

SEXUAL REPRODUCTION IN THE AVOCADO

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SUMMARY

Differences in time of maturity of the male and female elements of flowers (dichogamy) are discussed, including the double opening. The flowers are described as functionally monosexual, although they are structurally bisexual. The cyclic nature of the double opening is discussed and the correlation of temperature fluctuation with the erratic variation in the cycle of certain varieties is pointed out. Frequent overlap of first and second opening flowers probably minimizes the effect of these phenomena on fruit set. It is suggested that the cyclic dichogamy and variations with temperature could be important with certain varieties during prolonged periods of low temperature. These phenomena are very important in controlled pollination necessary for breeding work.

Avocado varieties can be perpetuated by budding and grafting so that, in theory at least, each Fuerte tree is identical to every other Fuerte tree with respect to heredity, each Anaheim to every other Anaheim, and so on if the rootstock is disregarded. The sexual process can be by-passed to this extent. However, sexual reproduction is important in the avocado because it is necessary to go through the sexual cycle in order to develop new varieties, obtain rootstocks or set fruit upon a tree when a framework is sufficiently developed to carry a crop.

The primary function of any flower is to favor crossing between different plants. This serves to maintain the variability essential to survival of a species in a constantly changing environment. Floral structures important in sexual reproduction are the pistil or female structure and the stamens or male structures. Superimposed upon the basic mechanism are devices which favor or ensure either cross-pollination or self-pollination. Special devices which favor cross-pollination are found in the avocado. They have been partially described in publications of Stout (8 and 9), Robinson and Savage (7), and others.

Examination of the flowers of newly opened buds, figure 1, reveals that the pistil is erect and prominent and that the stigma or pollen receiving surface is "bright" and receptive in appearance. The flower can be effectively pollinated at this time and the pollen grains will germinate and grow. Pollen of the Mexicola variety placed upon receptive flowers of the Hass variety will germinate within two hours under a variety of conditions. The filamentous sperm-bearing pollen tube from each germinated pollen grain will grow down through the style, the slender neck of the pistil, toward the ovary. There the egg and sperm unite, the embryo develops and fruit is set.

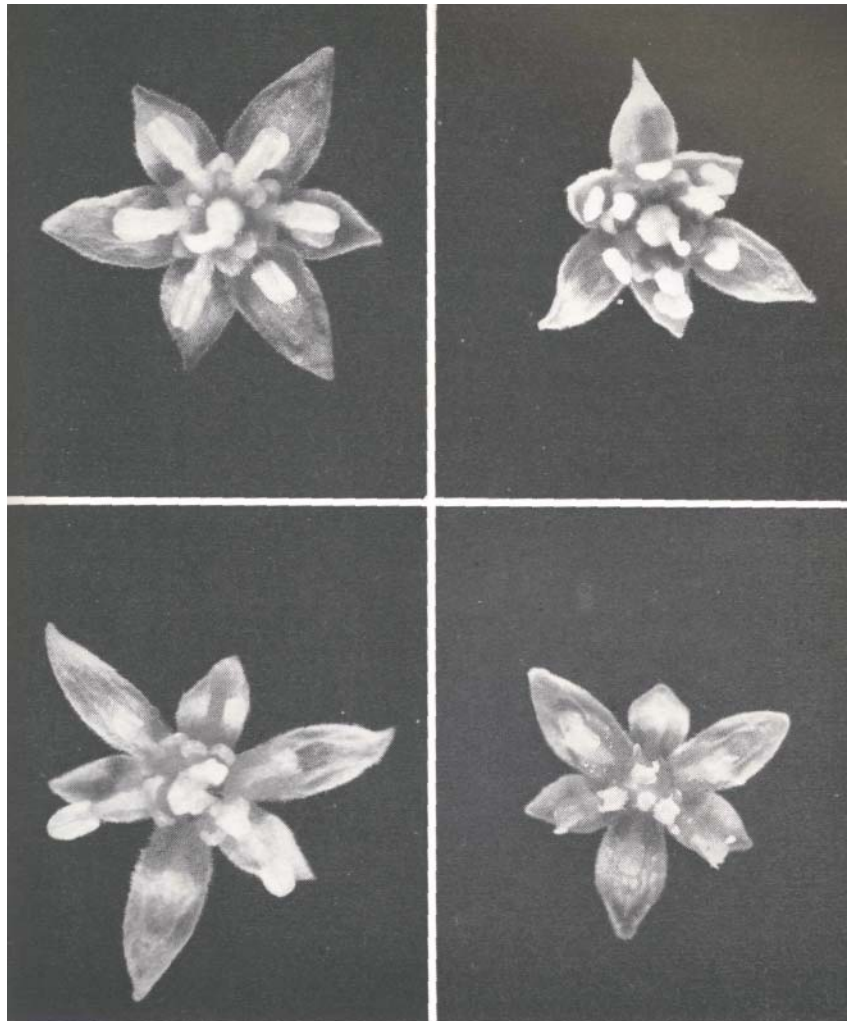


Fig. 1. (Top left) Early first opening, Mexicola. Greatly enlarged, photograph by Roy J. Pence.

Fig. 2. (Top right) First opening starting to close, Fuerte.

Fig. 3. (Bottom left) Early second opening—no pollen shed. Fuerte.

Fig. 4. (Bottom right) Second opening—pollen shedding. Zutano.

During this first opening, which may be termed stage I, the stamens are fanned out in a reflexed attitude, lying against the six sepals or petals, figure 1. Three pairs of stamens, one above the other, alternate with three singles, making a total of nine. Stamens are short in relation to the pistil at this time and the anthers, the pollen-forming capsules, are tightly closed. Pollen is not available at this time and the flowers are female in function.

Flowers remain in the first opening, stage I, for at least several hours. The time appears to be conditioned by temperature. Low temperatures will prolong the opening. Flowers on small tip-grafted Hass plants placed in a "walk-in" refrigerator at 40° F. after stage I commenced have been observed to continue in stage I for approximately 55 hours.

Flowers on comparable plants in the glasshouse, where temperatures ranged from a high of about 80° F. at the beginning to about 70° F. at the end, remained in stage I for about 5 hours.

As flowers close following stage I the pistil remains the prominent structure of the flower, figure 2. The stamens are still well away from the pistil, although they are perhaps a little longer. Pollen is not available. On certain days after cold or hot desiccating wind the stigma may no longer be receptive at stage I closing. It will appear brown and withered and under the microscope the long cells upon which pollen grains are deposited during pollination are shriveled and show evidence of breakdown. Attempts to pollinate the brown stigmas by hand at this time have resulted in no fruit set.

Systematic examination of the same flowers following stage I closing shows that a second opening, termed stage II, will occur from one to three days later. The time interval is evidently associated with temperature. Flowers on plants growing under glasshouse conditions regularly have the stage II opening the day after stage I for a given flower. The interval is frequently two to three days for comparable trees outside at Los Angeles. Prolonged exposure to a constant temperature of 40° F. will greatly increase the period between openings.

As stage II begins, the anthers have not yet, as a rule, shed any pollen. The flowers present quite a different aspect and the stamens are now the prominent structure, figure 3. Three stamens are erect and clustered tightly about the pistil and the other six surround the cluster in a raised position. They are now long in relation to the pistil.

Pollen is generally available shortly after stage II begins. Little valves or caps open on the sides of the anthers by bending outward, figure 4. Pollen can be observed clinging to the valves and the recesses in sticky clumps. These pollen grains will germinate if they are placed on the stigma of a receptive flower. The time of pollen shedding after the stage II flowers open is probably influenced by the relative humidity. Stage II flowers on plants situated in the near-saturated atmosphere of the humid section of a glasshouse shed pollen after a much longer period of opening than flowers on comparable plants in a glasshouse where no attempt was made to maintain high humidity. During stage II the pistil is relatively inconspicuous and the stigma often appears brown and shriveled. Attempts to pollinate even the "bright" stigmas have not resulted in fruit set. Flowers are now male in function.

Some mechanical means of bringing the male and female elements together is necessary since the sexual structures are functionally separated, though physically in close union. Large flying insects are pollinators, as several investigators have pointed out (2, 3, 4). Whole trees or parts of trees have been isolated from large insects by enclosure in screen cages and paper or cloth bags. No fruit has set under these conditions on a number of varieties, including Fuerte, Anaheim, Dickinson, Hass and others. A few fruits have set on Mexicola. There is ample evidence that the honeybee is an important pollinator, since the introduction of a small colony of bees into a caged tree will usually result in some fruit set. The profusion of ants crawling over flowers in some cages and bags has been a matter of concern, since they could conceivably transfer pollen. However, the absence of set fruit not accounted for by hand pollination would rule this out for all varieties except Mexicola.

The cyclic nature of the double opening may also have an important bearing on sexual reproduction. Whereas the difference in time of maturity of male and female structures, dichogamy, just described prevents auto-pollination of a given flower, it would allow a stage I flower to be pollinated by a stage II flower on the same tree. Early reports (8, 10) suggested that stage I and stage II flowers would not occur on the same tree at the same time. Varieties were classified as having only stage I in the morning and only stage II in the afternoon or *vice versa*, and interplanting was recommended to insure fruit set. Thus alternation of stages, if absolute, would make self-pollination of a given variety difficult, if not impossible. There is no good evidence to support this suggestion. Many investigators (1, 4, 5, 6, 10) point out that all varieties are erratic in this respect under ordinary conditions and the temperature fluctuation is important.

Hourly records of the flower opening stages on the Hass variety at Los Angeles were compared with continuous temperature records. Stage I flowers appeared about midday during relatively warm periods and on toward evening during relatively cold periods. On certain very cold days stage I flowers did not open at all. Furthermore the cyclic behavior was not absolute. There was frequently a one to two hour overlap period during which pollen was available at the time stage II flowers were closing and stage I flowers were opening. During warm periods this occurred about midday when bees are very active, affording an excellent opportunity for self-pollination to occur. Anaheim, Dickinson and Rincon are similar to Hass, but tend to open into stage I about an hour earlier than Hass. Lyon is different since individual flowers appear to be in stage I in the morning and by afternoon the same flowers are shedding pollen, having opened but once. Variation with temperature and periods of overlap are also evident in Fuerte. Mexicola had stage I and stage II flowers simultaneously on most days but the quantity and duration varied considerably.

The results of glasshouse experiments at Los Angeles (1) with minimum temperatures of approximately 65° F. indicated that the basic concept of cyclic opening is sound. Stage I occurred on the Hass and Anaheim varieties regularly in the morning and stage II in the afternoon. This is an essential reverse of the situation on comparable trees outside. More recent notes on the Lyon variety under similar glasshouse conditions indicate that it is out of phase in this respect with Hass or Anaheim. Stage II occurs regularly in the morning and stage I in the afternoon; the second opening of a given flower takes place the morning after its first opening.

There is no conclusive evidence at this time that the cyclic nature of the openings has a significant influence on fruit set. However, the fluctuations due to temperature might be important with varieties having a relatively short flowering season if prolonged periods of cool weather prevailed. First opening flowers would appear late in the day when insect activity is at a minimum. Where controlled pollination is necessary in a breeding program these factors assume great importance. Pollen can be collected and held for a reasonable length of time, but pollinations can be made only when receptive flowers are available.

LITERATURE CITED

1. Bringhurst R. S. Influence of glasshouse conditions on flower behavior of Hass and Anaheim avocados. Yearbook Calif. Avocado Soc. 1951: 164-168.

2. Clark, O. F., and Clark, A. S. Pollination and other experiments on avocados. Ann. Rpt. Calif. Avocado Assn. 1925-26: 85-94.
3. Lammerts, W. E. The avocado breeding project. Yearbook Calif. Avocado Soc. 1945: 74-80.
4. Lesley, J. W., and Bringham, R. S. Environmental conditions affecting pollination of avocados. Yearbook Calif. Avocado Soc. 1951: 169-173.
5. Nirody, B. A. Investigations in avocado breeding. Ann. Rpt. Calif. Avocado Assn. 1921-22: 65-78.
6. Robinson, T. R. Some aberrant forms of flower mechanism in the avocado. Yearbook Calif. Avocado Soc. 1931: 107-111.
7. _____ and Savage, E. Pollination of the avocado. U.S.D.A. Circ. 387. 1926.
8. Stout, A. B. A study in cross pollination of avocados in southern California. Ann. Rpt. Calif. Avocado Assn. 1922-23: 29-45.
9. _____. The pollination of avocados. Fla. Agric. Exp. Sta. Bull. 257. 1933.
10. _____ and Savage, E. M. The flower behavior of avocados with special reference to interplanting. Proc. Fla. Hort. Soc. 1925: 80-89.