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THE POLLINATION OF AVOCADOS

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CONTENTS

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THE POLLINATION OF AVOCADOS

A. B. Stout

INTRODUCTION

Pollination is the process by which pollen is carried from the stamens and deposited on the stigmas of the pistils in the flowers of plants. Then the growth of pollen tubes through the stigma to the ovary leads to the final acts of fertilization, which include the fusion of a sperm cell from the pollen tube with an egg cell in the ovule. This double cell develops into the embryo of the seed. It is certain that it is the rule that a fruit with a seed can mature on most of the avocados of the present day only when there has been a proper pollination that is followed by fertilization. Thus proper pollination constitutes an important step in the production of fruit.

But in avocados there is a most remarkable regulation in the development of the flowers and of their stamens and pistils which restricts and even prevents many self-pollinations[1], many close pollinations,[2] and also many cross-pollinations.[3]

This development and regulation is such that the flowers of one group of seedlings and clonal varieties (the "**A**" group) function as pistillates or females in the forenoon and as staminates or males in the afternoon while those of another group (the "**B**" group) function as males in the forenoon and as females in the afternoon. Thus there is an adaptation that restricts self-and close-pollinations and that provides for an alternation of the reciprocal cross-pollinations possible each day between certain members of the two groups.

But the horticultural practice of vegetative propagation by grafting and budding to obtain clonal varieties of avocados that are planted in solid blocks operates to prevent cross-pollination. In nature, or in plantings of seedlings only, every avocado tree is a seedling and any group of trees will be a mixture of **A** trees and **B** trees with opportunity for reciprocal cross-pollinations. When a seedling of merit is propagated by grafting or budding all trees of the clonal variety are alike in their trunk and branches (except for bud variation), they all have the same flower behavior, and there is no more chance for pollination from tree to tree (intra-clonal pollination) than there is for pollination from flower to flower on a single tree. In such cases proper interplanting to provide for natural cross-pollinations becomes desirable or necessary.

How the types of flower behavior operate in the clonal varieties now in cultivation, how they influence and determine the production of fruit, the extent to which these adaptations for cross-pollination make interplanting necessary or advisable, and what particular interplanting will promote increased and maximum yields of fruit in any or in all varieties are matters that are vital in the culture of avocados.

[1] Pollen taken from the stamens to the pistil of the same flower.
[2] Pollen taken from one flower to the pistil of another flower on the same plant or on another plant of the same clonal variety.
[3] Pollen taken from a flower of one plant to the flower of a different plant either a seedling or a plant of a different clonal variety.

THE GENERAL RULES OF FLOWER BEHAVIOR IN AVOCADOS

The flowers of all avocados thus far studied, except the Collinson, have both pistils and normally developed stamens—that is they are perfect flowers. Also the flowers are very similar in structure and appearance. They are rather small and inconspicuous in color; they are produced in large numbers; and a tree has a succession of sets of flowers that gives continuous flowering for at least several weeks and sometimes for several months! Each flower has one pistil, two sets of stamens arranged in an inner whorl of three and an outer whorl of six, and two sets of nectaries corresponding in number and relative position to the sets of stamens.

The flowers open synchronously in sets that have, normally, two distinct periods of opening. There is for each set (a) a period of first-opening when the flowers function as females, (b) an interval of being closed, and (c) a period of second-opening when they function as males, and these three periods constitute what may be called a cycle of dianthesis. The first-opening and the second-opening take place on different days and they cover different hours of the day. The succession of sets day after day brings a daily alternation of a new set in its first-opening with an older set in its second-opening and there is little or no overlap in the periods of opening of the two sets.

THE GENERAL RULES OF BEHAVIOR FOR THE "A" GROUP

Under favorable weather conditions the flower behavior for the A group of seedlings and clonal varieties is as follows:

The First Period of Opening:—In the hours of the early morning no flowers are open anywhere on the tree but during the early forenoon flowers begin to open almost in unison here and there in the various clusters of flower buds all over the tree. These flowers have not been open before. In this first-opening of flowers the six leaf-like segments of the perianth separate and bend outward; the two sets of six outer and three inner stamens follow and when the flower is fully open the stamens lie against the perianth and are nearly at right angles to the main axis of the pistil, as seen in the open flowers shown in Figure 1. Thus the pistil stands erect, alone, conspicuous, and fully exposed with the slightly expanded end (the stigma) white, fresh and evidently ready to receive pollen. Soon nectar appears as a glistening film or as droplets on the surface of the inner set of three nectaries which stand erect from between the inner set of stamens. Now bees and other insects seeking nectar can scarcely fail to brush against the stigma. The pistil is ready for pollination but no pollen is being shed from the stamens of the flower. The flower is, for the time being, functioning only as a female.

Directing attention to the numerous flowers open on the entire tree during the forenoon one finds that all the flowers which are open are in the same condition as the flower just described. No flowers are shedding pollen; all have pistils ready for pollination. This condition continues throughout the forenoon during which the entire tree functions as a female. About midday the numerous flowers of the set that was open during the forenoon close without shedding pollen. In doing this the perianth segments fold inward over the pistil until the flower is completely and tightly closed (see 3 in Fig. 2).

Thus an entire set of flowers, numbering several thousand for a large tree in the maximum of blooming, has been open and in the female stage during several hours of the forenoon, and during midday these flowers have all closed almost in unison.

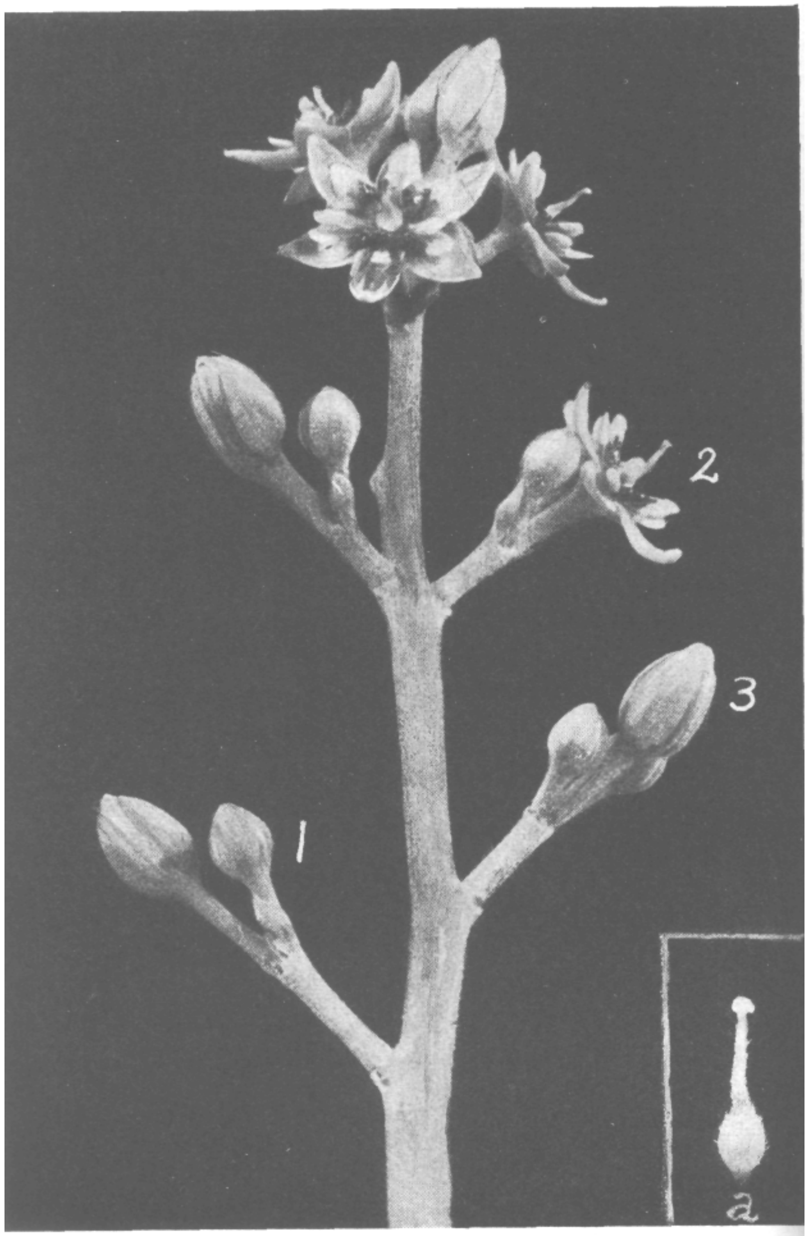

Fig. 1.—Avocado flowers in the first opening. a, Pistil with stigma fresh and receptive; 1, flower bud; 2, flower open in first period; 3, flower in the interval between first and second opening. Enlarged about two times.

The Second Period of Opening:—During the hours of midday, and usually while the flowers which were open in the forenoon for their first period are in the process of closing, the flowers of another set begin to open. To a casual observer it would doubtless appear that the same flowers open in the forenoon merely continue open during the afternoon. But if a number of individual flowers be tagged for identification the complete midday shift of sets can readily be determined and also the two periods of opening of a set of flowers can be observed and properly related to the daily sequence or alternation.

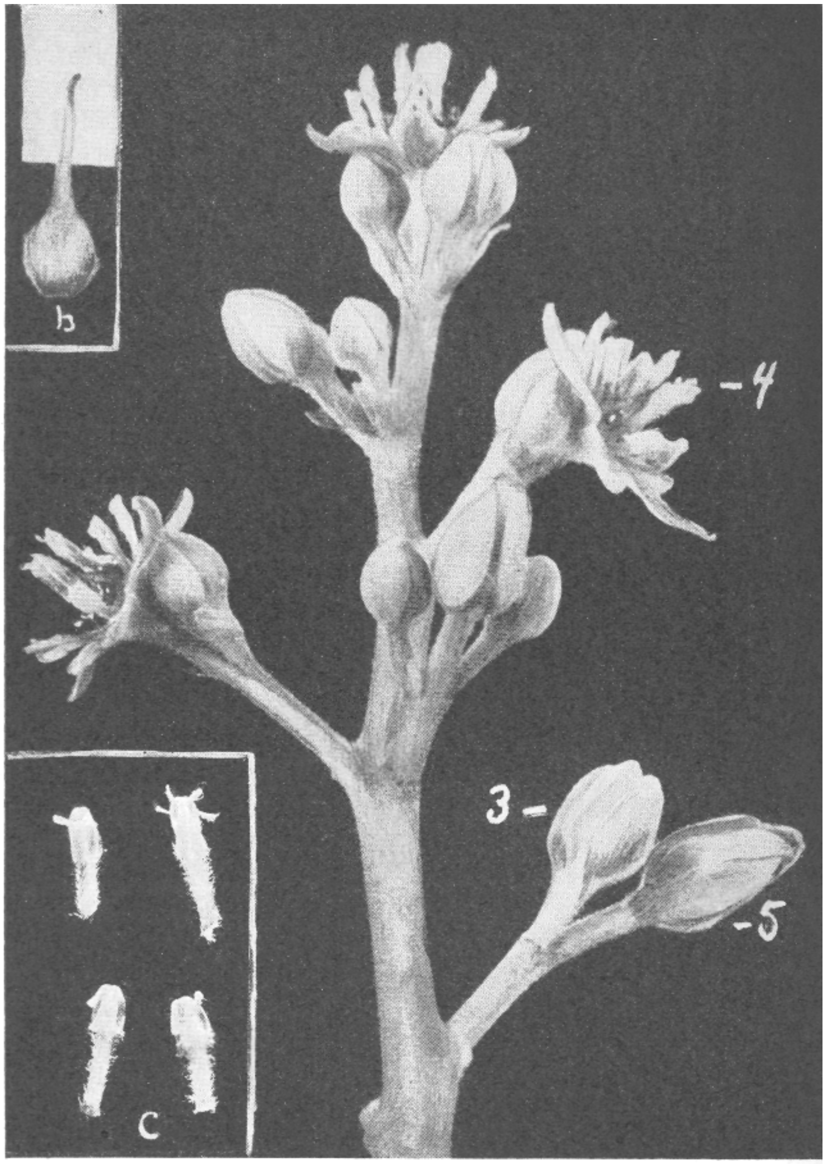

Fig. 2.—Avocado flowers in the second opening. b, Pistil with stigmatic end shriveled; c, stamens with uplifted valves on which pollen is exposed; 3, flower in the interval; 4, flower open in second period; 5, flower closed after the second opening. Enlarged about two times.

The flowers of a set opening for their second opening in the afternoon are distinctly different in appearance from those open during the forenoon (compare Figures 1 and 2). At this time the end of the pistil is frequently dark-colored and sometimes it is shrivelled and of course unable to receive pollen in proper pollination. The stamens are now noticeably larger and somewhat longer; the inner three stand erect in the middle of the flower around and overtopping the pistil and facing away from it; the outer set of six stamens stand at an angle of about 45 degrees. Not long after these flowers open, pollen begins to be shed. The pollen is ingeniously lifted out of each of the four chambers of an anther by a spoon-shaped valve that opens quite like a trap door [and bends upward. A somewhat sticky mass of pollen is gently held within the infolded margin of each valve, somewhat as one [1] might hold a ball of popcorn in an upraised hand. Thus the nine rod-shaped stamens of each flower stand bristling in different directions with pollen exposed in several directions from their summits. (Fig. 2). Below at the base of the outer set of stamens and between the stamens, a set of short-stemmed dome-shaped nectaries excrete thick films of nectar. In their efforts to obtain this nectar bees and other insects climb over the stamens, push in between them, and their hairy bodies become more or less smeared with the sticky pollen. But if pollen is not carried away by insects the sticky substance about and between the grains hardens and binds the pollen grains of each valve into a mass which then soon falls to the ground.

A careful census of the many flowers open on a tree of the A group during the afternoon will reveal that all the flowers that are open are in the same condition. They all shed pollen with the maximum of pollen shedding during the middle of the afternoon. Late in the afternoon the flowers of this set close almost in unison never to open again.

The Daily Alternation of Sets:—Thus during the hours of daylight two different sets of flowers open and close on trees of the A group and their periods of opening alternate. One set opens for the first or female opening during the forenoon; another set opens for the second or male opening in the afternoon. The maturity of the pistil or pistils and the stamens of the same flower at different times is known as dichogamy (14).* In avocados the dichogamy is synchronous for the entire tree.

The Cycle of Dianthesis:—The A varieties have flowers which open for the first period during the forenoon, close around midday and remain closed during that afternoon, the night following and the forenoon of the next day, and then open for the second period during the afternoon of the next day. Thus for a single flower there are two distinct and separate periods of opening or anthesis, a condition which may be designated as dianthesis. Between the two periods of opening there is an interval of about 24 hours. The entire time from the beginning of the first or female opening with the end of the second or male opening (the completed cycle of dianthesis) covers slightly less than 36 hours.

The succession of sets continues to operate on this schedule very regularly under favorable weather conditions and this brings two different sets into alternation or daily sequence each day. Each forenoon a new set opens for the first or female opening and this same set opens for the second or male opening on the afternoon of the following day. Each afternoon the set which opens for the second opening had its first period of opening during the forenoon of the previous day.

Each flower is perfect, it has two distinct periods of opening, it is mature as a female during the first period and as a male during the second period. There is the development of the two sexes in each flower at different times (dichogamy). The flowers open synchronously in sets and the two periods of opening occur during different hours of the day. Thus the flowers open on a tree at any one time are alike, and the development of the flowers is so coordinated or synchronized that the entire tree functions as a female in the forenoon and as a male in the afternoon.

THE GENERAL RULES FOR FLOWER BEHAVIOR IN THE"B" GROUP

The flowers of varieties of the **B** group are like those of the **A** group in structure and

* Numbers in parentheses (Italic) indicate references to literature to be found on page 44.

general appearance. Also they have the same two periods of opening and the flowers also open synchronously in sets. But the sets are normally open for the first or female period in the afternoon and for the second or male period in the forenoon either of the following day or of the second day. The succession of sets of flowers operating in this cycle gives a sequence in the daily alternation that is the reverse of that in class **A**. The flowers of a tree of a member of the **B** group function as males in the forenoon and as females in the afternoon.

THE DAILY RECIPROCATION BETWEEN "A" AND "B" VARIETIES

The relative flower behavior typical for **A** and **B** varieties and the reciprocation in pollination which results may be shown by comparing two clonal varieties such as Taylor and Panchoy.

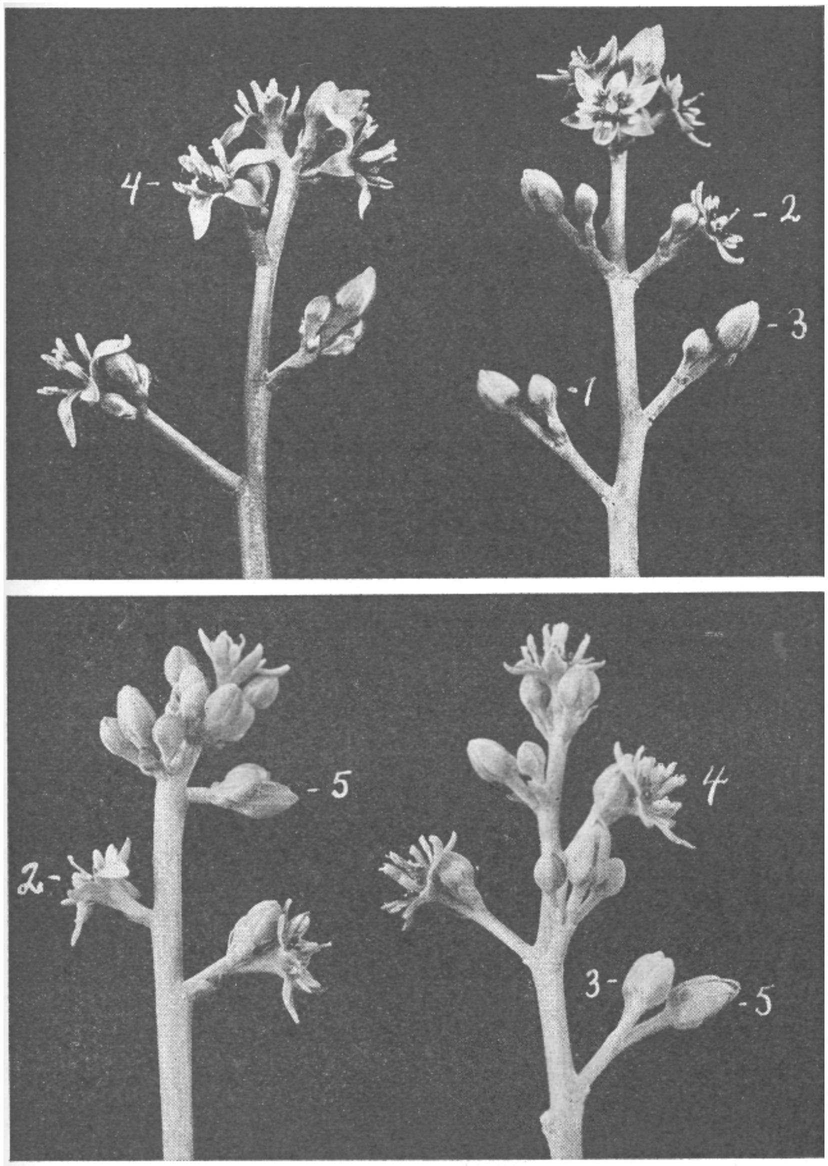

Fig. 3.—Flowers of Panchoy at left, of Taylor at right; upper for the forenoon, lower for the afternoon. 1, Bud unopened; 2, flowers in first period; 3, in the interval; 4, in the second period; 5, after the second opening.

During the forenoon, while flowers of Taylor are in the first period or female anthesis, the flowers of Panchoy are all of the second period or male opening (upper section of Fig. 3). Thus trees of Panchoy are shedding pollen during the forenoon at the time when the flowers of trees of Taylor are most ready to be pollinated. During the midday an alternation or change in sets occurs for each and then in the afternoon the flowers that are open on Panchoy are in the first period or female opening while the flowers open on Taylor are all of the second period or male opening (lower section of Fig. 3). These two varieties are, therefore, reciprocating in their daily alternations of sex. Taylor is female in the forenoon while Panchoy is male and then while Taylor is male in the afternoon Panchoy is female—all during the hours of a single day.

The adaptations for reciprocal cross-pollination are marked and evident. There is opportunity for pollen to be carried from Panchoy to Taylor during certain hours of the forenoon; during certain hours of the afternoon pollen can be carried from Taylor to Panchoy.

THE A AND B GROUPS IN NAMED VARIETIES AND SEEDLINGS OF PROMISE

A total of 413 clonal varieties of avocados are listed by name in the Year Book of the California Avocado Association for 1932. The flower behavior for most of these has either not been determined or there has been no record made in publications. In the following lists of **A** and B varieties several published lists have been combined with additional data obtained in Florida in 1932.

"A" VARIETIES

Varieties which normally have flowers open for the first or female opening in the forenoon and flowers open for the second or male opening in the afternoon.

Atlixco
Baker
Barker
Baldwin
Benik
Blakeman
Booth No. 1
Booth No. 7
Brooks
Butler
California
Cantel
Carlsbad
Challenge
Clower
Collason No. 1
Collason No. 2
Collason No. 3
Collinred C
Collinred D
Collinred E
Collinson No. 1 (pollen sterile)
Collinson No. 2
Colorado
Dickey
Dickinson
Dunedin
El Presidente
Family
Flamingo
Fuchs
Garcia
Gazzam
Gottfried
Grande
Hawaii
Hawaiian
Hollis
Ishkal
Kanan
Kashlan
Kay
Kosel No. 1
Kosel No. 3
Kosel No. 4
Kosel No. 5
Kosel No. 6
Lula
Mahan
Manik
Mayapan
McCann
Moanaloa
Mowry
Murrietta Green
Murrietta 2 lb.
Pankay
Perfecto
Peterson
Pinelli
Popenoe No. 3
Popenoe 51029
Puebla
Reasoner
Richardson
Sharpless
Simmonds
Sinaloa
Solano
Spinks
Taft
Taylor
Taylorson
Ultimate
Wagner
Waldin
Ward
Wester
S. P. I. 18729
S. P. I. 19205
S. P. I. 26698
S. P. I. 26703
S. P. I. 29137
S. P. I. 29379
S. P. I. 44626

"B" VARIETIES

Varieties which normally have flowers open for the second or male opening in the forenoon and flowers open for the first or female opening in the afternoon.

Akbal
Big Tree (Seedling)
Bitte (Seedling)
Booth No. 6
Booth No. 8
Butternut
Cabnal
Cardinal
Champion
Chisoy
Coban
Colla
Collinred A
Collinred B
Collins
Collinson x Trapp (S. P. I. 61740)
Collinson x Trapp (Broad leaf)
Cook
Dorothea
Eagle Rock
Earle's Late
El Oro
Estelle
Fuerte
Fulford
Ganter
Hanson
Hardee
Harmon
Hosack
Ishim
Itzamna
Knight
Kosel No. 2
Kosel No. 7
Lamat
Linda
Lyon
Mattair
McClure
McDonald
Meserve
Montezuma
Nabal
Nimlioh
Nimliohson
Nirody
Northrup
Nutmeg
Panchoy
Pollock
Popenoe 51105
Queen
Rey
Rome (S. P. I. 34831)
San Sebastian
Schmidt
Simpson
Steffani
Stephens Choice
Surprise
Tertoh
Trapp
Tumin
Val de Flor
Verde
Walker
Whitcomb
Winslow
Winslowson (Rolfs)
S. P. I. 2689
S. P. I. 26700
S. P. I. Seedless 32400
S. P. I. 44856

The above lists include most if not all of the most important varieties in culture at the present time in California and Florida. It is of significance that the **A** and the **B** types of behavior are apparently about equally distributed among avocado seedlings.

THE RELATIVE FLOWER BEHAVIOR OF DIFFERENT VARIETIES

The relative flower behavior of numerous varieties, members of the **A** group and members of the **B** group, may now be considered with reference to the exact time during the day when the two sets open and close and the bearing which this has on the reciprocations in pollination. In obtaining such data many flowers are tagged with distinguishing numbers and observations are made and recorded for trees of several varieties throughout the same day. The observations are made from tree to tree as quickly as possible, especially during the midday shift of sets, and the condition of the flowers is indicated and checked on squared paper for 15-minute intervals. The records for the day are then assembled into a chart (see explanation of charts for symbols used) with the varieties arranged according to the time when the sets of first-period flowers started to open. Such a chart gives a graphic picture of what the flower behavior of the different varieties has been during the day and what reciprocations for cross-pollination are most complete.

The data for such charts have been collected for many days of observation in Florida in 1925 and in 1932 and also in California in 1923 covering the same varieties and often the same trees for a series of successive days including normal behavior during favorable weather and abnormal behavior of various degrees during unfavorable weather. Figure 4 shows by diagrams the normal flower behavior typical for **A** and **B** varieties.

Fig. 4.—A record of normal flower behavior in Florida for a day rather late in the season of blooming. In this chart, as in those that follow, the continuous line indicates for each variety the entire time when flowers were open for the first opening. The dots indicate the time during which flowers of the second period of opening were shedding pollen and the dashes show the time before and after the pollen was being shed when these flowers were more or less open. As a rule pollen is shed most abundantly near the middle of the period covered by the dots.

A survey of this chart clearly reveals the following important features regarding the flower behavior of the several varieties studied.

1. There is a daily alternation in the synchronous dichogamy.

For each variety there were two different sets of flowers open during the day. The flowers of one set functioned as females, those of the other as males. Each set opened and closed in unison and the two sets were open during different hours of the day. While there was frequently a short interval of overlap of the two sets during the shift in midday, the rule is that no pollen was shed while flowers in the female condition were open for the second period, then it was scant for a time and later the maximum of pollen-shedding was reached after which pollen again became increasingly scarce.

It may be noted that unless pollen is carried away by insects the masses of pollen harden and become dried into little balls that fall to the ground. It also seems most probable that the pistils are not fully receptive for fertilization during the entire time flowers are open for the first period and that in the charts a line representing the most receptive condition of pistils would be much shorter than the entire shown in the various charts. But considering the entire periods of opening, in every case the synchronous alternation of sex as graphically shown in the chart most decidedly limits self- and close-pollination.

2. There are two main groups of varieties. The varieties studied on the date in question fell into two groups which reciprocated with respect to the relative sequence of the daily alternation in the development of the two sexes. The members of one group, called for convenience the **A** group, were female in the forenoon and male in the afternoon; while the members of the other group—**B**—were male in the forenoon and female in the afternoon.

This record of daily behavior is typical and fully representative for the various clones listed, for the **A** and **B** varieties in general, and for the range of differences seen within the **A** and **B** groups as these occur normally. Day after day during the more favorable weather conditions the behavior of each of the varieties listed in the chart will be quite similar.

3. There are varietal differences within the groups. It will readily be noted in Fig. 4 that there are certain marked varietal differences within each of the **A** and **B** groups in respect to the exact time when the sets of flowers open and close. These are features that are characteristic of the respective varieties. This aspect of flower behavior was first noted and reported by *Nirody(5).*

For the **A** varieties studied on the day of this record there was a difference of more than an hour in the time when the flowers started to open for the first period. These flowers of Perfecto opened at least 1½ hours earlier than flowers on Waldin, and thus there was some chance for the first-period flowers of the late Waldin to be pollinated from the second-period flowers of earlier varieties as Grande and Perfecto. In general, however, the hours of opening were somewhat similar for all the **A** varieties, and there was for all of these except Manik a short period of overlap when the set in the first period was closing and the set in the second period was opening.

For the **B** varieties very noticeable differences appear in the time when the flowers open for the first period. Thus on this day, for Meserve the first opening started early in the afternoon and was completed before the first opening began on Taft's Golden. Also for Trapp and Pollock the period of first opening came late in the afternoon and continued until after dark. For El Oro and Winslow the period of second opening was a relatively short interval. For some of the **B** varieties there is a slight overlap of sets, but for the ones listed at the bottom of the chart there is actually an interval of several hours after the closing of the set m the second period before the new set starts to open—a feature of the dichogamy which was observed by Nirody *(5).* All of the **B** varieties are, however, quite alike during the forenoon in respect to the opening for the second period.

The differences shown in the chart in the relative flower behavior of various varieties are remarkably constant day after day. The bearing which these types of behavior have on pollination will be discussed later.

4. Reciprocations in pollination. Thus any variety of **B** furnishes pollen at a time suitable for the pollination of any **A** variety. But some of the **B** varieties have the period of first opening late in the afternoon after pollen shedding has ceased or has almost ceased by the **A** varieties, and for these there is a decided limitation in the chances that ANY pollinations can be made during the first period of opening. The relation which this habit of late afternoon opening has to the second opening may now be viewed in a consideration of the cycles of the sets of flowers.

THE NORMAL CYCLES OF DIANTHESIS

The entire time from the first opening to the final closing of a single flower or of a set of flowers, which includes the two periods of opening and the interval of being closed, may be called the cycle of dianthesis, the flowering cycle, or merely the cycle. In considering these as represented in Fig. 5 one follows the behavior of the flowers of a set continuously from the time they first open until they close never to open again.

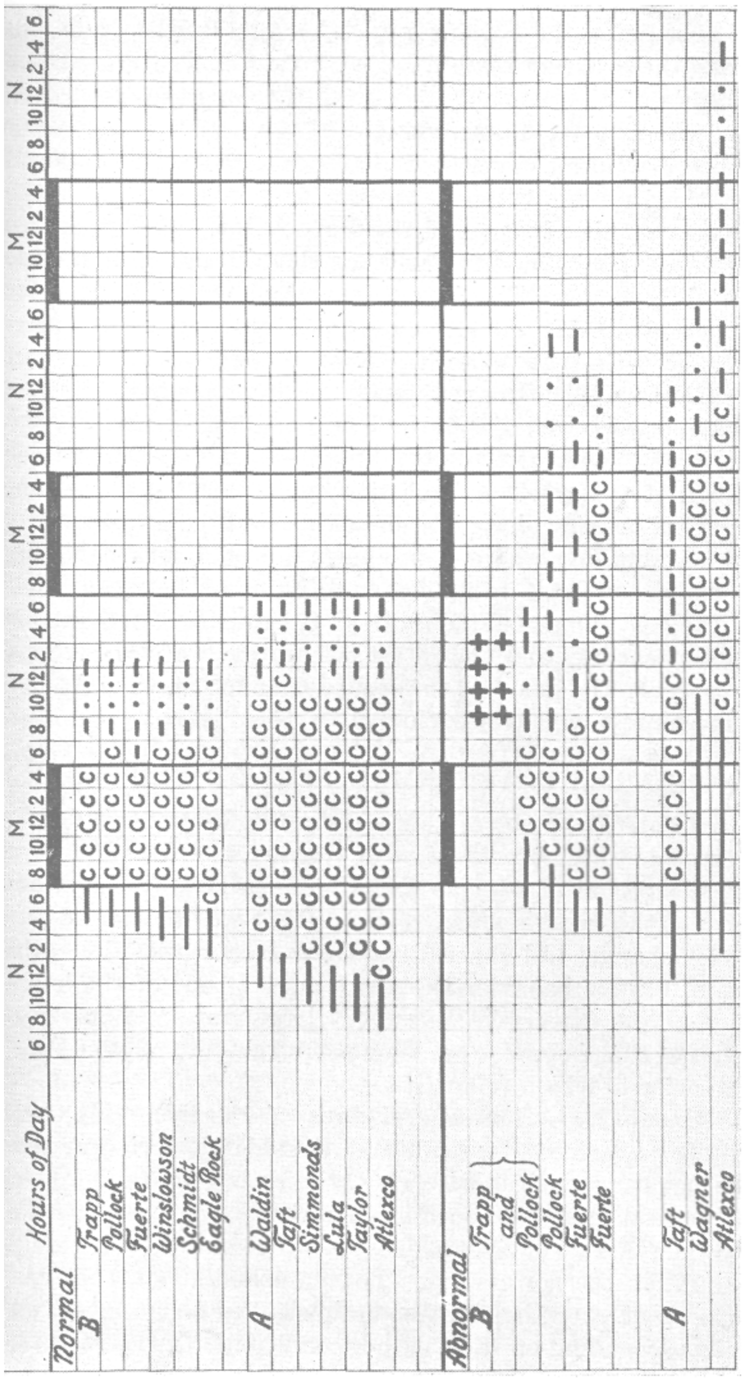

Fig. 5.—Chart showing diagrammatically the main types of normal and abnormal cycles in the opening of the flowers of avocados. An interval of time covering four periods of daylight and three intervening periods of darkness are represented. The interval between the two openings of flowers is indicated by the letter C. Under abnormal opening the barred dash (+) indicates single opening.

The shortest normal cycles of dianthesis are seen in the **B** varieties that habitually open for the first period late in the afternoon as do the Trapp and the Pollock but the **B** varieties which open earlier in the afternoon, as Eagle Rock, have a cycle that is slightly longer. The **A** varieties which regularly open for the first period latest in the forenoon, as the Waldin, have a somewhat shorter cycle than those like Atlixco and Taylor that start earlier in the day. The chart shows that there are more marked differences between varieties in the hours of the first-period opening than in the hours of the second-period opening. Thus when **A** and **B** varieties are selected and arranged according to the time of first-period opening, based on data collected on the same day or on comparable days, there is, as shown in Fig. 5, a rather graduated series from Trapp to Atlixco and the break between Eagle Rock of the **B** group and Waldin of the **A** group is less than that between the earliest and the latest within each of the groups. But in respect to the hours of the second opening the **A** and the **B** groups are more completely exclusive.

IRREGULAR AND ABNORMAL FLOWER BEHAVIOR

The particular behavior of sets of avocado flowers opening on any one tree as to the precise time of opening, the duration of an opening, the period of overlap and the lapse between sets, and the length of the cycle is affected by weather conditions and particularly by changes in temperature. In extreme cases the entire sequence of normal behavior is thrown entirely out of stride and the action of the flowers becomes very irregular. Various sorts and grades of such behavior are shown diagrammatically in Fig. 6 and in the charts which follow it.

Single Opening:—After several days of relatively high and rather uniform range in temperatures a sudden lowering of temperature may cause such short-cycle varieties as Trapp and Pollock to omit the first or female opening of an entire set or of part of a set and then this set of flowers may open the next day for a single opening. Then the flowers may shed no pollen at all, they may shed pollen poorly, or they may sometimes shed pollen freely and quite fully, depending on the weather conditions.

Skutch *(9)* has also observed that more pollen-shedding flowers may be open on certain trees during a forenoon than there were flowers in the first period during the preceding afternoon. This condition has frequently been seen by the writer and the observation made that it may involve flowers which open but once for a pollen-shedding period or it may involve flowers that operate on a 48-hour cycle, as reported under "B2" and "B3" types of flower cycles *(13).* Sometimes counts will show more flowers open on **B** varieties during the afternoon than in the following forenoon in which case certain flowers may not open for the second opening or they may do so on the second day following. That some varieties may be quite regularly **A** or **B** while others of **B** are more erratic is a frequent observation (see Figs. 6 and 7). This condition illustrates varietal differences.

Another type of single opening occurs when first-period flowers do not entirely close during the night but enter into an extended single opening. If the following day is favorable such flowers may shed pollen.

The writer has carefully studied single-flowering and diligently searched for seedlings or varieties which may have **ONLY** single opening in the hope that this might be associated with self-fruiting. This behavior is strongly developed in the "late" **B** varieties, but no variety has been found which maintains single opening to a noticeable degree under the most favorable conditions of weather.

Delayed Opening and Reversal of the Daily Alternation:— Under unfavorable weather conditions the first or the second opening is often delayed; the first opening of **A** varieties may be delayed until in the afternoon, and that for **B** varieties may be delayed until the following forenoon and thus the normal daily sequence is for the time being temporarily reversed (see especially Fig. 9). A set of flowers that would normally open during any one day may be delayed until the following day or until the second day. In extreme and continued inclement weather the development and maturity of flowers is greatly retarded and the opening of flowers in sets that are synchronous and alternating is scarcely in evidence.

Extended Cycles:—Unfavorable weather conditions or marked changes in weather while a set of flowers is open often extend the cycle of dianthesis either in the period of first opening, in the interval, or in the second opening, or in two or more of these conditions. Various types of this are shown in the table of Fig. 5. For example, a single set of flowers of Atlixco which normally has a cycle of about 36 hours may have an extended cycle of 80 hours.

Under certain conditions some of the **B** varieties, as the Fuerte, will have the sets of flowers operating in a cycle of 48 hours, but with a daily periodicity and alternation that appears to be quite normal. This appeared to be the rule of the behavior for certain **B** varieties in California during February, March and April of 1923 in those orchards where the writer made continued observations. Again this same variety and even the same tree that is operating on a 48-hour cycle will shift to a short cycle of 24 hours. One of the most surprising types of behavior is that in which part of the flowers of a set have a cycle of 24 hours and the rest have a cycle of 48 hours. In this case nearly always the pistils of those flowers opening for the second opening in a cycle of 48 hours are at that time blackened and obviously unable to function to pollination and these flowers open as much as an hour in advance of the flowers of the shorter cycle. The presence of pollen-shedding flowers of both short and long cycles may make decided differences in the number of flowers counted on successive days. In the present discussion it is considered that the 48-hour cycle for **B** varieties may be classed as abnormal but it should be noted that the flowers of a variety may continue in this cycle for some time.

The normal and the abnormal behavior of numerous varieties have been studied repeatedly in the same grove on different days. Typical records for such studies are presented in Figs. 4, 6, 7 and 8 and it may be stated that the observations recorded in these charts were all taken in the same grove (that of the late Wm. J. Krome at Homestead, Florida) and for the same tree when any one variety is noted in different charts.

The record of Fig. 6 is for a day following rather low night temperatures. There was decided delay in the opening of both first-period and second-period flowers and for several of the **B** varieties which normally have first-period flowers opening late in the afternoon there was omission of this set and continued opening (indicated by arrow heads) from the previous afternoon. But for most varieties there was the daily alternation of two sets complete, there was no overlap of sets when pollen was being shed and the reciprocation between many **A** and many **B** varieties was good. On this day there were no first-period flowers open on Estelle and Taft's Golden. Some of this set opened for a single opening during the next day.

Fig. 6.—Record of flower behavior for a day after a night of somewhat unfavorable temperatures.

Figure 7 is for two successive days and illustrates the effects on flower behavior of a sudden drop in temperature to a maximum of 77° and a minimum of 46° after several days of temperatures ranging about 10° higher. The opening of sets was delayed but the **A** varieties and most of the **B** varieties had two sets in daily alternation. The late **B** varieties were most irregular with single opening of both types and with much extended opening. On both days Estelle had only flowers of a single opening, and Trapp had most of its flowers in a single opening. On the day of this record there was for many varieties no overlap of sets and for none was there overlap for a considerable portion of the period of pollen shedding.

Various sorts of extreme off-stride flower behavior, frequently observed both in California and in Florida, are shown graphically in Fig. 8. The 9th and the 10th of February had been warm with maximum temperatures of 84° and 91° and the flower behavior had been normal and regular quite as shown in Fig. 10. Heavy rain on the 11th was followed by clear cold weather and northerly winds with a drop to a maximum temperature of 64° on the 12th, and on the night preceding the 13th there was the only frost experienced during February and March of that year in the orchard where the observations were made. As the chart indicates the two sets of flowers, which in favorable weather would have opened and closed on the 12th, actually required two days for their opening. There were both delayed and extended antheses and most of the time the flowers were semi-open with feeble and incomplete action of the flower parts and the shedding of pollen was slow, irregular, and incomplete. On the 12th there was no overlap of sets with one shedding pollen for any variety studied. On the 13th there was decided overlap for Atlixco, Wagner, Fuerte, Harmon and Pollock.

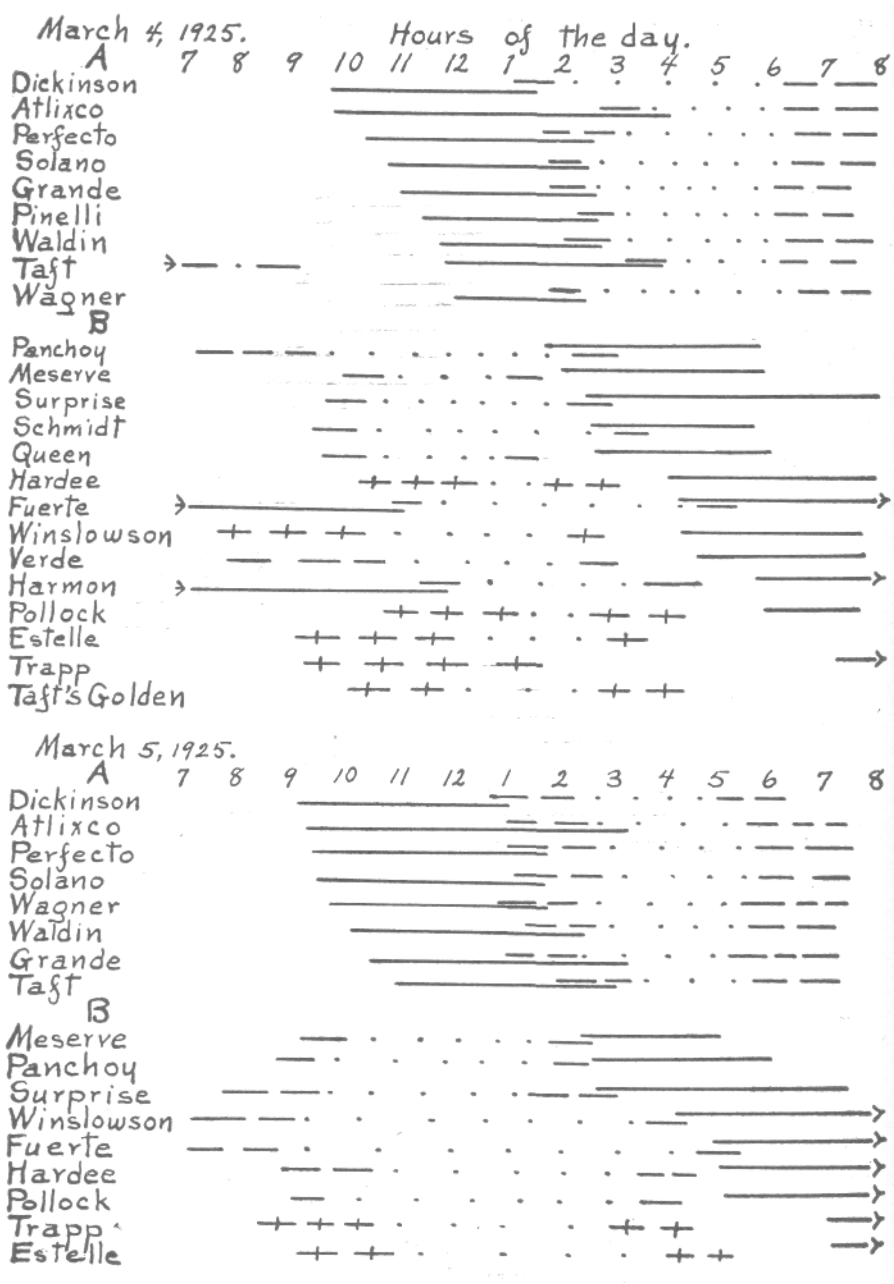

Fig. 7.—Records of flower behavior for two days showing delayed opening, extended opening, and single opening.

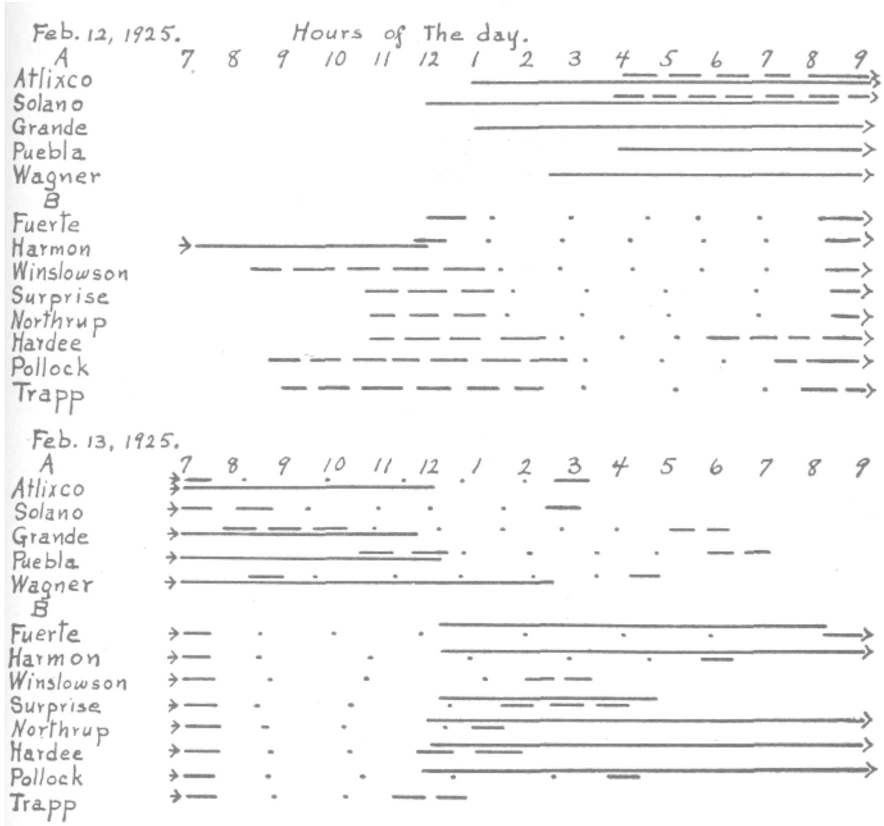

Fig. 8.—Record for two successive days showing much delayed and extended opening of flowers.

Thus the daily behavior of any one tree may differ from day to day in response to weather conditions. With continued inclement weather the flowering may be erratic for several days, for several weeks, or even throughout most of the entire season of blooming. Then it may be difficult to determine whether varieties are to be classed as **A** or **B**. From certain of the records obtained in California the behavior of the same trees of three **A** and three **B** varieties on three different days have been combined in Fig. 9 to illustrate the point in question. On May 5 the daily alternation of dichogamy was complete and in normal sequence. On May 17 under unfavorable weather there was for Sharpless and Taft a reversal of the daily sequence, no pollen shedding by flowers of Dickinson, extended opening and overlap for two sets on Queen and Panchoy, and for Linda only one set was open. During the forenoon of the 19th, there was the return of sunny weather and warmer temperatures. For the **A** varieties the set of flowers delayed or continued from the previous day shed pollen and closed about noon, then first-period flowers were open and these were followed by a set of second-period flowers. Of the **B** varieties Queen had three different sets of flowers open but Panchoy and Linda had but one set and these were second-period flowers.

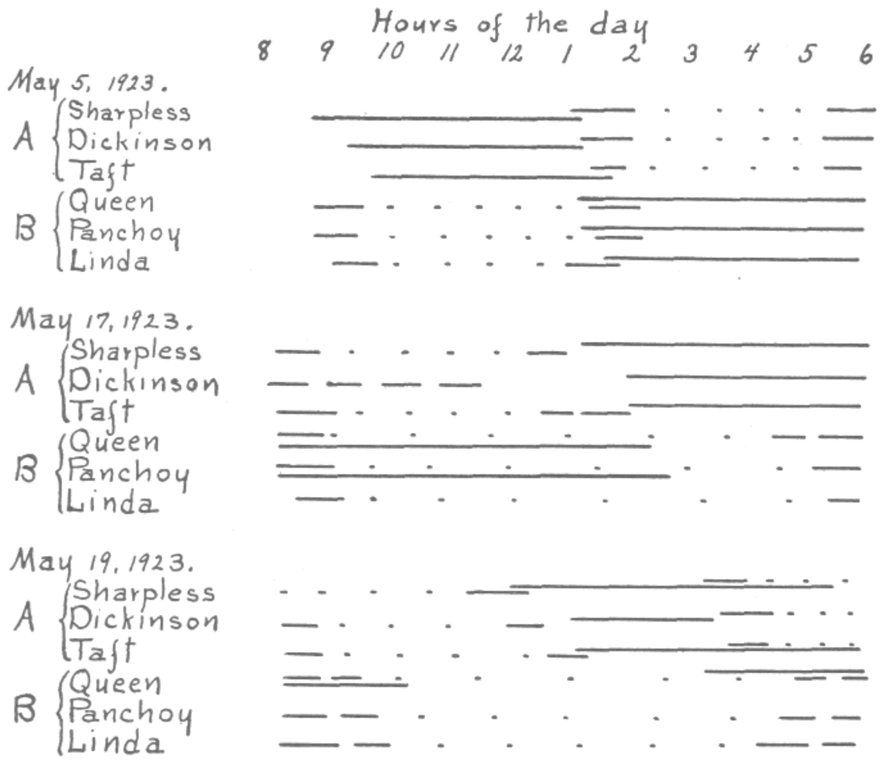

Fig. 9.—Records of flower behavior for six trees on three different days.

The various conditions of abnormal flower behavior were fully described and discussed and some of them illustrated by photographs and charts in the first reports made by the writer *(10,11, 12)* as well as in a more recent publication *(13).* Others have reported and discussed such behavior (see especially *7).* Erratic behavior, often to the degree that there was no definite daily alternation, was the rule in California during February, March and part of April in 1923, wherever the writer made observations.

Flower Behavior Throughout the Season of Flowering:—During 1925 the flower behavior of a tree of the Taft variety and a tree of the Trapp variety was observed carefully for most days of the season of bloom.

For the tree of Taft (see Fig. 10) there was considerable variation in the hour when the sets of flowers opened but there was for each day a definite alternation of two sets. Except for a few minutes on the first day of record there was no opportunity for pollen to be carried from second-period flowers to first-period flowers open on the tree. The flower behavior was most normal during the warmer weather of the last half of the season of bloom and then the shift of sets occurred more nearly at the noon hour.

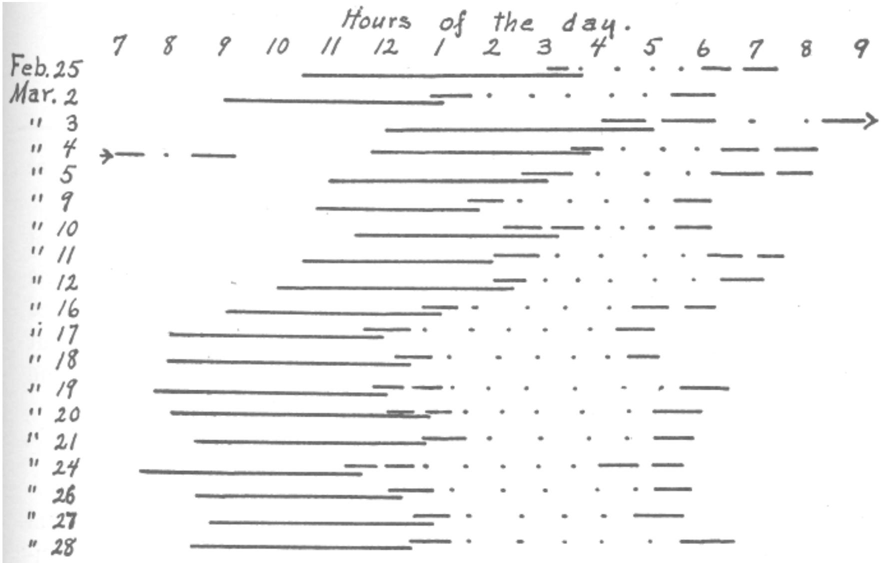

Fig. 10.—Records of the flower behavior for trees of the Taft variety in one locality in Florida during the season of 1925.

The record for the tree of the Trapp variety is shown in Fig. 11.

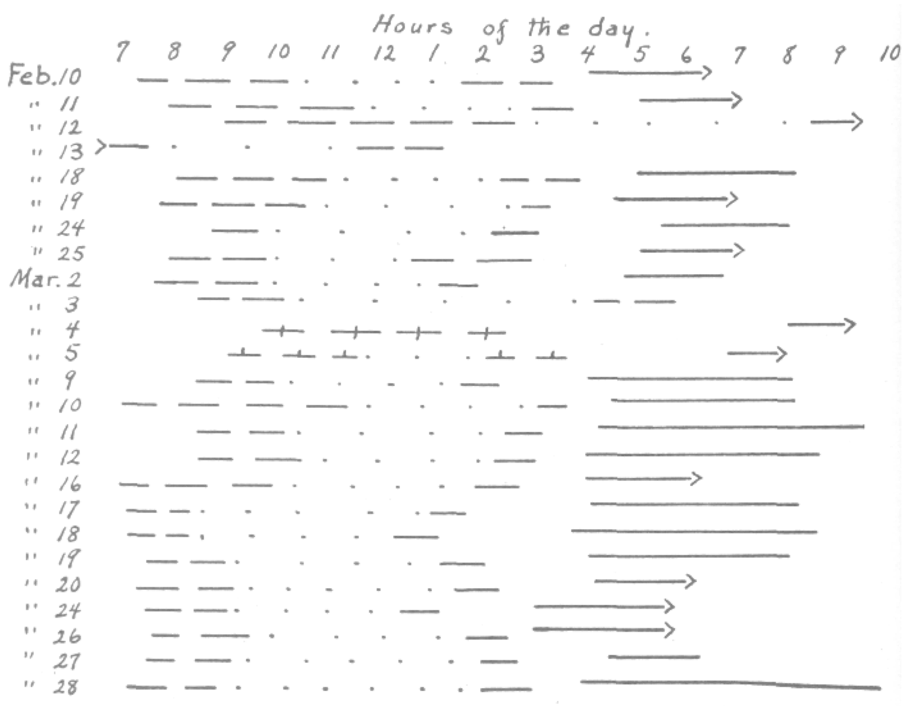

Fig. 11.—Records of the flower behavior for trees of the Trapp variety in one orchard during the season of 1925.

There were three days (Feb. 11 and 13 and March 3) when a set of first-period flowers failed to open. Only on two days did the first-period set open as early as 3:00 p. m.; usually this set opened late and remained open until after dark. At no time throughout the many days of observation were there any first-period and second-period flowers open together.

CHANCES FOR SELF- AND CLOSE-POLLINATION

Self-Pollination:—In avocados self-pollination of individual flowers can occur only during the normal second-period of dianthesis or during a single opening when pollen is being shed. Then considerable pollen of both self- and close-pollinations must, it would seem, reach the stigmas especially as a result of the activities of insects. If the stigmas are still receptive, the conditions favorable for pollen-tube growth, and the ovules and their eggs still ready for fertilization and responsive to self fertilization some fruit should result.

It would seem that the **B** varieties with shortest cycles, such as Trapp and Pollock, would be most likely to set fruit to pollinations made during the second period of the cycle. The flowers open for the first period late in the afternoon when pollen is not abundant on **A** varieties and the chances for any kind of pollination at this time are greatly reduced. If the pistils remain receptive until the next forenoon self-pollination or cross-pollination with other **B** varieties may be responsible for some or even all of the fruit that may be set at certain times by such varieties. It would seem that the flowers of the **A** varieties are less liable to remain receptive to pollination until the second opening. In fact the stigmas of such flowers are often disintegrated, blackened, and shrivelled and obviously in no condition to function to any kind of pollination. Such flowers, it would seem, must be properly pollinated during their first opening if they are to yield fruits. The same is true of the **B** varieties for those flowers that open in a long cycle of 48 hours.

Close-pollinations (from flower to flower on same tree) may be of two sorts; (a) between different flowers all of which are shedding pollen, or (b) pollination of first-period flowers from pollen of flowers in the second-period. The latter may be designated as dichogamous close-pollination.

The first mentioned type can occur at all times when flowers are shedding pollen and is presumably quite the same as self-pollinations except when a short-cycle set and a long-cycle set are both shedding pollen together. It is certain that for many varieties these pollinations do not lead to the setting of fruit.

Dichogamous close-pollinations can occur (1) during an overlap of sets and (2) when insects force flowers during the interval when they are closed after the first opening. During normal flower behavior there is, for most varieties thus far studied, very little overlap of sets during the time when pollen is shed. For a large majority of the flowers opening normally there is no chance for close-pollination of first-period flowers. The rule of normal behavior is that while the two sets may overlap slightly there is no pollen shed by flowers of the second opening during the time of the overlap. This is amply shown in Figs. 4, 6 and 7 for the daily behavior of numerous varieties and also in Figs. 10 and 11 which record the flower behavior of individual trees of the Taft and the Trapp varieties during a season of bloom.

During various types of irregular and erratic flower action there may be many chances for dichogamous close-pollination.

THE ROLE OF FERTILIZATION IN THE SETTING OF FRUIT

Pollination is but a first step in the series of events that are necessary in most avocados for fruit production. It is followed by the processes of fertilization including the growth of pollen tubes in the pistils and the fusion of sperm and egg in the ovule, all of which are processes which involve intricate physiological interactions.

In dichogamy, such as occurs in avocados, the condition of the pistil, and especially of the stigma at the time when pollen reaches it, is a factor which determines whether pollen tubes will grow. It seems clear that the rule is that in avocados the pistils are most receptive to pollination during the first period of a normal flower behavior, and that many pistils are less able or entirely unable to set fruits to any pollinations during the second period of opening.

In many plants, of which the apples, the pears and the sweet cherries may be cited, it is known that self-pollinations and also certain cross-pollinations made at the time when pistils are fully receptive are not effective in fertilization and in such cases only pollinations between varieties that are compatible in fertilization result in satisfactory sets of fruits. Certain varieties may be somewhat self-fruitful but will yield much larger crops to proper cross-pollination. Whether somewhat similar conditions exist in avocados in addition to the dichogamy is not definitely known.

At the present time little direct knowledge is available on the processes and events of fertilization in avocados. H. van Eiden found (reported by Hodgson, *4)* that for various Mexican and Guatemalan varieties the egg apparatus is developed and ready for fertilization when flowers are in the first period of opening and he found cases of fertilization at this stage. This is what one would expect from the flower behavior, but it does not necessarily indicate that the pistils of a few flowers on many varieties or that the pistils of many flowers of certain varieties do not remain more or less receptive until the second opening.

During 1932, T. W. Young in cooperation with the writer made studies of several varieties as to the structure of the pistil and the growth of pollen tubes in the style after various sorts of pollination. These studies indicate that there may be abnormalities in the structure of certain pistils which reduce or prevent their functioning in fruit production. It is possible that further study will show that these have a relation to abnormal flowering, to conditions of climate or culture, or to season of flowering or that they are rather characteristic of certain varieties. It also appears that " the number of pollen tubes which can penetrate through the style is restricted to few tubes or possibly to one tube. Further studies of the actual processes of fertilization should be made in respect to determining the conditions essential to the production of fruit, and to learning just what pollinations are most likely to yield fruit.

There is a tendency for a few varieties, as the Fuerte, to produce fruits which contain no seeds. Two clones which are said to produce only seedless fruits (F. P. I. Nos. 14889, and 14890) were obtained from Mexico in 1905 for trial in the United States. Another avocado, F. P. I. 32400, from C. P. Taft of Orange, California, is described as having "fruit absolutely seedless but very small, 3 to 5 inches in length and 1/2 to 1 inch in diameter." **A** tree of the F. P. I. 32400 is now growing in the Plant Introduction Garden at Chapman Field, but I am informed by T. A. Fenneil in charge of the Garden that it has not yet bloomed. It is not definitely known whether such fruits develop without pollination as parthenocarpic fruits (as do the fruits of the naval orange) or whether there is death of embryos after fertilization as is the case for certain seedless grapes. The seedless fruits which appear on avocados are relatively small and somewhat irregular in shape and give little promise of commercial value. It is possible, however, that good seedless sorts whose fruits are parthenocarpic may in time appear or be developed by selective breeding.

It has several times been suggested to the writer that certain avocados may be able to produce fruits containing seeds without any pollination or fertilization. Such a condition, which is called apogamy, is known to occur in relatively few of the seed plants. There is at present no proof or even very suggestive evidence that apogamy does occur in avocados. That certain trees of the same clone, as the Fuerte, are highly self-fruitful through apogamy in one orchard while other trees a short distance away are not is very improbable and is not to be accepted unless proven.

In summary, it may be emphasized that in the chain of events which lead from flower to fruit in avocados there are several weak links due in large part to the element of chance in the play of circumstances. Chances for fruit development depend on the presence of a seed. Chances for a seed depend on the presence of an embryo in the very young fruit. Chances for this embryo depend on proper fertilizations. Chances for fertilization depend on proper pollination which in turn depends on flower behavior, on the reciprocation of varieties in pollination and on the activities of insects. On all links of this chain the external conditions of weather and cultural conditions and the internal conditions of nutrition and development exert their various influences. Proper pollination, fertilization after pollination, and the holding and maturing of fruit are three weak links in this chain.

THE RESULTS OF POLLINATIONS MADE BY HAND

Self- and Close-Pollinations:—In California during 1923 several thousand self- and close-pollinations were made by hand mainly for the varieties Harmon, Fuerte, Northrup, Puebla, Dickinson and Taft, but for these not a single fruit was set. For Carton and Queen small fruits set, even when flower clusters were enclosed in paper bags and when there was no pollination except possibly that of incidental selfing, but none of these matured.

Cross-Pollinations:—As previously reported (Stout, *12* and *13)* it is to be recognized that relatively few cross-pollinations which are made by hand result in fruit. Of a total of 3,430 carefully executed cross-pollinations made in California during February, March, April, and May, 1923, only 173 flowers started to set fruit and some of these failed to develop. Similar results were obtained for pollinations made in Florida in 1925. In 1932 T. W. Young and the writer made 63 different kinds of controlled pollinations involving a total of 1,151 flowers. Of these flowers 754 were cut for microscopic study of the processes of fertilization. Of those left on the tree, 45 selfs promptly fell without even starting to form fruits and of the 352 flowers cross-pollinated only 14 set fruits. None of these 14 matured, but had all fallen a few weeks later (last check made 4-20-32). The cross-pollinations were reciprocal and they were nearly all made during normal flower behavior. It was later noted that considerable fruit set during the same period to open pollination especially on Winslowson. This fruit set rather abundantly at a time when its flowers were opening normally, when there was no overlap of sets, when bees were frequent visitors and during which there was opportunity for reciprocal cross-pollination with nearby and adjacent trees. Evidently insect pollination was much more effective than hand pollination. In certain cross-pollinations involving Lula, Winslowson, Fuerte and Hawaiian the stigmas were stippled with a fine stiff-haired brush to break the stigmatic glands with the thought that such injury may be accomplished by insects and may promote pollen-tube growth. But such pistils showed no better pollen-tube growth than did unstippled pistils and the flowers thus treated and left on the tree all fell. Such results do not enable one readily to determine what are the relations of pollination to the setting of fruit, what kind of pollinations are responsible for the fruits which mature on a tree and to what erratic setting of fruit is due.

Observation clearly shows that a large majority of the flowers produced by avocados do not set fruits and this condition continues even after the careful cross-pollination by hand of first-period flowers. Possibly (1) the pollinations are not made in a way necessary for success, or (2) the pistils of many flowers are unable to function in any relation except when conditions are favorable to a normal development either in the structure of the pistils or in their physiological condition, or (3) the most effective relations in cross-fertilizations were not involved in the crosses attempted.

Fig. 12.—Showing fruit set by tree of Winslowson to open pollination during a period when flower behavior was decidedly regular, when bee visitors were frequent, and when reciprocating cross-pollinations were possible from nearby trees. During the same period, careful self- and cross-pollinations on the same tree all failed to give sets of fruit.

FRUIT SETTING BY TENTED TREES

The extent to which avocado trees are able to produce fruit without cross-pollination may, it would seem, be determined experimentally by enclosing a tree in a cheesecloth "house" or "tent" during the entire period of flowering. Also trees or parts of trees of two varieties may be enclosed together. Bees to make the pollinations may or may not be supplied.

Tests of this sort were first made for avocados at the Theosophical Homestead, Point Loma, California. The results have been published and discussed *(1, 2* and *3).* In these tests Fuerte, Tinsley, and to some degree Dickinson were found to be self-fruitful provided bees were enclosed to effect self- or close-pollinations and it was concluded that at least the Fuerte is adequately self-fruitful. There were somewhat conflicting results. For example, part of a tree of Fuerte set no fruit when enclosed with part of a tree of Spinks with two hives of bees. If trees of Fuerte are adequately self-fruitful the enclosed portion of the tree in question should have borne fruit to selfing irrespective-of any cross-pollination with the Spinks. The result seems to indicate either that the insects did not effect cross-pollinations or that such pollinations did not lead to fruit setting.

During 1925 in the orchards of Wm. J. Krome at Homestead, Florida, a tree was tented with a hive of bees enclosed of each of the varieties Linda, Panchoy, Taft, and Trapp *(13)* (Fig. 2). About eight weeks after the close of the flowering period the Taft tree had seven fruits, the Panchoy two, the Linda 22, and the Trapp 18. There was no question that the flowers of these tented trees received abundant visitations daily by the enclosed bees

which effected self- and close-pollinations (including forced pollination of first-period flowers) far in excess of what flowers of any orchard tree is likely ever to receive. If these varieties readily set fruit without cross-pollination the tented trees should have set fruit more abundantly.

The flower behavior of adjacent trees of Taft and Trapp was studied during the season (see Figs. 10 and 11). For each there was a rather complete daily alternation with chances for self-pollination or for close-pollination of first-period flowers only through the forcing of flowers by the bees. The results obtained with the tented trees show that almost no fruit was set to enforced self- and close-pollinations and that proper cross-pollinations were necessary for adequate fruit production.

THE POLLINATION AND THE FRUITING OF THE COLLINSON AVOCADO

The fruiting of the Collinson avocado is of special significance in regard to the amount of cross-pollination which may occur under orchard conditions. This clonal variety is completely pollen-sterile *(15, 18* and *13)* and it furnishes no pollen for any sort of pollination. Tests under tents *(6)* show that trees of Collinson are unable to produce fruits without cross-pollination. This variety has been rather widely planted in Florida where it is usually highly fruitful. In fact, it received first place by vote in a questionnaire sent out to growers in 1931 as being very uniformly fruitful and highly desirable for general culture. Robinson and Savage *(8,* page 8) state that "The fact that this excellent variety fruits well in mixed plantings is convincing evidence that cross-pollination is the regular method of fruiting with avocados generally, and in this case it is the only possible explanation of fruitfulness."

The fruiting of the Collinson may be confidently viewed as the result of cross-pollinations with some other variety or varieties and as evidence that when conditions are favorable cross-pollination may rather readily be accomplished.

ON INTERPLANTING AVOCADOS

The advantage to be gained by interplanting avocados lies in the chance that there will be cross-pollinations which increase the yields of fruit over that obtained in solid-block plantings of one variety.

CONDITIONS WHICH DETERMINE CROSS-POLLINATION AND THE SETTING OF FRUIT IN ORCHARDS

Three conditions are important in determining whether an interplanting will be liable to increase the production of fruit.

1. The varieties interplanted should so reciprocate in flower behavior that there is opportunity for cross-pollination.

2. Means for effecting the pollinations must be operating year after year.

3. The pollinations when made must lead to fertilization and to the development of fruit.

1. Any interplanting of an **A** with a **B** variety will increase the chances for cross-pollination and these will be greatest when the **A** and **B** varieties used most fully reciprocate in the hours of the daily sequence and also bloom together over a considerable part of the flowering season. On the basis of flower behavior the proper interplanting of any variety will increase the chances for the pollination of flowers especially when they are in the first-period of an thesis and evidently most receptive to pollen.

An interplanting of only **A** or of only **B** varieties will give very little increased opportunity over solid-block planting for the normal pollination of first-period flowers. It is, however, quite possible that certain short cycle **B** varieties as the Pollock and Trapp will benefit by cross-pollinations with other **B** varieties during the second-period of anthesis provided the pistils remain receptive.

2. An interplanting can only afford an opportunity for cross-pollinations. Means for making the pollinations must be operating. Fortunately honey bees are very fond of the nectar of avocado flowers and they also collect pollen from the flowers. They freely visit the flowers during both of the periods of opening. Various other insects visit the flowers of avocados and some of these may be important agents in effecting pollination. But hives of the honey bee may be placed in the avocado orchards and to a considerable degree kept under control and for this reason the honey bee is to be considered as the most promising agent for orchard pollination.

Insects in their visits to the flowers automatically effect many self- and close-pollinations during the second period of opening but it seems obvious that the pistils of many such flowers are not receptive. They may also effect close-pollinations of first-period flowers when these are possible through overlap or through forcing. But to effect reciprocal cross-pollinations an individual insect must fly from one tree whose flowers are shedding pollen to another tree whose flowers are in the first period of opening. In general the insect must fly from **B** to **A** trees in the forenoon and from **A** to **B** trees in the afternoon (see Figs. 3, 4, 6 and 7).

During 1932 in Florida a special effort was made to study the activities of honey bees in their visits to avocado flowers. Mrs. W. J. Krome and W. K. Walton obtained several hives for distribution in the groves and E. Morton Miller and various of the students of the Department of Zoology at Miami University made special studies of the activities of the bees. One important feature which they determined is that certain bees collect pollen only from avocado flowers while certain other bees from the same hive collect nectar only. It is certain that many individual bees that are active among the avocado flowers do not make cross-visitations. They are liable to work on a single tree. Also it should be recognized that those bees which collect only pollen confine their attention to trees in the second period of the daily alternation or to second-period flowers where there is overlap and in so doing they make few or no reciprocal cross-pollinations. The desired reciprocal cross-pollinations are made chiefly or only by those bees which collect nectar and which in doing this fly directly and repeatedly from a tree whose flowers are shedding pollen to a tree of another variety whose flowers are in the first period.

Furthermore, it is possible that the qualities of the nectar produced by different varieties influence the activities of insects. Nectar differs in color and apparently also in thickness and in amount. The differences in the flavor and the odor of the nectar produced by certain pairs of varieties may be such that individual bees may not collect from the two during any one period of work. Thus many bees, and other insects as well, may be very busy in collecting nectar or pollen and yet be effecting no reciprocal cross-pollinations.

It can readily be observed that honey bees do travel through avocado groves to a considerable distance from the hive but whether this is due to preference for some one variety or to some other influence is not known.

Possibly bees are more liable to make cross-visitations at times when the open flowers are relatively few, when bees are relatively numerous, and when other pasturage is scarce. At certain times bees may be attracted away from avocado flowers to other flowering plants, especially to nearby citrus trees or even to cover crops. Certainly avocados should not be inter-mixed with other fruit crops such as citrus which not only separate the avocado trees but which may also be in flower at the same time.

In respect to the supply of hives of bees to be recommended for properly interplanted orchards of apples, pears, or sweet cherries, it is frequently considered that one strong colony to the acre is sufficient (see Bulletin No. 577, New York State Agri. Experiment Station). But in avocados the daily synchronous alternation of dichogamy restricts opportunity for proper pollination and, it would seem, makes it desirable to employ more than one hive to an acre, at least for the present time until experience gives more specific guidance.

3. The matter of affinities between varieties in respect to the processes of fertilization after cross-pollination may be an important one in the setting of fruit by certain avocados. The late William J. Krome frequently stated to the writer that he believed there is a decided cross-affinity between the Guatemalan and the West Indian types. If this be true, certain pairs of varieties may be more fruitful in reciprocal cross-pollination than are others. This matter requires careful analysis by direct studies of fertilization, by special tests with tented trees, and by comparison of fruit yields in adequately interplanted orchards in which the same varieties are employed in different combinations.

OTHER FACTORS DETERMINING FRUIT PRODUCTION

It is to be emphasized that reciprocating interplantings, adequate pollination, and affinities in fertilization can not and will not eliminate various other factors for unfruitfulness such as habits of alternate bearing, unfavorable conditions of weather, the attacks of fungi and of insect pests, and faulty methods of culture particularly in irrigation, soil fertilization and pruning.

Such factors operate to influence yields of fruit and often they are the limiting factors in fruit production. They are vital in the culture of fruits like the navel orange which requires no pollination whatever. In avocados they influence fruit production in addition to the factor of proper pollination. Possibly in certain localities unfavorable conditions of climate, of soil, or of culture are the chief factors which are responsible for lack of fruit on avocados and under certain conditions even the most proper reciprocal cross-pollinations may not be effective.

Frequently varieties of avocados set large numbers of fruits (see Fig. 11) which soon fall. Some of this abscission of fruit is due to physiological conditions either unfavorable to the retention of the fruit or of the nature of competition between fruits for food and water. Some of the fruits which are without embryos or which have dead embryos may be due to lack of pollination or to abortion after fertilization and these are doomed to fall unless there is development as seedless fruits. When there has been proper setting of fruit the holding of fruit until maturity is no doubt chiefly a matter of the influence of environmental and cultural conditions.

METHODS OF INTERPLANTING

The simplest type of interplanting is that which includes one **A** variety and one **B** variety. In such plantings, three arrangements of the trees may be considered as follows:

```
A B A B        A   A          A B A B
                 B   B
A B A B        A   A          B A B A
                 B   B
A B A B        A   A          A B A B
                 B   B
A B A B        A   A          B A B A
                 B   B
 (2a)           (2b)           (2c)
```

In 2a and 2b a vertical row is composed of only one variety and in 2c the trees of each variety are in diagonal rows. In plan 2b the two nearest trees are always of the same variety but there are four of the reciprocating variety next in the line of the diagonals. In 2a each tree has two adjacent reciprocations in the same lateral row. In the plan 2c each tree has for its four nearest neighbors trees of the other variety, and this would afford opportunity for the greatest number of reciprocations in cross-pollination. In any such interplanting the two varieties should be in flower together at least during a considerable part of the season of bloom and neither should be decidedly alternate in bearing.

An interplanting of only two varieties gives opportunity for only one kind of cross-pollination. The nectar of the two varieties concerned may be so different that cross-visits by insects may be reduced in number or it is possible that there may be lack of affinity in the processes of fertilization.

When four varieties, two of the **A** group and two of the **B** group, are interplanted the arrangement that seems best is as follows:

A1	B1	A2	B2	A1	B1
B2	A1	B1	A2	B2	A1
A2	B2	A1	B1	A2	B2
B1	A2	B2	A1	B1	A2

In this case each tree has immediately surrounding it in the four nearest distances two trees of one reciprocating variety and two trees of another reciprocating variety. Thus there are for each tree chances for two different reciprocating cross-pollinations and each operates from two trees. There is the chance that one of the two cross-relations may be more effective than the other, and hence the interplanting of four varieties is in general more likely to give fruit than an interplanting of only two varieties. If, however, cross-pollinations are not effective between any two, as let us say **A1** and **B1**, then the **A1** and the **B2** and the **B1** and the **A2** should reciprocate. If it is determined that they do this perfectly the two pairs may be planted to greater advantage in a two-variety interplanting.

When three **A** varieties and three **B** varieties are interplanted the maximum opportunities for cross-pollination are obtained when the varieties of each group are arranged in repeating sequence in diagonal rows which alternate as shown in the following diagram:

A1	B2	A3	B1	A2	B3
B1	A2	B3	A1	B2	A3
A1	B2	A3	B1	A2	B3
B1	A2	B3	A1	B2	A3
A1	B2	A3	B1	A2	B3
B1	A2	B3	A1	B2	A3

In this arrangement any tree has as a female the chances for three different inter-varietal reciprocations in pollination from the four nearest trees and one of these is duplicated in the two trees adjacent in the same vertical row. The **A** and the **B** varieties are arranged in pairs which alternate in the same vertical row and hence these two should be most fully reciprocating and also most fully similar in season of bloom, habits of growth, and cultural requirements. This arrangement would also promote cross-pollination of any one short-cycle **B** variety during the second period of opening with pollen of two other **B** varieties standing next in the diagonal rows.

Special means of promoting cross-pollinations in avocados have been suggested and to some extent employed. Trees of two or more varieties may be planted close together so that their branches somewhat interlock and combine to make one compact group. Another method is to so graft that the branches of two or more varieties are grown on the same trunk and root system to form one tree. This has been done to some extent both in California and in Florida but the results have not been satisfactory. In reporting his experiences with this method the late Wm. J. Krome stated (see Proceedings Florida State Hort. Soc. for 1925, p. 90-91) that "I have never found that it was a wise thing to do. The stronger variety will almost every time dwarf the weaker variety, and you will wind up with only one variety on the stock." The writer knows of no reports on the results of tests in compact group-planting but the success of such a method would probably involve the grouping in one unit of trees that grow with almost the same vigor.

PRACTICAL MATTERS REGARDING INTERPLANTING

At the present time definite answers can scarcely be made to the numerous practical questions which growers of avocados are certain to ask regarding interplanting. Yet enough is known to attempt statements which seem most safe and reasonable both in regard to the known facts and to the means which are most likely to lead to the best, the quickest, and the least expensive solution of the pollination problem in the culture of avocados.

Will all varieties be benefited by proper interplanting? Every clonal variety and every seedling thus far studied in California and Florida has shown a daily synchronous alternation of dichogamy which unmistakably limits and restricts self- and close-pollination. In the sequence of these daily alternations there are the two main groups from which various clonal varieties may be selected which afford the most complete and the most remarkable reciprocations for cross-pollination. Cross-pollination should greatly increase the chances that fruit will be produced in abundance and with greater regularity. In normal flower behavior and also during various grades of abnormal flower behavior the rule is that flowers can not be pollinated during the first period of opening unless by reciprocating cross-pollination.

To what extent are any varieties self-fruitful? In regard to this point the writer stated in 1923 *(3*, pp. 42-93) that "Experience seems to indicate that possibly some varieties may set fruit when there is no opportunity for cross-pollination" and also the irregular and off-stride flower action which gives opportunity for dichogamous close-pollination was fully described.

A later report *(15*, p. 84) published after the studies of 1925 in Florida may be quoted as follows: "Thus the setting of fruit by isolated trees or by trees of a solid planting of one variety and particularly by trees abundantly worked by bees in tenting experiments may be expected. It is possible that a peculiar set of local weather conditions may sometimes favor setting of fruit year after year without cross-pollination. Some varieties such as the Trapp may have a flower behavior that enables them to be more self-fruitful than are other varieties. But even for such varieties there is no doubt that a proper interplanting will increase the chances of many more proper pollinations and to this extent insure the production of more uniform crops."

There seems to be considerable evidence that at least certain varieties may be self-fruitful, especially along the coastal region south of Los Angeles in California. Observations and tenting experiments at Point Loma have been interpreted by Clark *(1, 2* and *3)* to signify that certain varieties are self-fruitful in that location. In a recent statement Dr. J. Eliot Coit remarks as follows: "However, so many other factors enter into the question that throw the regular rhythm out of stride that the practical growers I know who have been watching this question of cross-pollination over a period of years have come to the conclusion that these other factors are more important than the normal opening or closing time of the blossoms. I can take you to any number of groves where solid Fuerte or Taft plantings standing alone produce heavily. One particular instance is three Taft trees where there are no other avocado trees near for a long distance that are outstandingly heavy and regular producers. Therefore, the tendency of the growers today is to go ahead and plant the varieties they want to plant that will produce most money for them and trust the trees for their own pollination" (Year Book, California Avocado Association for 1931, p. 111).

In answer to inquiries regarding the pollination of avocados J. G. France, Farm Advisor of San Diego County, California, makes the following published statement: "I hope we are going to find out after a while. There are some funny things about it. Some people have Fuertes and nothing else and have good crops, and some have everything else and have poor crops, and then vice versa. Without a little more careful observation, I can't even hazard a guess. I have an opinion, though. I'm inclined to think that temperature conditions are more important at the time of setting than having a number of avocado trees around" (Year Book, California Avocado Association for 1931, p. 112).

The statement quoted above that temperature is an important factor in fruit setting is pertinent both as to the effect on flower behavior in relation to pollination and to the effect on the processes of fertilization after pollination. Under what may be called the more favorable temperatures flower behavior is more regular and complete in the alternation and there is less opportunity for close-pollination. Without doubt there are temperatures which prevent fertilization to any kind of pollination. Those temperatures which tend to favor the processes of fertilization after self- and close-pollination can be assumed also to be more favorable to fertilization after proper cross-pollination.

Robinson *(7)* has recently surveyed the evidence for self-fruitfulness and considered the flower behavior that may be involved, and he concludes that "Despite the observed instances where certain avocado varieties are evidently not dependent on cross-pollination for fertilization of the flowers, it is believed that under most circumstances interplanting of reciprocating varieties, together with the use of bees as pollinating agents, provides a worthwhile measure of security against faulty pollination.

According to present knowledge the self-fruiting of any avocado which has seeded fruit depends (1) on dichogamous close-pollination during an overlap of sets or when there is the forcing of flowers by insects, or (2) on self-pollination of flowers whose pistils remain receptive until pollen is being shed from their stamens.

The writer is inclined to believe that flowers in abnormal opening are, as a rule, unable to function in any relation. Yet rather slightly abnormal cycles produced by moderately inclement weather, especially if it be long continued, may promote self-fruiting especially when insects are active. It also seems to the writer that the forcing of flowers and the self-pollination of certain flowers by insects during normal opening will be more liable to lead to self-fruiting. On account of the shorter cycle of dianthesis it would appear that self-pollinations are more likely to yield fruit on **B** than on **A** varieties except when their flowers are open in the long cycle of 54 hours.

How to make avocados bear adequately and regularly has long been and still is a matter of concern to avocado growers both in California and in Florida. The erratic and poor bearing of certain varieties has been a chief factor in their being discarded from general culture. The flower behavior of all varieties clearly indicates a remarkable adaptation for cross-pollination which can best be provided for by proper interplanting and by supplying honey bees in abundance.

To ignore this condition by planting in solid blocks invites low yields of fruit. This means financial loss to growers especially during the period when the relatively few most self-fruitful varieties are being discovered and the areas are being delimited in which the environmental conditions favor or induce a type of flower behavior that is most favorable to self-fruiting.

It is without doubt advisable (1) to interplant avocados on the basis of their flower behavior, (2) to supply bees in abundance to effect pollinations, (3) to make special experimental tests of various types of interplanting with different combinations of the most promising varieties, (4) to make definite studies of existing commercial orchards regarding the yields of each tree and the disposition of the different varieties, and (5) to continue careful studies of normal and abnormal flower behavior, of the means of pollination, and of the processes of fertilization.

The combined results of such efforts should rather quickly and definitely reveal what, if any, varieties are self-fruitful and under what conditions and to what type of flower behavior and pollination they thus operate. The results thus obtained should also reveal to what extent varieties require cross-pollination and what particular combinations of these are most favorable to fruit setting. Perhaps it is not too much to hope that in time a group of ideal avocados may be discovered or developed by selective breeding which among other desirable qualities are fully self-fruitful. That such varieties are not now in existence among the varieties commonly cultivated is evident. Until such varieties are definitely known it is a safe and wise plan to interplant on the basis of flower-behavior and with due consideration of other qualities and cultural requirements.

There appear to be few legitimate objections to the interplanting of avocados. In making interplantings along the lines that now seem most promising the grower has nothing to lose and there is the chance that he will profit by increased production.

ACKNOWLEDGMENTS

This bulletin is a report chiefly of the investigations which the writer made in Florida in 1925 and 1932, but to some degree the conclusions and the data involve the earlier studies in California during 1923.

The investigations in 1925 were made under the auspices and with the financial support of The New York Botanical Garden and the Farm Bureau of Dade County, Florida. During most of that period of work E. M. Savage of the Bureau of Plant Industry, U. S. D. A., participated in the investigations as did also T. Ralph Robinson for a part of the time. Valued assistance and cooperation were rendered by various members and officers of the Florida Avocado Association and especially by the late Wm. J. Krome and by J. S. Rainey, county agent of northern Dade County.

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This bulletin draws freely from earlier publications of the writer and especially from the report on "The Flower Behavior of Avocados" published by The New York Botanical Garden in 1927. The illustrations of figures 1, 2 and 3 are from photographs used in that report and the plates of Figures 4, 6, 7, 8, 9, 10 and 11 are of those made for that report and here used by permission. This repetition is, it is felt, justified, first because a large number of the separates of that report which were printed for distribution to avocado growers in Florida were destroyed in Miami during the hurricane in 1926, and, second, because these photographs and charts very fully illustrate the matters involved.

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