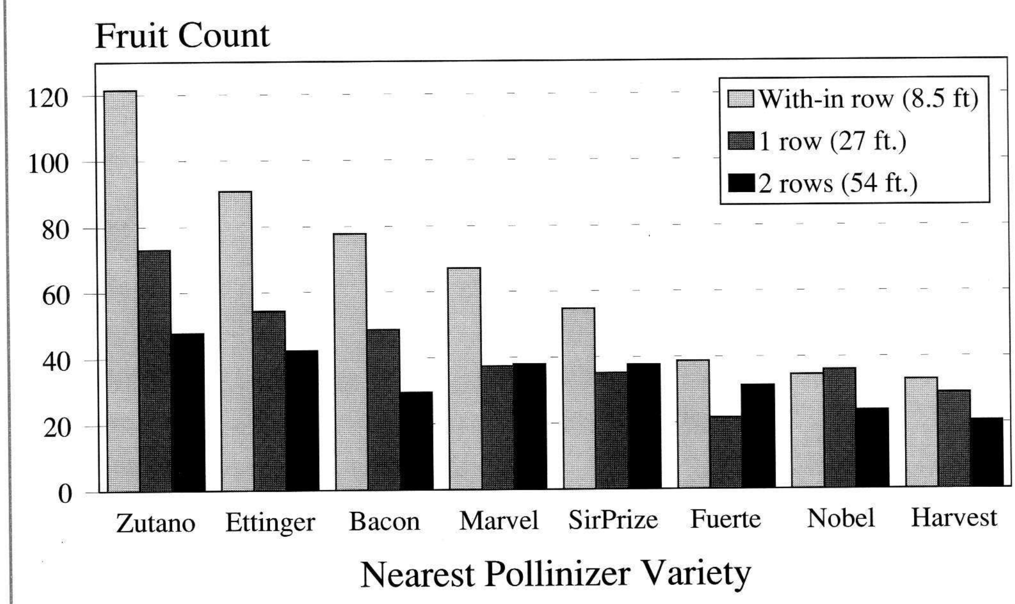

Figure 2. The influence of pollinizers on 'Hass' fruit yield in March 2001. Data were collected from 'Hass' trees located at varying distances from interplanted rows of pollinizers in a grove containing honey bees at a density of 2.5 hives/acre.

types selections, it appears that the 'Marvel' may also serve as a good pollen donor. This is of interest since the 'Marvel' tree is considerably smaller than the 3 top pollinizer varieties. Hence our preliminary work confirms previous observations by others on the potential benefit of using pollinizers to boost the yield of 'Hass' avocado in California.

III. Future directions

We plan to continue the studies outlined above with ongoing funding from the California Avocado Commission (to A. E. Fetscher, N. Waser, T. Davenport, and T. Chao). In the upcoming season, we will collect additional data from the pollinizer site to determine if patterns detected from the 2000 fruiting season are repeated. We also will monitor the incidence of receptive stigmas persisting into the male phase of flowers at this site, as well as the frequency of visitation by both NWC and IT honey bees to 'Hass' and the other cultivars, and we will study floral biology and phenological patterns of the various cultivars. In addition, we will examine a similar set of variables in other groves in Ventura County CA and elsewhere.

Can You Make Money Growing Cherimoya in the Coastal Regions of California? A Sample of Establishment and Production Costs and Profitability Analysis

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Cherimoya production in the coastal regions of California has been developing, and several farm advisors at the University of California have been gathering information regarding production practices and the economic feasibility of the crop. In this article, I provide estimates of the costs and capital needs for producing cherimoya in the coastal regions of California, as well as a basis for evaluating profitability using gross and net margins to determine economic profit. Because values of land and water vary tremendously within the region, I also provide guidelines to adjust gross and net margins to accommodate such variations.

Determining Establishment and Production Costs

Establishment and production costs for cherimoya in the coastal regions of California are determined based on information gathered from growers and shippers. In addition, growers and farm advisors suggest that some of the cost information from a recent study conducted for lemon production in Ventura County (Takele et al., 1997) will be applicable to cherimoya production. The following data and assumptions have been used in determining the cost of cherimoya production.

Operating assumptions and costs

Preplant and Planting: Land preparation costs $816/acre. Land preparation is performed on a custom basis and includes removing trees, subsoiling, and leveling. To determine planting costs, I based this analysis on 134 trees per acre (18' x 18' space planting). The cost of planting is calculated at $14.20/tree ($12.20 to purchase the tree and $2.00 for labor to plant trees). I am assuming there is a loss of 2 trees/acre in the first season. These are replanted in year 2.

Irrigation: Based on the lemon production cost study, the average cost of water purchased from the Coastal region of Ventura Co. is $190 per acre-foot. The amount of water applied is estimated to be 4 to 9 acre-inches/acre during the first two years of establishment and 16 to 20 acre-inches/acre during years three to five. After the trees have reached full production, water application is assumed at an annual rate of 24 acre-inches/acre.

Prune and Sucker: We calculated pruning and suckering costs based on data we have for lemon production. These operations cost about $100/acre during the first and second years of establishment, $220/acre during the third and fourth years, and about $500/acre during the fifth and production years. Because these operations are usually performed on a contract or custom basis, they are charged on a per acre basis.

Pest Control: Insect control during both the establishment and production years includes a biological control program using deccolate snails for snail control at $50/acre/year and chemical and or traps for ants and rodents at $150/acre/year.

Weed control: Weed control includes hand weeding, which was estimated to take 20 hours/acre/year during both establishment and production. Costs of hand weeding are calculated at labor rate. Also chemical herbicide control may be used. In this analysis, we used Roundup at 1qt/acre/year during both establishment and production.

Fertilization: According to growers surveyed, the rate of nitrogen (N) applied ranged from 17 lb/acre in the first year to about 204 lb/acre in production years. In addition, micronutrients (zinc sulfate and manganese sulfate) are each applied at the rate of 8 lb/acre each year during both establishment and production periods. The cost of N is approximately $0.17/lb and micronutrients cost an average of $0.37/lb. Fertilization is through the irrigation system.

Pollination: Hand pollination is required for production of cherimoya in California. Hand pollination is estimated to take about one hour/acre for each application of pollen during years four and five of the establishment period and two hours/acre for each application of pollen during the production years. Annually, pollination is done every other day for about two months. This brings the total time for pollination to 30 hours/acre each year during establishment years and 60 hours/acre each year during production. Costs of pollination are calculated at labor rate.

Labor: The average cost of labor is estimated to be $8.65/hour (the same rate used in lemon production costs) for both machine and non-machine workers. However, labor wage payrolls carry benefits in-