

AVOCADO POLLINATION BASICS – A SHORT REVIEW

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Introduction

All avocado types were evolved in the subtropical climates of Central America, and their flowers 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 many 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 in Central America, nor in the tropical weather of Florida. However, in Mediterranean climate countries, like Israel, California and South Africa, it presents a major limiting factor. Wind and spontaneous self-pollination of the avocado flower are not effective in these countries, and insect pollination is needed for fruit production. Its original pollinators from Central America are not present there, and the European honeybee (*Apis mellifera*) is there the main efficient and available avocado pollinator. During bloom, honeybee hives are introduced commercially to most avocado orchards there, and yet pollinator activity in the orchard is usually not enough, pollination rates are too low and yields are, respectively, far from the potential.

Too low cross-pollination rate is also a significant yield limiting-factor of the avocado in those countries. This may result from either lack of nearby pollen-donor trees, or from low efficiency of the insect pollinator, the honeybee, as a cross-pollinator. To summarize, to maximize avocado yield in the Mediterranean climate countries one needs: (a) enough effective pollination; which demands (b) enough activity of an efficient pollinator, the honeybee; (c) sufficient cross-pollination; which is depended on (d) enough pollen donor trees in close proximity.

A. Flowering (3, 6, 11, 14, 16, 17, 18, 27, 30, 35, 37, 38)

The bisexual avocado flower opens twice, with an intermediate closing. The first flower opening

is at a female stage and the second, usually on the following day, is at a pollen-releasing male stage. Both opening and closing of the female stage flowers, as well as of the male stage ones, occur simultaneously within the tree, and the cultivar, at a regular time daily. This unique flowering behavior, which is displayed by all avocados, termed diurnally synchronous protogyny dichogamous, with an intermediate closing.

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

B. Pollination (2, 4, 6, 7, 11, 12, 14, 16, 17, 26, 29, 31, 33, 35, 38, 40)

The avocado flowering behavior is a sophisticated mechanism that prevents self-pollination (within a flower), enables close-pollination (between neighboring flowers within a tree or cultivar) and encourages cross-pollination (between different cultivars), by preferring the cross- to the close-pollination.

Self-pollination occurs when pollen of a flower reaches the stigma within the same flower. This process does not necessarily demand pollinator involvement. It may be accomplished by wind, or even spontaneously, due to gravity. Self-pollination of the avocado flower may only occur with its male stage, where it is common and efficient phenomenon. Nevertheless, whether the self-pollination of the male-stage flower can succeed to lead to fertilization is an open question. A clear inability of the male-stage flower to achieve fertilization was demonstrated under the Mediterranean-type weather conditions, where mostly Mexican and Guatemalan cultivars, and their hybrids, are grown. However, in Florida, with the local West Indian cultivars and their hybrids, highly efficient male-flower fertilization was found.

Close-pollination occurs regularly during the daily self-overlap period of male and female-stage flowers within a tree and the cultivar. During cool weather it may also happen when the afternoon bloom is delayed till the next morning, and then self-overlaps with the normal opposite-gender morning bloom. Since male and female-stage flowers during close-pollination are at a very close proximity, the close-pollination efficiency may be high. It depends on the length of the self-overlapping period, on the percent of female flowers that are exposed to it, and on pollinator activity. As was mentioned above, most avocado cultivars in the Mediterranean countries present a daily efficient self-overlapping period, but this is not the case for many West Indian cultivars that are grown in tropic weather. Generally close-pollination is performed more efficiently in A-type cultivars, and less so in the B types. This is due to the more efficient self-overlapping of the A-type cultivars.

Cross-pollination occurs (during warm weather) between B-type male-stage flowers and A-type female-stage flowers in the morning, and vice versa in the afternoon. It may also eventuate between trees of the same flowering type, when there is an overlapping period between the male flowers of one and the female flowers of the other. Cross-pollination efficiency depends on the distance between the “pollenizer” (pollen donor) tree and the pollinated one, on the overlap-period efficiency between the former male bloom and the latter female bloom, and on pollinator mobility and activity. In many cases, cross-pollination of A-type cultivar by a B-type one is more efficient than the opposite way, since the overlap between the A-type female bloom and the B-type male bloom is more efficient than the vice versa.

C. Mass flowering effects (1, 2, 8, 9, 10, 12, 13, 14, 15, 25, 36)

An adult avocado tree, in a good season, may bear about one million flowers, but only several hundred fruits. Namely, only 0.05% of the flowers (one of 2,000) give fruits. This effect, which is very common for Sub-Tropical trees, was termed: “mass flowering”. For what does the avocado tree need that large excess of flowers?

Cooperation among flowers: the inflorescence effect. A single small flower produces very low attractivity for its potential pollinators. Its advertizing power for a distant pollinator is low, and the approaching visitor may receives a very limited amount of reward. However, an inflorescence, composed of many dense small flowers, may advertizes itself like a big flower, and can offer the visitor more reward. And most importantly, it forces the pollinator to visit many flowers at a time. The blooming avocado tree acts like a giant inflorescence, where thousands of flowers cooperate 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, in the cultivars 'Hass', 'Ettinger' and 'Reed', that a single pollen grain on the stigma has a very low probability of fertilization. Twenty pollen grains or more should reach the stigma to achieve a high fertilization probability. Namely, a cooperative effort of many pollen grains is needed to break through the style and into the ovary. An average of only 1-3 pollen grains are deposited on an avocado stigma by a single visit of a pollen-carrying honeybee. Therefore, more than one visit per flower is necessary to achieve the needed pollen amount. In addition, in many cultivars a higher likelihood of fertilization by out-cross pollen, compared to that by self-pollen was found. Moreover, it appears that pollen of certain cultivars is more potent as a cross-fertilizing agent than pollen of others, namely, the former result in higher fertilization rates. Therefore, simultaneously with the cooperation, a competition develops among the pollen grains, for fertilizing the single ovule that is waiting inside the ovary. The competition selects for the best pollen grain out of the selves, and furthermore for the most potent out-cross pollen, if available.

Competition and selection among fruits. Selective fruit-drop of self initial-fruits, while mostly cross-pollinated fruits remained on the tree, has been demonstrated in Israel for the main cultivars. As a result, the percent of cross-pollinated fruits on the tree was found to increase during fruit growth. In most of these cases, the resulting yield decreased significantly with increasing distance from the pollen source, and the resultant decrease of cross-pollination rates. The available data may support the assumption that the selection against the self-fruits was mainly evident under stress conditions of a very 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 not only stronger, but also larger than the self-pollinated ones. These phenomena are termed "metaxenic effects". Some avocado cultivars, like 'Ettinger', 'Bakon', 'Zutano' and 'Edranol', were found to produce a "positive metaxenic effects", namely, give an advantage to the out-cross pollen grains over the self grains, as well as to the out-cross fruits over the selves. These cultivars are termed "potent cultivars".

D. The honeybee as a pollinator of the avocado (1, 2, 5, 6, 11, 14, 16, 17, 18, 19, 20, 21, 24, 27, 30)

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, while visiting both stages, honeybees collect only nectar (“nectar collectors”), and then, while visiting pollen-carrying male flowers, they actively brush the pollen off the body. The nectar and pollen collector honeybees, as well as the nectar collectors, make 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, the nectar, and the nectar and pollen collector honeybees, but not the nectar collectors, appear to be efficient pollinators of the avocado.

However, in most Mediterranean climate countries the relative attractiveness to the European honeybee of the avocado bloom is low, in comparison with that of numerous local flowering species that are in bloom at the time, like citrus spp, and species of the Mint, Daisy and Mustard families (Labiatae, Fabaceae and Brassicaceae, respectively). Thus, in many cases honeybee foragers from hives, which are placed in an avocado orchard for pollination, abandon the orchard to visit a nearby competing bloom. It is quite evident that the avocado flowers are less adapted for supplying the European honeybee needs, than the local Mediterranean competing flowers.

Most field-worker honeybees forage within a limited area of 1 to 3 trees, and may perform cross-pollination only between trees of opposite flowering-type cultivars at a distance of up to two rows. A small percentage of the foraging honeybees (2-4%), however, move farther between rows and fields, and may carry avocado pollen hundreds of meters away from its source. These are the scout bees, which, for the sake of information collecting, move among different locations and flowering species throughout the food collecting flight. The efficiency of cross-pollination between close neighboring trees of opposite flowering-type is not much lower than that of the close pollination, but it drops dramatically with increasing distance from the pollen source.

E. Does pollination limit avocado productivity? (2, 4, 6, 11, 12, 14, 19, 20, 21, 25, 27, 30, 31, 36)

One may assume that, in the case of the avocado, pollination cannot play a role as a yield-limiting factor. As was pointed out above, a medium size mature avocado tree produces about one million flowers per blooming season, which lasts 30 to 60 days. Thus, the tree carries

10,000 to 40,000 new female flowers every day. Now, if a seasonal total of 400 to 600 flowers, that are successfully pollinated and fertilized, would be enough for a fair crop, it could be accomplished by 2 to 3 honeybees, during only 1 hr of close-pollination in one day (a forager honeybee visits about 6 avocado flowers per min, and about half of the flowers at that time are female-stage). But, as a matter of fact, a measurable initial fruit-set in the field demands activity of 5 to 10 honeybees per tree at least, during 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 combined result of both 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 efficiency of the honeybees as cross-pollinators, the resulting low rates of cross-pollination and the selective initial-fruit drop of mostly the close-pollinated fruits.

To summarize, pollination may be a limiting factor for avocado productivity where: (a) self-fertilization within the male flower does not happen, and (b) at least one of the two following conditions is exists:

1. Total-pollination rate is low, because of a low pollinator activity. This is due to a low level of available pollinator population, or to the presence of more attractive competing bloom.
2. Cross-pollination rate is low, because of low mobility of the pollinator insect, as in the case of the honeybee, or due to a relatively large distance between the pollinated tree and the pollen-donor cultivar.

F. What can be done to improve avocado pollination?

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

1. Introduce enough honeybee hives to the orchard: You need at least 5-10 honeybees per medium tree to achieve fair pollination, and more is much better. Check your trees twice a week during the blooming time. If bee density on the blooming trees is lower than 5-10 per tree, you should add more hives. Only rarely will one hive per acre be found to be sufficient, and in many cases up to four strong hives per acre are required. Keep the hives in the orchard throughout the blooming season. Be sure the bees have a near by fresh water source.

2. Add pollen-donor trees to the orchard: Most avocado cultivars need cross-pollination to achieve their yield potential. Cross-pollination is efficiently performed between adjacent trees, and not farther than two rows away from the pollenizer tree (about 12 m). Therefore, the best

orchard design would allocate a pollenizer tree adjacent to every pollinated tree, and the minimum density of the pollen-donor trees should be set to every 4th row. Not all cultivars may serve as efficient pollinizers. Find out what pollinizer cultivars you should use, according to your orchard cultivar composition.

3. Keep the orchard open: Direct sunlight should reach the lower branches of each tree. This would enable the lower branches to grow and to carry more bloom. The open orchard also encourages a higher honeybee activity and mobility, and would increase both total- and cross-pollination rates.

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