New Zealand and Australia Avocado Grower's Conference '05. 20-22 September 2005. Tauranga, New Zealand. Session 7. Flowering, fruit set and yield. 9 pages.

AVOCADO POLLINATION – A REVIEW

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Key words: avocado, cross-pollination, flowering, honeybee, pollination

INTRODUCTION

(Gazit & Degani 2002, Ish-Am & Eisikowitch 1998a, Ish-Am et al. 1999a, Ish-Am & Gazit 2002, Knight 2002, Smith 1966, 1969)

All avocado types were evolved in the tropical climate of Central America, where their flowers had co-evolved with the local insect species. The main pollinators of the avocado were Meliponinae bees and wasp species. The avocado fruits were consumed by the local human populations for thousands of years, and numerous cultivars were developed during its long domestication process.

The avocado fruits are solely a product of pollination and fertilization, since a parthenocarpic effect is not known. The need for pollination does not appear as an important yield limiting factor neither in Central America, nor in the tropical weather of Florida. However, in the Mediterranean climate, in countries like Israel, California and South Africa, it presents a major limiting factor. Wind and spontanous self-pollination of the avocado flower were found not to be effective in this climate, and therefore insect pollination is essential for fruit production. The avocado native pollinators from Central America are not present there, and the European honeybee (*Apis mellifera*) is the main efficient and available avocado pollinator. Honeybee hives are comercially introduced during bloom to most avocado orchards there for pollination purpose. Yet pollinator activity in the orchard is usually not high enough, pollination rates are too low and yields are, therefore, much lower than the potential.

A. FLOWERING

(Bergh 1969, Davenport 1986, Free 1993, Gazit & Degani 2002, Ish-Am & Eisikowitch 1991a, Ish-Am & Eisikowitch 1991b, Ish-Am & Eisikowitch 1993, McGregor 1976, Papademetriou 1976, Sedgley & Grant 1983, Stout 1923, Stout 1933)

The bisexual avocado flower opens twice, with an intermediate closing. The first flower opening is a female stage and the second, usually on the following day, is a pollen-releasing male stage. Both opening and closing of each flower population (female and male) occur simultaneously within the tree, and the cultivar. The male and female flowers open at different times of the day. This unique flowering behavior is termed: diurnally synchronous dichogamous protogyny, with an intermediate closing.

The avocado cultivars are divided into two complementary flowering groups, according to their daily flowering sequence. ‘A type’ cultivars, in warm weather, open female-stage flowers from the morning till noon, and the next day reopen these same flowers in the male stage from noon throughout the afternoon (a flower’s opening cycle of about 34 hr). ’B type’ cultivars, on the other hand, open female-stage flowers from noon throughout the afternoon, and reopen them in the male stage on the following morning till early afternoon (a flower’s opening cycle of about 26 hr). Thus, a daily effective overlap occurs between A-type female-stage flowers and B-type pollen releasing male-stage flowers during the morning, and vice versa at the afternoon. Furthermore, in most avocado cultivars a daily regular self-overlap phase also exists, of female-stage flowers and pollen releasing male-stage flowers of the same tree, which takes place for a period of 1-3 hr. In cool weather a delay of both female and male opening times occurs, which may result in a complete reversal as to the part of the day female and male-stage flowers are open. At both female and male-stage flower openings nectar is secreted, although by different sets of nectaries.

B. POLLINATION

(Bergh 1968, Bergh 1977, Davenport 1986, Davenport et al. 1994, Free 1993, Gazit 1977, Gazit & Degani 2002, Ish-Am & Eisikowitch 1991a, Ish-Am & Eisikowitch 1991b, Lesley & Bringhurst 1951, Papademetriou 1975b, Schroeder 1954, Sedgley 1977, Sedgley & Grant 1983, Stout 1933, Vithanage 1990)

The avocado flowering behavior is a sophisticated mechanism, which prevents effective self-pollination (within a flower), enables close-pollination (between neighboring flowers within a tree) and encourages cross-pollination (between different cultivars).

Self-pollination occurs when pollen grains reach the stigma within the same flower. This process could be accomplished by wind, or by gravity, and may be encouraged by a pollinator visit. Self-pollination of the avocado flower may only occur during its pollen-releasing period, at the male-stage opening, where it is a common phenomenon. However, the ability of this self-pollination to lead to fertilization (namely, to be effective) presents an open question. A clear inability of the male-stage flower to achieve fertilization was demonstrated under Mediterranean-type weather conditions, where mostly Mexican and Guatemalan cultivars, as well as their hybrids, are grown. On the other hand in Florida, where the local avocados are of the West Indian cultivars and their hybrids, highly effective male-flower fertilization was found.

Close-pollination, between neighboring flowers within a tree (or a cultivar), occurs regularly during the daily self-overlap period of male and female-stage flowers within the tree. In cool weather it may also happen with the afternoon bloom, which is delayed to the next morning, and then overlaps with the normal opening of the opposite-gender morning bloom. Since male and female-stage flowers exist in very close proximity during close-pollination, this process efficiency may be very high. It depends on the length of the self-overlapping period, on the percent of female-stage, and pollen-carrying male-stage flowers that are exposed to it, and on pollinator activity. As was mentioned above, most avocado cultivars in the Mediterranean countries present a daily effective self-overlapping period, though this is not the case for many West Indian cultivars in tropical weather. Generally close-pollination process is more effective for A-type cultivars, and less so for the B types, due to the more efficient self-overlapping of the former cultivars.

Cross-pollination occurs (under warm-weather conditions) between B-type cultivar's male-stage flowers and A-type cultivar's female-stage flowers in the morning, and vice versa in the afternoon. It may also occur between different cultivars of the same flowering type, if an overlapping period exists between the male-stage bloom of one of them and the female-stage of the other. Cross-pollination efficiency is a function of the distance between the "pollinizer" (pollen donor) and the pollinated trees, as well as of the male and female-stage flowers' overlap duration and efficiency, and on pollinator activity and mobility. In some cases, cross-pollination of A-type cultivar by the B-type one was found to be more effective than the opposite way, due to higher efficiency of the overlap between the A-type female-stage and the B-type male-stage bloom than the opposite overlap.

C. MASS FLOWERING EFFECT

(Bergh & Garber 1964, Bergh 1968, Degani & Gazit 1984, Degani et al. 1989, Eisenstein & Gazit 1989, Gazit 1977, Gazit & Gafni 1986, Gazit & Degani 2002, Goldring et al. 1987, Lahav &v Zamet 1999, Shoval 1987)

An adult avocado tree, in a normal season, may bear about one million flowers, but only several hundred fruits. Namely, only 0.05% of the flowers (one of 2,000) produce fruit. This effect, which is common in tropical trees, is termed: "mass flowering".

What may be the purpose of this avocado large excess of flowers?

Cooperation among flowers (the inflorescence effect): A single avocado flower has very low attraction for its potential pollinators. Its advertizing influence on a distant pollinator is low, and the amount of reward for those that do approach is very limited. However, a large inflorescence, composed of many clustered small flowers, may advertise itself efficiently, and can offer the visitor a large amount of reward. The large inflorescence also forces the pollinator to visit many flowers at a time. A blooming avocado tree has the effect of a giant inflorescence, of dozens of thousands of flowers cooperating in attracting the potential pollinators.

Cooperation and competition among pollen grains: Although the avocado-flower ovary holds only one ovule, it was demonstrated (in Israel, for the cultivars 'Hass', 'Ettinger' and 'Reed') that when only a single pollen grain reaches the stigma the fertilization probability is very low. Actually, twenty pollen grains or more must reach the stigma for a high fertilization probability. Thus, a cooperative effort of many pollen grains is needed for breaking through the style and into the ovary. Since an average of only 1-3 pollen grains are deposited on an avocado stigma by a typical single visit of a pollen-carrying honeybee, more than one visit per flower in necessary to achieve fertilization. In addition, for many cultivars a higher likelihood of fertilization by out-cross pollen, compared to that of the self-pollen was demonstrated. Furthermore, the pollen of certain cultivars appears to be more potent as a cross-fertilizing agent than pollen of others. Therefore, in addition to the cooperation, a competition between the pollen grains occurs, for fertilizing the single ovule, which is waiting inside the ovary. This competition may select for the best pollen grain out of the selves, and moreover, for the most potent outcross pollen, if available.

Competition and selection among the fruits: A significant selection, throughout the heavy initial-fruit drop, for cross-pollinated fruits and over the self-fruits, has been demonstrated in Israel for the main cultivars. As a result, the percent of the tree cross-pollinated fruits increases during fruit growth. In most of these cases, the resulting yield was found to decrease significantly with increasing distance from the pollinizer trees, due to the decrease of cross-pollination rate. The available data may support the assumption that the selection against the self-fruits was mainly evident under stress conditions of a windy, hot and dry spell, and minimized, or disappeared altogether, under milder conditions. Interestingly, a selective fruit drop had been found even within the self-fruits, preferring the self-heterozygote fruits to the homozygote ones. These selection effects result from the competition for resources, which is in effect both among the fruits, and between them and the new growth. In most cases the cross-pollinated fruits were found to be stronger and larger than the self-pollinated ones. These phenomena are termed “metaxenic effects”. Some avocado cultivars, like ‘Ettinger’, ‘Bacon’, ‘Zutano’ and ‘Edranol’, were found to produce a “male parent positive metaxenic effect”. Namely, their pollen grains have an advantage over the self-grains when they cross-pollinate other cultivars, as well as their out-cross fruits over the selves. These cultivars are termed “potent cultivars”.

D. THE HONEYBEE AS AN AVOCADO POLLINATOR

(Bergh & Garber 1964, Bergh 1968, Clark 1923, Davenport 1986, Free 1993, Gazit & Degani 2002, Ish-Am & Eisikowitch 1991a, Ish-Am & Eisikowitch 1991b, Ish-Am & Eisikowitch 1993, Ish-Am & Eisikowitch 1998a, Ish-Am & Eisikowitch 1998b, Ish-Am & Eisikowitch 1998c, Ish-Am et al. 1999b, McGregor 1976, Papademetriou 1976)

Honeybees visit both female and male-stage avocado flowers. When both flower stages are available they usually visit them alternatively, collecting nectar from both and pollen from the male flowers (“nectar and pollen collectors”). However, they sometimes visit only the male-stage flowers, collecting only pollen (“pollen collectors”). Occasionally honeybees are seen collecting only nectar (“nectar collectors”), and then, while visiting pollen-carrying male flowers, they actively brush the pollen off their body. Both “nectar and pollen collector” and “nectar collector” honeybees, while visiting avocado flowers, make an efficient contact with the male-stage flower stamens and the female-stage stigma, by the very same regions of their body. These body zones (the “pollen collecting zones”) were found to carry large amounts of avocado pollen. Thus, both the nectar, and the nectar and pollen collector honeybees serve as efficient pollinators of the avocado. The pollen collector honeybees, on the other hand, do not visit the female-stage flowers, and hence do not contribute to avocado pollination.

In most Mediterranean climate countries the relative attractiveness of the avocado bloom to the European honeybee is low, in comparison with that of numerous local flowering species. It is quite evident that the avocado flowers are less adapted to the European honeybee than the competing local Mediterranean flowers. These species are in bloom throughout the avocado flowering season (the spring), which is also the blooming season peak there. They consist mainly of the Citrus spp, and species of the Mint, Daisy and Mustard families (Labiatae, Fabaceae and Brassicaceae, respectively). Thus, honeybee foragers tend to abandon the avocado orchard, where their hives were placed for pollination purpose, and to visit a nearby competing blooming species.

Most field-worker honeybees forage within a limited area of 1 to 3 near-by trees, and therefore may perform cross-pollination only between trees at a distance of one or two rows. A small percentage of the foraging honeybees (2%-4%), however, move farther between rows and plots, and may carry avocado pollen hundreds of meters away from its source. These foragers are the “scout bees”, which, for the sake of information collecting, move among different locations and flowering species throughout their food collecting flight. The cross-pollination efficiency of adjacent avocado trees of opposite flowering-type found to be similar to that of the close-pollination. However, cross-pollination efficiency drops dramatically with increasing pollinizer distance.

E. DOES POLLINATION LIMIT AVOCADO PRODUCTIVITY?

(Bergh 1968, Bergh 1977, Davenport 1986, Free 1993, Gazit 1977, Gazit & Degani 2002, Ish-Am & Eisikowitch 1998a, Ish-Am & Eisikowitch 1998b, Ish- Am & Eisikowitch 1998c, Lahav & Zamet 1999, McGregor 1976, Papademetriou 1976, Schroeder 1954, Shoval 1987)

One may think that, in the case of the avocado, pollination cannot play a significant role as a yield-limiting factor. Since a mature avocado tree produces about one million flowers per blooming season of 30 to 60 days, the tree carries 10,000 to 40,000 (new) female flowers every blooming day. If a good seasonal crop of 400 to 600 fruits per tree demands pollination (and fertilization) of about the same number of flowers, it may be accomplished by only 2 or 3 forager honeybees, during 1 hr of the daily close-pollination period in only one blooming day. This results from the following data: A forager honeybee visits about 6 avocado flowers per min, which are about 360 flowers per hr. About half of these flowers, at that blooming phase, are female-stage, and they are efficiently pollinated through every honeybee visit. Nevertheless, in practice, a measurable initial fruit-set under field condition demands activity of at least 5 to 10 honeybees per tree, throughout the female bloom. One week of this visitation level is required to achieve a fair crop, and much more is needed for a good one. This seeming paradox can be understood as a result of the need for 20 pollen grains per stigma (or more) for an efficient fertilization and the low average number of pollen grains that is deposited on the stigma through a single bee-visitation. It may also stem from the low rate of cross-pollination, which results from the low efficiency of the honeybee as a cross-pollinator, and the heavy close-pollinated initial-fruit drop, which occurs due to the selection for the few cross-pollinated fruits.

To summarize, pollination may be a limiting factor for avocado productivity where:

(a) Self-fertilization within the male flower does not happen;

(b) Pollinator activity is too low (due to a low level of available pollinator population, or to the presence of more attractive competing blooms), and hence total-pollination rates are too low;

(c) Cross-pollination rate is too low, owing to a low mobility of the pollinator insect, or to a large distance from the pollinizer tree.

(d) A significant selection against the self initial-fruits occurs, mainly under stress conditions of a windy, hot and dry spell.

F. HOW TO IMPROVE AVOCADO POLLINATION?

I believe that an adequate treatment should be able to mostly overcome the pollination limits, and could allow the avocado to achieve its yield potential.

1. Enough honeybee hives in the orchard: One needs at least 5-10 honeybees per medium tree on the female bloom to achieve a fair pollination, and more is much better. Therefore, you should check the trees twice a week during the blooming time. If bee activity on the female-stage blooming trees is lower than 5-10 per tree, you should add more hives. Only rarely would one hive per acre be sufficient, and in many cases up to four strong hives per acre are required.

2. <u>Fair conditions for hive activity:</u> Place the hives in a sunny location, preferable facing the east. Keep the hives' vicinity, and especially the hive entrances, clear of vegetation. Assure a near by fresh water source for the bees. Keep the hives in the orchard throughout the blooming season. Check the hives regularly for health and normal activity.

3. Enough and close-by pollen-donor trees: Most avocado cultivars need cross-pollination to achieve yield potential. Cross-pollination is efficiently performed between adjacent trees, and up to two rows away from the pollinizer tree (about 12 m). The best orchard design would allocate a pollinizer tree adjacent to every pollinated one. Therefore, the minimum advised density of the pollinizer trees could be set to a pollinizer tree on every 3rd tree within the row, on every 3rd row. Not all cultivars may serve as effective pollinizers. Find out what pollinizer cultivars you should use, according to your orchard cultivar composition and location.

4. Open canopy: Direct sunlight should reach all the tree zones include the lower branches. This would enable the tree to grow and to carry bloom all over. Open orchard canopy also encourages a higher honeybee activity and mobility, and would increase both total-and cross-pollination rates.

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