

POLLINATION AND FRUIT SET OF AVOCADO

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The basic facts of avocado flower behavior have been deciphered and previously described (3, 4, 23). Its protogynous, diurnally synchronous, dichogamy operates under normal conditions in the following way:

1. Each and every flower opens twice. At the first opening it is functionally female – the pistil is mature, the stigma is receptive while the pollen sacs remain closed. At the second opening the flower is functionally male: dehiscence of the pollen sac occurs and pollen is being shed while the upper part of the style is frequently shriveled and brown.
2. All flowers of the tree or cultivar are female before noon and male in the afternoon (A group) or are female in the afternoon and male before noon (B group).
3. The elapsed time between the first and second opening is about 24 hours for A group flowers and about 12 hours for B group flowers.

Normal flower behavior occurs only during warm weather with minimal night temperature above 12°C and maximal day temperature above 22°C (for A group flowers) (22). Flower opening is delayed, the open period prolonged and the time between the 2 openings greatly increased in cooler weather (3, 4, 5). There is also increased overlapping of female and male opening on a single tree under these conditions (3).

Pollination and fertilization have been studied and described. These studies had been hampered by the lack of a good technique for dependably following pollen tube growth within the pistil and the lack of facilities to study the pollination requirements of the mature tree. The recent advent of the fluorescence technique enabled relatively easy observation of the pollen tube inside the style tissue (8). This method has been adapted for the avocado (22, 26) and used extensively in studies involving pollination and the fertilization process both in Israel (22, 26) and Trinidad (9, 10). Large scale use of caged trees enabled a study of pollination requirements under controlled conditions.

Successful fruit set is the culmination of a long chain of processes. It starts with the production of functionally normal male (pollen grains) and female (ovule and embryo sac) organs. Pollination has to be effected with viable pollen on a receptive stigma. The pollen grain has to germinate and the pollen tube penetrate the style into the ovary through the micropyle to enter the embryo sac where fertilization occurs with the formation of a diploid zygote and triploid endosperm. These processes were reviewed recently (3, 4) so I will try to emphasize new data or a different interpretation.

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The Male Organ—Pollen

The anther has 4 pollen sacs that open 1-2 hours after the second flower opening (Fig. 1). The sticky pollen tends to adhere to the inside surface of the open valve (Fig. 2). The individual pollen grain is spherical with short spikes (Fig. 3), about 40 μm diameter (19). There are about 5,000 - 10,000 pollen grains per flower (21).

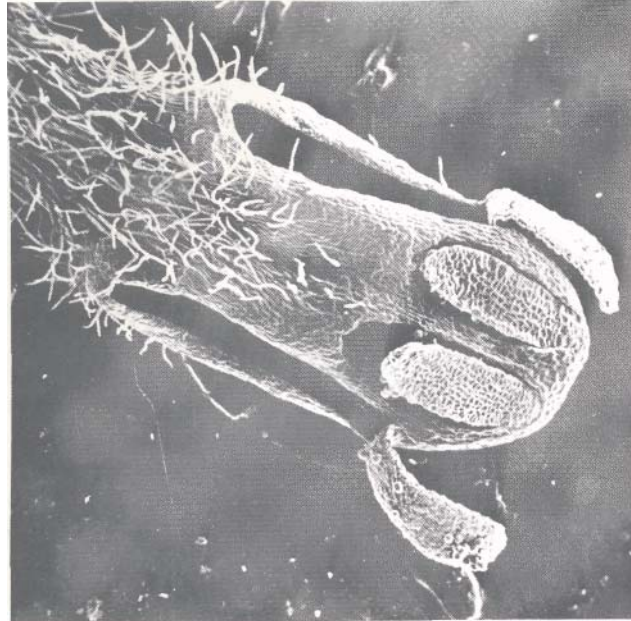


Fig. 1. Avocado anther with 4 open valves.

Avocado pollen does not germinate well on artificial media. Partial success has been reported recently (6) but, according to our experience, germination percentage is extremely erratic and the growing pollen tubes seem to be defective. This situation does not enable us to use this easy method for determination of pollen viability. Fortunately, the same pollen will almost always germinate when placed on fresh stigmas of either attached or detached flowers. Using this technique, we could confirm earlier findings that fresh pollen of commercial varieties collected even during the first and cooler part of the flowering season always shows a high percentage of germinating grains (22). The case of the male sterility found in 'Collinson' is the exception to the rule (17).

We could not confirm the reported long storage life of pollen (18), but frequently found that pollen stored under low humidity remained viable for 4 days (22). Pollen of several West Indian varieties kept in the orchard retained its viability for more than 6 days (9).

The Female Organ—Ovule

A normal avocado pistil (Fig. 4) seems to be an exception. Its ovule abnormalities and degenerations are many (19, 28) and the percentage of unequivocally normal ovules was found to be only 2-20% (28).



Fig. 2. Pollen adhering to the inside surface of an open valve.

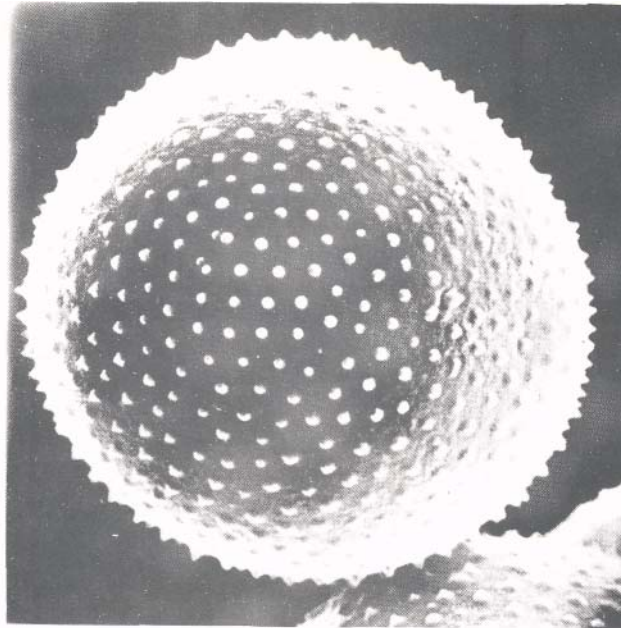


Fig. 3. 'Fuerte' pollen grain.

Pollination

Many studies have demonstrated conclusively the need for the presence of large insects (that are excluded by regular window screen nets) to obtain regular fruit set. The honey bee is probably the chief pollinator but wasps and flies may play an important role. The use of honey bees for avocado pollination is hampered by the clear preference of the bee to citrus flowers over avocado flowers. As long as there is a flowering citrus

orchard in the vicinity (at a distance of 2-3 km), the bees will get out of their hives at the avocado orchard and take a direct course toward the citrus orchard, neglecting the avocado flowers. Fortunately in Israel, the citrus flowering season ends when even 'Fuerte' is still flowering. The necessity of honey bees for appreciable fruit set is accepted both by the USA (3) and Israel.

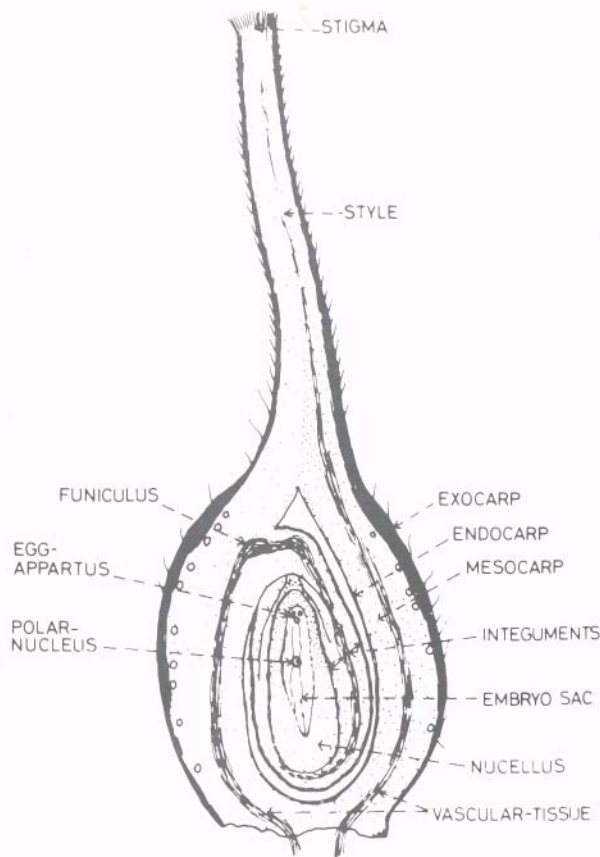


Fig. 4. Schematic longitudinal section of an avocado pistil showing the normal position and relative dimension of the ovule.

Caged 'Fuerte', 'Hass' and 'Tova' trees were found to attract small insects by the large amount of nectar accumulated in the flowers. Nevertheless, percentage of efficiently pollinated flowers (whence the pollen grain began to germinate so that it did not wash out during preparation for microscopic analysis) was practically nil and only a few fruits were set per tree (Table 1).

Fertilization Process

Pollen Germination and Pollen Tube Growth in the Style and Penetration into the Embryo Sac

Pollen grains and pollen tubes stained with aniline blue emit a distinct yellowish fluorescent light when exposed to a strong UV light (8, 22, 26). This phenomenon

facilitated easy and direct observation of the pollen tubes inside the intact, but cleared and squashed, style and ovule (22, 26). Usually, numerous pollen grains will germinate on the stigma and penetrate the upper part of the style, however, only 1 or 2 of the pollen tubes will reach the base of the style and enter the ovary (26). The pollen tube can be observed further until it reaches the ovule and enters the embryo sac.

Table 1. Effect of different pollination regimes on 'Fuerte', 'Hass' and 'Tova' production in 1972 and 1973.

Experimental trees ^z		Caged trees ^y			Uncaged trees ^y
Cultivar	Pollinizer	With pollinator	With bees	With bees and pollinator	
Fuerte	Tova	2a	14 b	65 c	82 c
Hass	Fuerte	5a	24 b	73 c	82 c
Tova	Fuerte	2a	40 b	98 c	110 c

^z 4 trees each.

^y Number of fruit/tree/year.

Rate of Pollen Tube Growth

It took about 2-3 hours for pollen tubes to reach the base of the style (temperature 18-24°C, 'Hass' and 'Fuerte', style length 20-25 mm) (22). At 32.5°C, it took 1-2 hours in Trinidad (10). Penetration of the pollen tube into 'Fuerte' ovules occurred 24-48 hours after pollination.

Fertilization and First Stages of Fruit Development

The exact length of time that elapses from pollination to the fusion of the egg cell with one of the generative pollen nuclei and the formation of the diploid zygote and the polar cell with the second generative nucleus to form the triploid endosperm has not yet been determined (18, 25). It has been established that development of the endosperm precedes that of the embryo. First divisions of the endosperm were found 3-7 days after pollination while the zygote started to divide about 2-9 days after pollination. A 3-week-old normal fruit was found to have a spherical, small (60-150 μ) proembryo and well-developed endosperm. Anatomical examination of fruit during the first month after pollination revealed that only about 10% were normal. Most of these fruit were without embryo, endosperm or both. This situation was found both in 'Fuerte' and 'Tova', a very prolific, new cultivar (21).

Factors Affecting Fertilization and Fruit Set

Pollination with viable pollen during the first flowering stage (female) is considered to be a prerequisite for successful fertilization and fruit set. It has been found that pollen may germinate on stigmas pollinated at the second flower opening (19, 22) but it has not

been found to result in fertilization. We now have the technique to study this problem and it should be clarified in the near future. Percentage of flowers pollinated at the female opening is usually quite high (19, 22, 28), but fruit set in many cultivars is often very low. Temperature and the need for cross-pollination have been considered to be main factors influencing fruit set (4, 7).

Temperature

Low temperatures seem to adversely affect fruit set. Fruit set usually starts only when average temperature and especially the minimum night temperature are above a certain threshold value (3, 4, 17). It is believed that fruit set of the commercial varieties grown in California and Israel may occur only when the minimal night temperature will be above 12-15°C (4, 21). Mexican types start setting fruit before the commercial varieties, probably because they are more tolerant to low temperatures.

Cross-pollination

For many years it has been thought that planting of 2 complementary varieties in close proximity is important for securing pollination. Studies of pollination in caged trees with bees showed this belief to be a fallacy. It was found that adequate pollination at the female stage occurred (7) with any presence of another variety from a complementary group (28). The explanation for this is based on the fact that bees and wasps tend to carry West Indian pollen grains on their bodies for a long period of time and self-pollination within the same variety may occur (6, 28).

Nevertheless, it was found that some pollinizers will increase fruit set considerably (Tables 1, 2, 3) (2, 3, 4, 7). The fact that not all pollinizers have the same influence emphasizes the fact that pollination is not the limiting factor, but pollen quality.

The fact that Mexicans were found to be more efficient pollinizers in California and Israel and Guatemalan types were found to be good pollinizers in Florida may be explained by the hypothesis that the more cold resistant pollen has a better chance in the fertilization process.

Table 2. Effect of different pollinizers on 'Fuerte' production.^z

Year	Caged trees and bees ^y			Topa Topa	Open pollinated trees ^y
	Self	Hass	Tova		
1974	64	94	159	139	133
1975	103	50	102	95	156
Average	84 b	72 b	132 a	177 a	145 a

^z 4 trees per combination.

^y Number of fruit per tree.

Table 3. Effect of different pollinizers on 'Tova' production.^z

Year	Self ^y	Ettinger ^y	Nabal ^y
1974	9	74	25
1975	56	211	65
Average	33 a	143 b	45 a

^z 4 caged trees and a bee hive per combination.

^y Number of fruit per tree.

Summary

The protogynous nature of the avocado flower tends to prevent self-pollination within the flower. The synchronous dichogamy of all flowers of the same cultivar tends to encourage cross-pollination between cultivars belonging to complementary flowering groups.

Pollination is performed by relatively large insects like bees, wasps and flies. The viability of the pollen is more than 24 hours. This fact is probably responsible for the occurrence of a very high percentage of self-pollinations when trees are isolated from potential pollinizers. This is probably also the explanation for the fruitfulness of cultivars planted in large blocks without any pollinizers

Successful fruit set is the culmination of a long chain of processes. It starts with production of pollen and ovule. Pollen has to be deposited on a receptive stigma, the pollen grains have to germinate and penetrate through the style into the ovary and enter the embryo sac. Fertilization then has to occur with the formation of embryo and endosperm. It takes a few hours for the pollen tube to reach the base of the style, 1-2 days to reach the embryo sac and 3-10 days until endosperm and embryo start to divide and develop.

Cross-pollination usually increases fruit set under sub tropical conditions when the pollinizer is relatively cold-tolerant. The cold-tolerant pollen can probably successfully affect the fertilization process even when temperature is quite low and produce a more cold-tolerant embryo and endosperm.

Selected References

1. Bergh, B. O. 1957. Avocado breeding in California. *Proc. Fla. State Hort. Soc.* 70:284-290.
2. _____. 1968. Cross-pollination increases avocado set. *Citrograph* 53:97-100.
3. _____. 1969. Avocado (*Persea americana* Mill). In: Outlines of perennial crop breedings in the tropics, F. P. Ferwerda and F. Wit, eds. Wageningen, Netherlands, p. 23-51.

4. _____. 1975. Avocado. *In: Advances in fruit breeding*, J. Janick and J. N. Moore, eds. Purdue Univ. Press, West Lafayette, IN. p. 541-567.
5. Bringhurst, R. S. 1952. Sexual reproduction in the avocado. *Calif. Avoc. Soc. Yrbk.* 1952:210-214.
6. Free, J. B. and I. H. Williams. 1976. Insect pollination of *Anacardium occidentals* L., *Mangifera indica* L., *Blighia sapida* Koenig and *Persea americana* Mill. *Trop. Agr.* 53:125-139.
7. Gustafson, C. D. and B. O. Bergh. 1966. History and review of studies on cross-pollination of avocado. *Calif Avoc. Soc. Yrbk.* 50:39-49.
8. Lammerts, W. E. 1943. Progress report on avocado breeding. *Calif. Avoc. Soc. Yrbk.* 1942:36-41.
9. Lesley, J. W. and R. S. Bringhurst. 1951. Environmental conditions affecting pollination of avocado. *Calif. Avoc. Soc. Yrbk.* 1951:169-173.
10. Martin, F. W. 1951. Staining and observing pollen tubes in the style by means of fluorescence. *Stain Tech.* 34:125-128.
11. Papademetriou, M. K. 1975. A study of the viability of avocado pollen under natural conditions. *Calif. Avoc. Soc. Yrbk.* 58:74-76.
12. _____. 1975. Pollen tube growth in avocados (*Persea americana* Mill.). *Calif. Avoc. Soc. Yrbk.* 58:99-102.
13. _____. 1976. Percentage of fruit set in avocados (*Persea americana* Mill.). *Calif. Avoc. Soc. Yrbk.* 59:1 35-142. 14.
14. Peterson, P. A. 1955. Avocado flower pollination and fruit set. *Calif. Avoc. Soc. Yrbk.* 39:163-169.
15. _____. 1956. Flowering types in the avocado with relation to fruit production. *Calif. Avoc. Soc. Yrbk.* 40:174-179.
16. Robinson, T. R. 1930. Pollen sterility in the 'Collinson avocado. *J. Heredity* 21:34-38.
17. Schroeder, C. A. 1942. Pollen germination in the avocado. *Proc. Amer. Soc. Hort. Sci.* 41:181-182.
18. _____. 1952. Floral development, sporogenesis and embryology in the avocado *Persea americana*. *Bot. Gaz.* 113:270-278.
19. _____. 1954. Some aspects of pollination in the avocado. *Calif. Avoc. Soc. Yrbk.* 38:159-162.
20. _____. 1955. Pollen production in avocado. *Calif. Avoc. Soc. Yrbk.* 39:184-186.
21. Slor, E. and R. Spodheim. 1972. Selection of avocado varieties in Israel. *Calif. Avoc. Soc. Yrbk.* 55:156-157.
22. Snir, E. 1971. Flowering, pollination and fruit set in avocado. M.Sc. Thesis, Faculty of Agriculture, The Hebrew University, Rehovot, Israel (Hebrew).

23. Stout, A. B. 1933. The pollination of avocado. Fla. Agr. Expt. Sta. Bul. 257.
24. Tomer, E. and M. Gottreich. 1975. Observations on the fertilization process in avocado with fluorescent light, *Euphytica* 24:531-535.
25. _____ and _____. 1975. First stages in avocado fruit development. *Alon Hanotea* 41:411-414 (Hebrew).
26. _____, _____ and S. Gazit. 1976. Defective ovules in avocado cultivars. *J. Amer. Soc. Hort. Sci.* 101:620-623.
27. Torres, J. P. 1936. Some notes on avocado flower. *Phillipp. J. Agr.* 1936:207-227.
28. Zakai, S. 1977. Factors affecting pollination and fruit set in avocado. M.Sc. Thesis, Faculty of Agriculture, The Hebrew University, Rehovot, Israel (Hebrew).