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History and Review of Studies on Cross-Pollination of Avocados

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Introduction:

For many years researchers, growers, and others have been intrigued by the avocado tree. They have attempted to study its growth habit, its flowering behavior, and various other aspects of this interesting plant. One of the important but puzzling aspects of avocado growing is whether or not certain varieties need pollination from different varieties to assure a good crop. In a commercial operation fruit production each year is of utmost importance. If cross-pollination is the answer to more consistent and heavier crops, then a practical method utilizing this phenomenon must be developed.

The purpose of this paper is to bring together, in summary form, some of the important work that has taken place in the field of cross-pollination and its effect on increasing production in avocados.

History of Cross-Pollination Work:

Beginning nearly 50 years ago, researchers and growers in Florida, Hawaii, and California experimented with the avocado, attempting to explain the flowering of this particular plant and its relationship to production. They grafted different varieties on a single trunk in hopes of increasing fruit production (1). Studies of the importance of bees in pollination of avocado flowers were many. The flowering cycle was studied to determine what varieties might be good pollinators.

During 1922-1923, a practical research man by the name of Orange I. Clark began his observations on the influence of bees on pollinating avocado flowers. The work was done by the Homestead Horticultural Department, International Theosophical Headquarters, Point Loma, San Diego, California. The orchard was located about one mile from the ocean on the east slope of the ridge. It comprised three acres of trees from one to eight years old. About 30 varieties and a considerable number of seedlings were planted in this test area. In the last reported blooming season, 17 hives of bees were placed in the orchard. At this time a drought in Southern California resulted in less outside bee pastures than usual and so the bees worked very well on the avocado blossoms. The bee behavior was carefully observed and notes made of it (2). Mr. Clark concluded that the heavy crop that had set on much of the orchard trees was a consequence of the greater amount of bee work on the blossoms.

Orange I. Clark observed that the bees did not work as freely on avocados as on other fruit blossoms. They seemed to prefer other bee pasture to the avocado orchards.

When bees are abundant or other pastures scarce, they do work freely on avocados. It is interesting to note that bees had a strong preference for sticking to one avocado tree at a time. For this reason it was not easy to obtain the maximum amount of cross-pollination of avocado varieties such as occurs with other tree fruits. It could be observed that bees cross freely when the foliage of two varieties interlace with very little space between.

An interesting observation by Clark was that very few avocado flowers closed tightly after shedding pollen. Many remained open half way with abundant pollen on the anther valves. Bees were constantly walking across these half-closed flowers in search of open flowers. Frequently they probed with their hairy tongues the loosely-closed flowers which have been shedding. At times they forced open receptive flowers which had not yet opened for the first time but would open within a few hours. They sometimes probed flowers in all stages in rapid succession. They do less of this if fewer bees were at work in proportion to the number of flowers open.

In the coastal climate the overlapping of the receptive and pollen-shedding periods of many varieties is considerable. This and the frequent probing by bees of blossoms not fully opened provides for the self-pollination of many varieties. The daily periodicity of the Fuerte is such as to permit considerable self-pollination, by the overlapping of the male and female periods. But this does not prove that self-pollination will produce as many mature fruits as cross-pollination.

Clark found that the avocado blossoms are supersensitive as compared with flowers of other plants. If the blossom clusters are experimentally ruffled or subjected to winds, they are much less likely to set fruit.

In 1923, Dr. A. B. Stout (3), Director of Laboratories, New York Botanical Garden, spent some time in California and was intrigued by the avocado flowers. He made a study of cross-pollination of avocados in Southern California and arrived at certain basic factors and principles of flowering. He said that cross-pollination is necessary for the best setting of fruit in avocados and he set out to prove this.

Dr. Stout found the flower behavior to be of two types, A type and B type. In the A type, the first period flowers (functioning female) opened in the forenoon and the second period flowers (functioning male) opened in the afternoon. These two openings are sometimes called Stage I and Stage II. A given A-type flower would open for the first time (Stage I) one morning, then close and remain closed for about 24 hours, reopening (Stage II) the following afternoon, after which the flower closes for good.

In the B type just the reverse openings occurred. In other words, the first opening was in the afternoon, with the second opening of that particular flower the following forenoon, weather permitting. With this cycle, the entire tree functions as a male in the forenoon and as a female in the afternoon. The A type pollen was shed between about 2:30 and 4:30 at a time when the stigmas of the type B flower were receptive. The B type pollen was shed between about 10:30 and 12:30 when the type A stigmas were receptive. These reciprocations occurred fairly regularly on warm sunny days, but when the weather was cool and cloudy, flower openings became irregular and retarded. The foggy nights and rainy weather affected the regularity, continuity, and sequence of blossoming and flower opening.

Dr. Stout observed that the majority of flowers of any variety open and close for each of the two periods in unison. During certain hours of a day one can find on a tree of any variety only flowers opened for the first time. Later that day, or the following morning, these flowers are closed and another set will be open for the second time. This habit of the alternating opening of flowers of one condition in unison or in rhythmic cycles, decidedly limits the opportunity for pollen to be carried from one flower to another of the same variety. A single tree or a group of trees of one variety may bloom day after day and be visited continuously by many bees and yet very few or even no flowers may be pollinated. This makes cross-pollination between the varieties highly necessary for the setting of much fruit.

However, experience indicates that some varieties may set fruit when there is no opportunity for cross-pollination. In varieties that set fruit abundantly and consistently, there is frequent overlapping of flower periods with apparent opportunity for close-pollination. "Close" pollination means that the flower is pollinated, not by its own pollen but by pollen from another flower of the same variety. The ideal avocado, from the standpoint of self-fruitfulness, is one that normally, and rather continually, overlaps its male and female periods of opening; in addition, it is self-compatible in the close-pollinations that are thereby possible. Overlapping does occur more or less on every variety, frequently involving different sides of the tree according to exposure to sun and wind. Occasional setting of fruit from close-pollination may be expected for any variety and it is possible that peculiar local conditions may be favorable to close-pollination.

It was suggested by Dr. Stout that cross-pollination would be best promoted by interplanting a variety of group A with a variety of group B provided that they blossomed during a considerable part of the same calendar period. The Fuerte and Dickinson seemed able to cross-pollinate reciprocally. But since the Dickinson period of flowering is. somewhat later than that of the Fuerte, it did not seem that these would be an ideal combination.

In certain areas, local conditions may keep one or the other, or perhaps both, out of the normal sequence of bloom more or less continually. At the lower and cooler edge of a certain grove the flowers on the Fuerte trees are repeatedly two, three, or more hours late in opening for the first time, as compared with the flowers of the Fuerte trees grown on ground at the upper end of the grove. This local condition, such as pockets of cool air or fog at night, may adversely affect the efficiency of a particular interplanting. Growers should give careful attention to these matters to be most successful in securing good crops of fruit. Actually, the cross-pollinators need to be close together, which means the same microclimate, which means a similar delay for both — which is fine.

The time for the most favorable and successful pollination is decidedly limited. Pistils are most receptive for only a short time and many cross-pollinations effected while flowers are open for the first time are doomed to be failures. The most successful interplanting is that which favors frequent and continued cross-pollination during the limited time when pollen and pistils are '"most right.[1]' This is without a doubt best provided for when a variety normally shedding pollen in the forenoon is interplanted with the varieties whose flowers open for the first time (Stage I, which is female) during the forenoon. Further selection of particular sets of varieties for interplanting, of course, must be determined by cultural requirements, habits of growth, quality of fruit, and season of maturity with reference to the demand of the trade.

Dr. Stout, in summarizing his work, said that different procedures for grove planning could be followed. One procedure is a mixed close interplanting of trees of two complementary varieties such as the Fuerte and a Type A variety. A second way would be to plant two trees perhaps only a foot apart. Finally, one can graft two or more varieties that complement each other on one tree. All of these methods would necessitate a change in cultural practices, specifically increased pruning, to maintain a proper tree balance.

Continuing in 1924, Orange Clark of Point Loma investigated the blossom behavior of the Fuerte and other varieties (4). He had found earlier that bees were helpful in the cross-pollination of Fuertes. He felt that the trees and branches that had fully developed mature leaves and were well supplied with nutrients, but that did not make too "sappy" new growth in the spring, would be more likely to set well.

In 1930 Dr. R. W. Hodgson, Dean of the College of Agriculture, University of California, Los Angeles, and a long-time research worker on avocados, reported on a two-year study on cross-pollination of the avocado (5). He had verified the findings of Dr. Stout and Orange I. Clark, and found in addition that there was plenty of "offstride" blooming, exceptions to the rhythmic alternation, to provide ample opportunities for close-pollination under all conditions. He concluded that for commercial fruit production the clocklike opening and closing described by Dr. Stout, which apparently minimizes the possibility of cross-pollination, is probably not of great importance. Mr. H. Van Elden, a graduate student working with Dr. Hodgson, found evidence that at the first opening of the flowers of both Mexican and Guatemalan varieties, the embryo is in the proper condition for fertilization. He also found evidence that by the second opening of the flower (at which time the pollen is shed), fertilization had already occurred. This means that fertilization results from pollen of a different flower, with a different behavior pattern. The pollinating flower could be an adjoining one on the same tree, from a different tree of the same variety, or from a different variety.

In 1932, Dr Stout did additional work with avocados and their peculiar flowering habit (6). First of all, he summarized the flower behavior of the two groups. He was certain that much of the poor bearing of some varieties in the avocado industry is due to lack of proper pollination, and that maximum and reasonable uniform yields, at least by most varieties, can only be expected when there is abundant and proper cross-pollination between the A and B varieties. Proper interplanting, or inserting a different variety into an individual tree, will greatly increase the chances for fruit production—if insects, which make the pollinations, are working effectively. This depends on the bee population and the proper climatic conditions for bee activity.

In 1940, Dr. C. A. Schroeder, Plant Physiologist, University of California, Los Angeles, worked on the floral arrangement of the avocado. He compared the normal flower with abnormal types (7). For this discussion we will describe only the normal flower. It has a single pistil and nine stamens. The pistil is free from the other floral parts and has a simple, bulbous, smooth ovary, and a somewhat elongated style terminated by a slightly enlarged stigma. The stamens are inserted in two whorls. The inner whorl consists of three stamens that have 3 staminodes (sterile or abortive stamens) alternating between them. The outer whorl of six stamens is placed opposite the parts of the inner whorl so that for each outer stamen there is either an inner stamen or a staminode on the same radius. Each of the inner stamens has two small nectaries, one on each side of the filament at the base. The anthers shed their pollen by means of four valves which are hinged at the top. The inner stamens open outward while the outer stamens are directed inward.

The floral envelope consists of six parts which are so similar in appearance they are referred to generally as perianth parts. However, in some varieties there is sufficient differentiation to identify them as sepals and petals. All of the floral parts are covered with hair except on the stigmatic tissue, the nectaries, and tips of the staminodes.

In 1942, Dr. Schroeder experimented with pollen germination. He found that pollen germinates at 40 degrees F. and higher on avocado stigmas (8).

In 1951, Dr. Schroeder studied flower bud development in the avocado (9). Knowledge concerning the time when flower (fruit) buds are formed in the avocado can be helpful to an understanding of the growth and bearing behavior of the tree and may be useful in connection with certain orchard management practices.

The avocado may exhibit two or more growth flushes during the year in contrast with the single annual growth period observed in most deciduous trees. The normal period of bloom for the avocado in California is during the fall months, November and December, for some varieties and seedlings of the Mexican race, and extends well into the spring and early summer, May and June, for varieties of the Guatemalan race. The bloom period for any given variety may be from one to six months or more, depending upon the favorableness of conditions for fruit setting during the bloom.

The fruit-bud system in the avocado is derived from terminal and subterminal buds on growth of the previous season. Ordinarily the buds are mixed and contain both floral and vegetative primordia.

Avocado flowers set fruit if conditions of climate, especially temperature, are favorable, but less than 1 percent of the flowers are usually sufficient for a good fruit crop. The bloom period usually is terminated and vegetative length growth begins in the shoot concurrent with the set and development of young fruit. When climatic conditions are not favorable for fruit set and all the flowers have fallen, there frequently is developed on the same shoot an entirely new series of inflorescence branches with many new flowers. This second series of flower buds apparently is initiated and develops within the period of a few weeks prior to bloom.

The evidence that flower buds may be formed a relatively short time before the developing buds can be discerned with the naked eye, is obtained by tracing the development of shoot tips by means of microscopic examination in the laboratory. Dr. Schroeder showed in his study that the Fuerte tree, which was in full bloom in December, already snowed microscopic evidence of flower buds the preceding October, whereas the other Fuertes, which bloomed in early February, contained evidence of well-developed flower buds the preceding November.

This initiation of avocado flower buds only a few weeks prior to blossoming is different from the situation observed in decidious fruit trees, for the latter initiate buds at least several months before bloom begins. The avocado is thus typical of evergreen subtropical plants, which are in active growth during much of the year. Checking of vegetative growth in subtropical plants by drought or excessively high temperature may be sufficient stimulus to cause flower bud formation any time during the year. In any given flower, the floral envelope or perianth parts are first to develop followed by the stamens, and finally, the pistil with the single ovule.

In 1951, Dr. J. W. Lesley and Dr. R. S. Bringhurst, Plant Geneticists, University of California, Riverside and Los Angeles, studied the environmental conditions affecting pollination of avocados (10). Their observations on orchard trees indicated a strong correlation between temperature and the flower opening. When the maximum temperature did not exceed 70°F. and the minimum 53°F., Fuerte, a type B variety, either had no fully-expanded Stage I (female) flowers or they appeared so late in the day that pollination was unlikely. Likewise type A varieties may have Stage I flowers in the morning during a warm period and in early afternoon to late afternoon, or not appearing at all, during a cold period. Throughout the latter part of the blooming season, when other tree conditions, both internal and external, apparently are most favorable for fruit setting, climatic conditions at Riverside are such that Stage I flowers are relatively infrequent. During the same period at Los Angeles, Stage I flowers appeared quite regularly. They observed that conventional definitions of Type A and Type B varieties are probably valid only at certain temperatures which in some localities are the exception rather than the rule.

Some additional evidence is given that in California honeybees are important for fruit setting. Their activity is much affected by weather conditions. Low temperatures are unfavorable for their activity as well as for the proper sequence of flower opening.

In 1953 and 1954, Dr. Schroeder conducted a study on the pollen and its behavior in relationship to fruit setting (11). While avocado pollen in most instances appears normal in all respects, it has been found impossible to germinate on artificial media but grows readily on the avocado stigma. Most varieties grown commercially in California produce sufficient and abundant pollen for adequate fruit set if other factors are satisfactory. Following is a table giving the average number of pollen grains in the different varieties:

VARIETY# POLLEN	**GRAINS/FLOWER**
Frey	10,500
Lyon	9,918
Mexicola	8,757
Hass	7,641
Puebla	7,578
Topa Topa	7,254
MacArthur	7,119
Lula	6,903
Fuerte	4,743

As it requires only one grain to germinate on the stigma, and subsequently to grow down the style to fecundate the egg cell, it appears that pollen production itself probably is not a limiting factor for fruit set in Southern California.

Among other factors which can influence the process of fruit development is the actual mechanical transfer of the pollen from its place of origin in the anther to the stigma. This transfer could conceivably be by wind or birds or insects, or by actual mechanical contact of the anther with the stigmatic surface. Most researchers have found that the avocado is pollinated primarily by bees, although there is a possibility that pollen is occasionally transferred by other methods.

The style is approximately 4 millimeters long, from the stigma to the location of the egg. If a constant pollen tube growth rate is maintained, approximately 28 hours will elapse between germination and fecundation. Temperature and variety will influence the growth rate, some varieties requiring as long as 66 hours from germination to fecundation of the egg. The result of fecundation is the embryo. The embryo is sensitive to (1) low or high temperature, (2) desiccation, and (3) nutritional deficiencies. One or all of these will result in aborted seeds; the young fruit then either drops or develops into a "cuke." An interesting observation on the variation of pollen grain development, as given by Dr. Schoeder in his study of the Fuerte variety (12), is as follows:

AREA	**#GRAINS**
Coastal Los Angeles	4,743 (standard yield)
Coastal Los Angeles	6,705 (high yield)
Coastal Los Angeles	4,266 (low yield)
Inland Fillmore	8,101
Inland Fallbrook	9,747

In 1955, Dr. Peterson, Plant Geneticist, University of California, Riverside, conducted experiments on avocado flower pollination and fruit set (13). It was a follow-up to earlier such work, as well as a new experiment on the effect of bees on setting of fruit. He found that the trees which were caged and had bees, set far more fruit than caged trees without bees. Two trees were caged from each of the Zutano and Hass varieties. For each variety, one tree had a hive of bees inside its cage and the other did not. The results of that test are as follows:

NUMBER OF FRUIT ON EACH CAGED TREE

	Beeless	**Bees**
Zutano	4	120
Hass	5	284

Dr. Peterson confirmed the work of Clark, Stout, and others that there were two distinct stages to the avocado flower cycle. Stage I of the individual flower cycle is the female or pollen-receptive stage, while Stage II is the male or pollen-shedding stage. The avocado flower stigma comes in contact with its own anthers containing valves loaded with pollen only during Stage II. (Schroeder had shown that in an individual flower in Stage II, pollen was transferred to its own stigma and subsequently germinated.) In other experiments, Peterson's hand pollination on the most receptive, fresh-appearing Stage II stigmas never resulted in the setting of fruit. Under greenhouse conditions of high humidity and moderate temperature, pollen grains germinated on Stage II stigmas in the Zutano and Fuerte, although they did not effect fertilization after such a Stage II pollination. Thus, 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.

Since an individual flower does not set fruit after self-pollination, some agent of pollen transfer must be necessary. Peterson said, a "tree can self itself" (close-pollination) through the medium of bees, when the two stages overlap so that for brief periods of the day pollen and receptive stigmas are present on a tree at the same time. In addition, "residual" pollen might be carried on the bees and remain viable for effective pollination even if no overlap of the stages occurs.

Most experiments to date designed to test the effectiveness of close-versus cross-pollination have clearly shown that the latter is more effective. Dr. Peterson related an example of Robinson and Savage's work in Florida concerning a 10-acre planting in Lake Eloise, Florida. It contained Fuerte avocado trees, 10 to 12 years of age which had failed season after season to produce any fruit. When a young, adjoining grove containing other varieties first produced flowers, the row of Fuerte trees next to this new planting set a full crop of fruit. In the second row, there was a fair set of fruit, and in the third row, only one tree out of twelve set any fruit, while no fruit could be found in any of the succeeding rows. This indicates the response of Fuerte trees to varieties in the complementary flower cycle (Type A) and suggests the limitation in range of bees and pollinating activity at least in the area of Florida. This seems to correspond with our results here in California (14). Dr. Peterson's conclusions were (1) some agent of pollen transfer is necessary to effect pollination, and honeybees are known to be good pollinators, (2) there is only a short period during the cycle of the avocado flower during which pollination can be effective.

In 1956, Dr. Peterson observed some additional data on the influence of temperature on flowering (15). Low night and day temperature delays flower development. A night temperature of 45°F. or less delayed the opening of Type A flowers from morning until afternoon. For a Type B variety, such as the Fuerte, the flowers opened very late in the day, or not at all, so flowers were not adequately pollinated by bees. Cool weather causes the bees to be sluggish, so there are two factors working against fruit setting: (1) bees are not working properly, and (2) flower opening is delayed or inhibited.

Following is a list of varieties that are commonly grown in the industry today, with the type of flower of that variety:

VARIETY	**FLOWER TYPE**	**VARIETY**	**FLOWER TYPE**
Anaheim	A	Lyon	B
Bacon	B	MacArthur	A
Dickinson	A	Mayo (Covocado)	A
Duke	A	Mexicola	A
Edranol	B	Puebla	A
Emerald	A	Rincón	A
Fuerte	B	Ryan	B
Hass	A	Topa	A
Jalna	A	Zutano	B

In 1957, the authors, in consultation with an avocado grower in Pauma Valley, San Diego County, came to the conclusion that there was some cross-pollination effect on the grower's property and a test plot was established with the growers, Mr. and Mrs. John Best.

It was generally believed in the industry that cross-pollinization was of little or no practical commercial importance to avocado fruit set in California. According to Chandler (16) and Hodgson (17), Fuerte trees seemed to fruit about as well in large solid blocks or as single isolated trees as in closely mixed plantings. If cross-pollination increases its crops, that increase is too small to be detected among the results of other influences. Earlier Hodgson had written, "no case has yet been brought to light in this state where the provision of cross-pollination has measureably improved either regularity of bearing or the amount of yield of individual trees." (17)

In the John Best grove, in San Diego County, actual fruit counts were started in October of 1957. Fuerte trees had been planted in 1950, at a spacing of 28 feet. In February 1951, seedling trees were planted between the Fuertes at 10-row intervals. The seedlings were top worked in September, 1951 to Topa Topa. The Topa Topa interplant rows were for wind protection. As a follow up to the interesting data obtained the first year, Topa Topa grafts were placed in the top of Fuerte trees to measure the influence of the graft in the large tree itself. (18).

In 1964, Bergh and Garber reported the results of a study of avocado groves in southern California (14). The study showed an apparent beneficial effect of cross-pollination where two or more varieties were interplanted. They found a beneficial effect on Fuerte set where varieties of Topa Topa, Hass, and Zutano were nearby. They found the Zutano set improved with the interplanting of the Rockwood variety. MacArthur had a good effect on the Edranol set; and Hass, Zutano, and Rincon appeared to affect the MacArthur set.

In 1966, Bergh reported orally the results of the tests on the John Best grove in Pauma Valley, San Diego County. The overall fruit increase due to cross-pollination was 40% over an eight-year period. Also, more fruit has been produced on the Fuerte trees in which Topa Topa grafts are present. In only two years out of the eight was the "effect" apparently not working. This could be due to the flowering of the Fuerte and Topa Topa not coinciding. Such could result from weather conditions influencing the flowering cycle of one or both varieties.

It is as yet too early to make a general recommendation as to what type of pollinators should be planted, or in what manner they should be placed in an orchard. It is felt that a branch graft in each tree would be most desirable. For newly planted trees, tests are now being conducted, with the first trees planted in the spring of 1966. In this test two trees are being planted in the same bole. The trees are a Topa Topa on Topa Topa rootstock and a Fuerte on Topa Topa rootstock. Another combination is Covocado on Topa Topa in the same hole with a Fuerte on Topa. Another combination is Topa Topa on a Duke rootstock and a Fuerte on Topa Topa. In addition, there are planted new Topa Topa on Topa rootstock trees next to two-year-old Fuerte trees. The spacing is about six to eight inches from the trunk of the older tree.

Interesting field observations have been made during spring and summer of 1966 indicating that other varieties such as the Covocado, Jalna, Puebla, and Zutano, are influencing increased Fuerte set. While the Zutano is of B-type like the Fuerte, cross-pollination may occur fairly readily if the daily opening and closing rhythms are a little different, as is true of nearly all varieties. We have statistically significant evidence that the Hass variety (which is an A type, and opposite to the Fuerte) also increases Fuerte set to a less marked degree. It is thought that the Mass variety tends to bloom too late to coincide best with the flower-setting period of the Fuerte. It could be that the Zutano has a sufficient-better time of blossoming to compensate for its flower type.

More observations are needed and tests conducted before a definite recommendation can be given on any varieties other than the Topa Topa. The authors urge growers to study their orchards carefully when Fuerte trees are growing next to or near other varieties, observe the Fuerte set. Plan to keep individual tree production records, if possible on those Fuerte trees next to different avocado varieties, to compare with the grove average.

SUMMARY

Summarizing the data on cross-pollination as it affects Fuerte fruit set, we can say:

1. The avocado flowering behavior consists of two-stage sexual openings with reciprocal daily patterns classified as A and B types
2. Climatic conditions of temperature, humidity, rain, cloudiness affect proper operation of flowering and influence bee activity
3. Pollen must reach the stigma at the proper time in the flower cycle.
4. Pollination of some type, close or cross, must take place for fruit
5. Bees are necessary for pollination of avocado flowers
6. There is overlapping of the receptive and pollen-shedding periods in certain varieties which accounts for some varieties setting fruit without cross-pollination.
7. Cross –pollination produces more Fuerte fruit than close-pollination.
8. Mixing Type A and Type B varieties in a planting enhances the chance for increased production.

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