Book 1

Chapter 3

Avocado Flowering and Pollination

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A typical full grown healthy avocado tree in California can produce up to a million flowers a year, but, on the average, fewer than 200 flowers per tree will set fruit that will hold and develop to maturity and harvest (about 10,000 lbs/acre, or less). Upon occasion, we have seen some groves with trees setting an average of 500 flowers per tree (25,000 lbs/acre), but this is rare. More commonly, only 100 flowers (or less) per tree will set and hold fruit to maturity (5,000 lbs/acre or less), much to the distress of growers. In short, there is a significant yield potential in most groves that has not been achieved. While there are many factors that contribute to poor yields, some of this failure to reach high yields is related to factors that affect flowering, pollination and fruit set, and probably more factors remain to be discovered. In addition, the avocado flower has a very interesting bisexual quality in which the flower opens twice; first opening in the female stage, then closing and opening the next day in the male stage. This chapter will discuss several factors that influence the ability of trees to flower and set fruit, and the interesting flowering behavior found in avocado will be described.

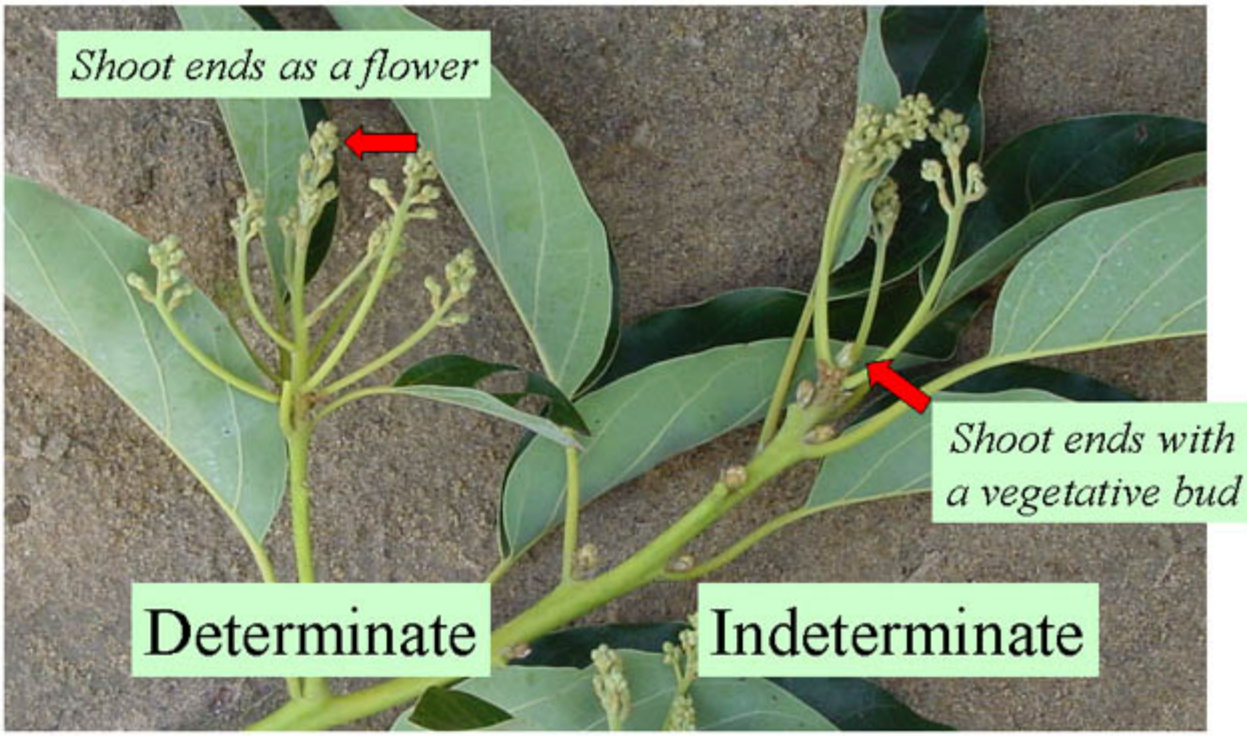
1. Factors that Affect Flower Formation.

The following factors affect flowering in avocado. Further information can be found in the review of avocado reproductive biology by Gazit and Degani (2002).

a. Juvenility. Most grafted avocado cultivars will not begin to flower until the third year after planting. Some cultivars are more precocious; 'Gwen' and progeny siblings with the 'Gwen' line of genetics, such as Lamb Hass, will often flower in the second year after planting. Most un-grafted seedlings have a long juvenile phase and may not flower for 10 – 15 years after planting.

b. Phenology. Flower primordia are found in terminal or subterminal buds on shoots that grew in the spring and summer flushes of growth. Recent research has shown that differentiation from vegetative buds to reproductive buds takes place at the end of shoot expansion of the summer growth, usually in August in California (Salazar-Garcia et al. 1999). Later, these reproductive buds grow to form multi-branched panicles upon which the flowers form. A tree can have hundreds of panicles and the tree as a whole can have up to a million flowers (Bergh 1986). The panicles are usually determinate (no leafy buds emerging from the panicle), but some are indeterminate (with leafy buds eventually growing from the panicle). Usually these panicles are found on the outer surface of the tree, with maximum exposure to light. This presents a problem in a pruning program; when doing hedgerow pruning or shaping later in the season, many of those shoots that are ready to form panicles and flowers are removed. Research is underway which should address the question whether late season pruning is more detrimental than early season pruning.

Figure 1. Example of determinate and indeterminate inflorescences in avocado



The length of the flowering season is variable according to race, cultivar and temperature. In general, Mexican cultivars flower earliest, West Indian cultivars next, and pure Guatemalans last.

West Indian cultivars flower well in tropical climates, but often flower poorly in the subtropical climate of Southern California. On the other hand, Guatemalan and Guatemalan x Mexican hybrids flower poorly in tropical climates, but flower profusely in California. The lack of flowering in a tropical climate is the reason 'Hass' (a Guatemalan x Mexican hybrid) is not grown as a commercial avocado cultivar in Florida and Hawaii. The 'Hass' cultivar in San Diego County usually has the bulk of flower opening occurring over a six week period from late March to early May. 'Hass' in the more northern counties may have a flowering period about 2 to 4 weeks later than San Diego. However, in some years in San Diego, flower opening begins as early as late January. Flower timing can also vary considerably in a given location. In one grove in San Diego County, in an attempt to apply a bloom spray at 50% flower opening, it was discovered by the author that this occurred on April 7 one year and April 30 the next year.

The length of flowering season for 'Hass' is reduced at higher temperatures. One report has the length of flowering season at 85, 42 and 15 days at 17/12, 25/20 and 33/28 C (day/night respectively) (Sedgley and Annelis, 1981).

Flowering is usually seen to start earlier in the warmer areas of the grove, along the grove roads where there is abundant light and perhaps warmth from the asphalt roads, and on the southwest side of the trees where there is long exposure to sun in the afternoon.

c. Temperature. Flowering in 'Hass' and the other subtropical avocado cultivars is induced by a period of low temperature. 'Hass' did not flower when kept at temperatures of 30/25, 25/20 or 20/5 C (day/night), but did flower when exposed to 3-4 months of 15/10, 18/15, 20/15 and 23/18 C (day night). Under the two last temperature regimes the flowering was delayed and sparse (Buttrose and Alexander, 1978).

d. Day Length. Day length does not seem to be a factor in flower induction in avocados. In Mexico, off-bloom in Hass (known as 'crazy bloom') is induced in September after long (greater than 12 hr) day length. Certain cultivars in California, most notably 'Pinkerton', have a significant off-bloom in the summer. Buttrose and Alexander (1978) reported that 'Fuerte' flowered under both 15 hr day lengths and 9 hr day lengths.

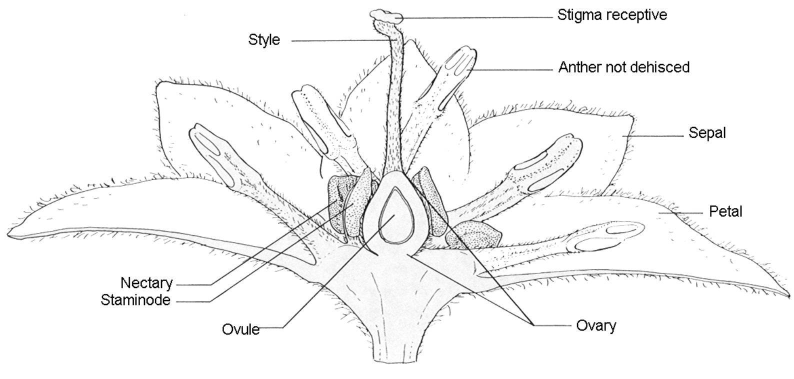
e. Water Stress. Water stress did not appear to increase flowering in trees subjected to either high temperatures or low temperatures. Flowering was delayed after the water stress (compared to the non-stressed control trees) and occurred about a month after cessation of the stress (Chaikiattiyos et al. 1994). It has been observed by the author that water stress in California usually results in less flowering the following spring because water stress almost always leads to chloride tip burn, and eventual leaf drop. With severe tip-burn, leaf drop is excessive and an abnormal leaf flush in the spring is necessary to replace leaves that have dropped. It is believed that the resources in the tree are diverted to leaf growth rather than flower development. Controlled water stress as it affects flowering in avocado has not been studied in California.

f. "On Year" vs. "Off Year". More information needs to be learned about why avocados have "on" and "off" years, but it is suspected that starch levels and perhaps certain growth regulators need to reach certain levels and in balance with each other for the tree to flower heavily. It has been noted that not all shoots develop flowers; in an "on" year 46% of shoots developed flowers but only 13% of shoots developed flowers in the "off" year (Salazar-Garcia et al. 1998, Salazar-Garcia and Lovatt 2000). In the year after an extremely heavy crop, some trees do not develop flowers at all.

2. Basic Flower Structure.

Female Stage: The avocado flower opens twice, opening first as a female, closing overnight, then opening as a male for the final opening. The female flower has all nine stamens bent at almost a 90-degree angle to the central erect pistil. The stigma is white and receptive to pollen, but the pollen has not yet been released from the closed pollen sacs at the ends of the stamens. Nectar is secreted from the three staminodes.

Figure 1. Female Stage



Male Stage: After closing overnight, the flower opens as a functional male. The six stamens of the two outer whorls fold closer to the pistil (about a 30 to 40 degree angle from the pistil). The three stamens from the inner whorl stand erect next to the pistil. Nectar is secreted by three pairs of nectaries. Anther dehiscence (splitting to release pollen grains) occurs 1-2 hours after the second flower opening. The surface of the stigma sometimes will remain white, sticky and receptive to pollen, but normally the stigma is brown and shriveled by the time pollen is released. About half of the avocado cultivars open as female in the morning, and the other half as female in the afternoon, leading to the classification of "A" and "B" cultivars (Lahav and Gazit, 1994). (See "The Remarkable Avocado Flower" below for further information).

Figure 2. Male Stage

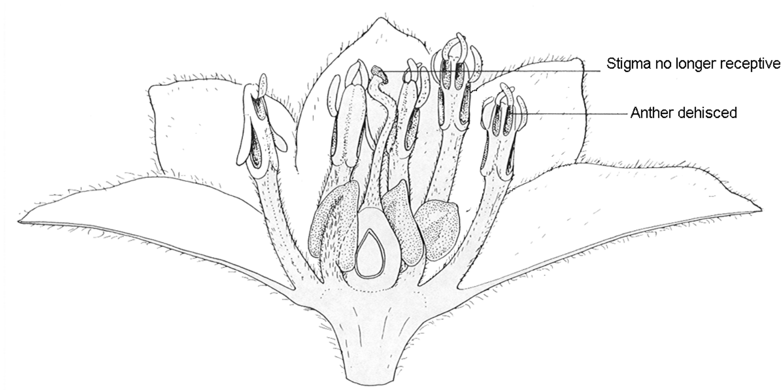


Figure 3. Stage 1 Floral Opening

Figure 4. Stage 2 Floral Opening

Photos courtesy of Dr. Tom Davenport,
University of Florida

The Remarkable Avocado Flower (adapted from Bergh, 1974 and Silva, Lovatt and Bergh, 2002).

"Avocado flower behavior is noteworthy – nothing quite like it is known in any other plant. The avocado flower has both female and male organs, which means it is structurally "perfect", or "bisexual", which is not unusual. What is unusual is that the avocado male and female organs within one flower do not function at the same time. Each avocado flower is functionally unisexual. Each flower is female when it first opens. That is, its stigma will receive pollen from other avocado flowers, but its stamens do not shed pollen at this first opening."

The female-stage avocado flower has a receptive stigma but also nonfunctional male parts (Figure 1). The female stage flower opens first, but for only 2 or 3 hours. The flower then closes and remains closed the rest of the day and that night. The following day, the flower opens again. But now the stigma will ordinarily no longer receive pollen. Instead, the flower now sheds pollen, and is known as a male-stage flower. After remaining open for several hours on the second day, the male-stage flower closes again, this time permanently. Thus each avocado flower is female at its first opening and male at its second opening.

In California, honeybees transfer pollen from male-stage flowers to stigmas of female-stage flowers. Once pollen has been successfully transferred to the stigmas, a process known as *pollination*, the pollen germinates, producing a pollen tube that advances through the style and ovary tissues to the ovule, which contains the egg. Depending on temperature, the pollen tube requires only about 2 to 4 hours to reach the ovule. Once the pollen tube delivers the sperm to the egg inside the ovule, the sperm and egg must fuse, a process known as *fertilization,* which results in formation of the embryo. The process of fertilization initiates the development of the ovary into a mature avocado fruit, and the ovule into the seed, inside of which is the embryo. This embryo can then develop into the young seedling avocado tree of the next generation. The seed provides plant growth regulators necessary for fruit set and fruit development.

Nature has provided for avocado cross-pollination by creating two kinds of botanical varieties. The A type flower is functionally female in the morning of the first day and functionally male in the afternoon of the second day, if the weather is warm. The B type flower is functionally female in the afternoon of the first day and functionally male in the morning of the second day, as diagrammed below.

	First Day		Second Day	
	Morning	Afternoon	Morning	Afternoon
A type	Female (stigmata receptive)			Male (sheds pollen)
B type		Female	Male	

Since different flowers open on different days, the two types of avocado cultivars complement each other with their diurnal synchrony. Both are functionally female on their first day and functionally male on their second day, but they differ in the time of day that they are male and female. A variety of one type provides pollen (functionally male) when a variety of the other type is receptive (functionally female). Therefore, the pollination and fertilization necessary for fruit set can occur.

On trees of an A-type cultivar, flowers open for the first time in early or midmorning, remain open and pistil-receptive until about noon, then close and remain closed until about noon of the second day, when they reopen and begin shedding pollen with the pistil no longer receptive. Finally, they close permanently that night. On a single tree, there may be thousands of flowers that open for the first time the same morning and then follow the same behavior pattern synchronously hour after hour for their 2-day existence. The total opening cycle on an A-type tree covers about 36 hours. Flowers on trees of a B-type cultivar function analogously but with transposed timing. The opening cycle on a B-type tree spans about 24 hours. The difference in cycle time reflects the relative length of the closed period between openings.

The two flowering types behave with clocklike exactness only when the average temperature (night minimum and day maximum) is above about 70°F (21°C). As the temperature falls, the daily openings for the functionally male and female flowers become delayed and irregular such that a single tree may have flowers in both the female and male stages at the same time, which explains how large blocks of just one cultivar set heavy crops via self-pollination. With colder temperatures, the second (male) opening may be delayed 1 or more days, and other abnormalities in flower behavior may occur. Either opening may continue through the night and into the next day. Below 60°F (16°C), however, there may be zero fruit set.

Recent research at University of California, Riverside has shown a weak positive correlation between cross-pollination and yield in some Hass avocado orchards, but the total data suggested that self-fertilization was responsible for a substantial portion of fruit set in California groves. However, in earlier studies, when an A-type and a B-type variety grew with their branches overlapping or at least close together, fruit set increased by 40 to 150 percent. Many commercial growers plant B-type cultivars to provide a complimentary source of pollen for the Hass avocado, an A-type, and place beehives in their orchards. Since home gardeners are not concerned about yield and bottom-line profit like a commercial grower, they do not need to make provision for cross-pollination. Nevertheless, it is useful to understand the factors that can influence fruit set and that can be used to increase fruit set, if desired.

A sampling of cultivated varieties classified as A types or B types are listed below:

- A-type cultivars: Hass, Gwen, Pinkerton, Reed, Anaheim, Lamb Hass
- B-type cultivars: Fuerte, Zutano, Bacon, Whitsell, SirPrize"

Under typical California weather conditions, which are subtropical, both the A- and B-type cultivars bloom continuously for about 2 months, and it is rare for the earliest cultivar to finish blooming before the latest begins. Whereas summer flush vegetative shoots of the Hass avocado in California transition to reproductive shoots and initiate inflorescences sometime from the end of July through August, individual avocado flower buds are initiated at most about 2 months before the tree is in full bloom. The seasonal cycles of flowering, fruit set, and fruit development for the Hass avocado in San Diego—Riverside environmental conditions are shown in figure 5.

Avocados produce two types of floral shoots: determinate floral shoots, in which the apical bud is a flower, and indeterminate floral shoots, in which the apical bud remains vegetative and produces a vegetative shoot. Determinate floral shoots occur along the branch, and indeterminate floral shoots are formed at the end of a shoot (branch). The number of flowers per inflorescence of the Hass avocado is approximately 150.

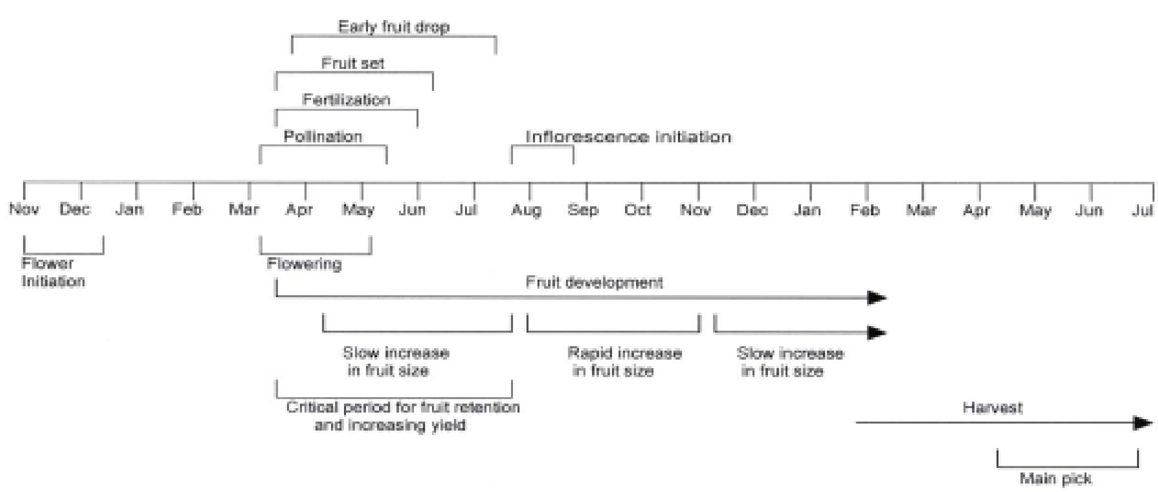


Figure 5. Flowering, fruit set, and fruit development of the Hass avocado in California.
Source: After Lovatt 1999; based on San Diego-Riverside environmental conditions

Hass avocado trees in California produce approximately 90 percent indeterminate floral shoots. This type of floral shoot sets less fruit than a determinate floral shoot. However, fruit set should not be a concern since a single tree will likely have a million flowers in bloom during a single spring bloom period. Despite the fact that less than 0.1 percent of this total results in fruit that hold to maturity, good yields are obtained. A yield of 200 8-ounce (229-g) fruit, or about 100 pounds (45 kg) per tree, results from approximately 0.02 percent fruit set.

Avocado trees have a strong tendency to alternate or biennial bearing, alternating moderate to heavy crops one year with light crops (low yields) the next year. This condition can be initiated by climatic or cultural conditions that result in excessive fruit drop and poor yield or by optimal conditions for fruit set that result in a bumper crop. Spring flush vegetative shoots arising from indeterminate floral shoots that set fruit do not produce inflorescences the following spring. Thus, when trees are carrying a heavy crop, the number of shoots that can produce inflorescences the next spring is significantly reduced. This is the cause of the low fruit set and yield that occur in the year following the heavy crop.

3. Problems Created by Low Temperatures.

As mentioned by Bergh (see above), flower opening and closing follows a regular pattern when the average night minimum and day maximum temperature is above 70 F (21 C). As night minimum temperatures and day maximum temperatures drop, flower opening is delayed. The female opening of A flower cultivars may be delayed into the afternoon, while the B flower cultivars may open as females at night or the next morning. Under these cooler conditions there might be 2-4 days between opening of the female/male flower phases.

The B flower cultivars may completely fail to open as female flowers at the lower temperatures. When exposed to maximum day temperatures between 18 and 21 C, and minimum night temperatures between 7 and 12 C, no female flower opening occurred in Fuerte (B flower) (Leslie and Bringhurst 1951). Under these conditions, Hass (A flower) completed the proper flower cycle.

While cooler temperatures may delay flower opening, this may be a benefit to some degree because overlapping of female and male flowers increases, presumably insuring pollination in a grove of pure "A" type flowers such as Hass. An overlap of 45 min to 90 min was found to occur in Hass during the mid-day (Ish-Am and Eisikowitch, 1989).

In addition, cooler temperatures (and cloudy skies) reduce the bee activity in the grove.

4. Types of Pollination.

There are three types of pollination in avocado; cross-pollination, self-pollination, and close pollination.

Cross pollination occurs when pollen is transferred from male flowers of a type A cultivar to female flowers of a type B cultivar, and vice versa. The flowering behavior of avocado, in which one type will be in the female stage while the other type is in the male stage, seems to promote cross pollination. Indeed, there are several observations and studies that indicate increased yield when type A trees are close to type B trees, with bees present to move the pollen from flower to flower (Nirody, 1922, Stout, 1923, Peterson, 1955, Bergh and Garber, 1964, Gustafson and Bergh, 1966, Degani, et al. 1989, Markle and Bender, 1992). The efficiency of cross pollination depends on the distance between the pollen-donor (pollinizer) tree and the pollinated tree. The yield-increasing effect is best when A and B trees are one or two rows away from each other; if the trees are farther away there may not be a substantial yield increasing effect. Also, there must be a substantial overlap between the male and female bloom, and bees must be at sufficient density to carry the pollen back and forth from pollinizer trees to pollinated trees.

Isozymes and RAPD genetic markers have become useful tools for determining the amount of out-crossing (cross-pollination) in avocados. Recently, using RAPD markers, Kobayashi et al. (2000) found a weak correlation between yield and the rate of cross pollination in Hass in California, concluding that most of the pollination in their study was by close pollination or self-pollination. However, their yield data indicated that there was a definite effect when the B flower trees were adjacent to Hass (4 year average = 205 fruits per tree). When the B flower trees were 5 rows away the 4 year average yield was 90 fruit per tree, and the when 15 rows away the 4 year average was 54 fruits per tree.

In another study in Israel, Degani et al. (1989), using Fuerte and Ettinger as pollinizers, found that Hass fruitlets one month after set were mostly 'selfs' (Hass pollinated Hass), but as the season progressed, the percentage of Hass selfs decreased and the percentage of Hass hybrid fruitlets increased. By the end of fruit abscission, most of the fruitlets still on the trees were found to have been hybridized by pollen from Ettinger. Hybridization from Fuerte was not near as strong as it was from Ettinger. They reported "the Hass fruit yield was found to correlate significantly with the rate of out-crossing with Ettinger". The conclusion was that hybridized fruit tend to stay on the tree better; selfed fruit have a higher drop rate.

Ettinger is not normally grown in California, but Zutano, Bacon and Fuerte are B flower cultivars that should (in theory) serve as cross pollinizers. Lacking data to indicate which is best, it can only be said from observations in the field that Zutano, followed by Bacon, seem to consistently give good yields to nearby Hass trees.

In the past it was recommended in California to plant a pollinizer tree at every third position in every third row (Lee, 1973), but this recommendation was in an era when the fruit from the B flower trees had a relatively good market. As the market declined for greenskins (in favor of Hass), some growers tried using B flower Zutanos and Bacons as windbreaks around the grove. The age-old questions remains: does the yield increase in the Hass near the pollinizers make up for the loss of yield when a Hass is replaced by another variety that does not have a good market? The answer to this question still has not been answered to any satisfaction, but in our observations in California it appears that if a grove is subjected to cool temperatures in the spring, there may be a definite benefit from pollinizer trees. There might not be a benefit when temperatures are mild.

One idea being tried by some growers is to thin a crowded grove (removing every other tree on the diagonal) and graft a Zutano bud into a sucker on the stumps of the removed trees. The Zutano tree would be kept small; essentially the trees would be used only as pollinizers and not as a crop to be harvested.

One of the main goals of the avocado breeding program in California is to develop a B flower Hass-like cultivar that could be inter-planted into every other row in a Hass grove, and be harvested and sold as Hass.

Close pollination occurs when pollen from male flowers land on stigmas of female flowers during the daily overlap period of male and female stage flowers in the same tree (or between neighboring trees in the same cultivar). During cool weather, the afternoon bloom may not occur until the next morning and overlaps with the normal morning bloom, but cool weather also slows down bee activity that could lead to less pollination. We have observed male/female overlap around noon in most groves, some more pronounced than others. With good bee activity, close pollination is probably most important during this time period.

Self pollination occurs in a single flower. In avocado, self-pollination happens only in a male-stage flower when a stamen releases pollen that falls into the stigma that is still receptive. This process may be completed by wind blowing the pollen a short distance, or by gravity. In California, caged tree studies without bees or an alternate flowering cultivar has always led to very poor fruit set. Because of this, we assume self-pollination in Hass is not important. Gustafson and Bergh (1966), in a review of pollination in avocado, stated "an individual flower apparently cannot pollinate itself and subsequently produce a fruit. It is important that the pollen not only reach the stigma, but that it arrive there at the proper time in the flower cycle." This statement has been somewhat controversial because cages invariably add a windbreak factor, a shading factor, and a cooling factor to the experiments. In the more tropical climate of southern Florida, however, Davenport et al. (1994) have shown evidence that pollination in the male stage is important, possibly because the stigmas stay white and receptive to pollen germination in the more humid climate.

In the dry Mediterranean climate of California, cross pollination and close pollination are probably most important for fruit set because the stigmas in the male-phase flowers dry quickly, precluding self-pollination. When humidity is high (as it is in Florida), self-pollination is probably the predominant method for setting fruit.

5. The Role of Bees in Pollination.

Bees appear to be very important for moving pollen from the male stage flowers to the female stage flowers, completing the pollination process in cross pollination and close pollination. O.I. Clark observed in the 1920's that heavy crops in avocado were associated with greater work by bees on the blossoms (Clark, 1922-23). He also observed some things that we see today:

- "Bees prefer other bee pasture to the avocado orchards." We often see bees flying over or around avocados to get to citrus in bloom or other sources of nectar.
- "When bees are abundant or other pastures scarce, they do work freely on avocados."
- "Bees have a strong preference to sticking to one avocado tree at a time." This inhibits cross pollination between cultivars, unless the trees are very close, or intermingling with each other. Ish-Am (2000) added "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."

The importance of bees was confirmed by University of California, Riverside geneticist Peter Peterson (1955) when he caged four trees, two Zutano and two Hass, and put a small hive of honeybees in one the Zutano cages and one of the Hass cages. The results from that test were:

Number of fruit on each caged tree

	Beeless	Bees
Zutano	4	120
Hass	5	284

Steps to take to Improve Pollination

1. Bring beehives into the grove. The University of California farm advisors have usually recommended 1 – 2 strong hives per acre, but Ish-Am (2000) suggests that 1 hive is rarely sufficient, and in many cases 4 hives are required. California growers usually have to rent hives (in 2002 hive rentals averaged $42 per hive), but sometimes beekeepers will drop a load of 80 hives for free if the grower has good bee forage nearby. Bees should have water available; floating boards on ponds or reservoirs enables them to land and drink without drowning.

2. Add pollinizers to the grove. Ish-Am recommends a pollinizer tree row be located at least every fourth row. Some growers in California use pollinizers as wind-breaks around the grove, and some replace thinned-out trees with pollinizers.

3. Keep the orchard open. Direct sunlight should reach the lower branches of each tree in order for the trees to produce a "wall" of flowers down the ground. In avocado production, this can only be accomplished by pruning the upper branches on a yearly basis. Keeping open channels through the grove encourages the flight of bees.

4. Other types of bees? Bumblebees have been reported to increase yield in avocados in Israel where honeybee populations were low. New World Carniolan bees have been used in an experiment in San Diego County for pollination: results were inconclusive as to whether they increased yield compared to Italian honeybees, but it was found that they gather more nectar from avocado (Fetscher et al. 2000). Work with these bees, and other wild bees, may eventually reveal a more efficient pollinator for avocado.

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