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The flower behavior of avocados

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THE FLOWER BEHAVIOR OF AVOCADOS*

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(with plates 24–28 and charts 1–10)

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In avocados the development of the two sexes in the hermaphrodite flowers is so regulated that the many flowers open on the entire tree function only as females during certain hours of the day and only as males during certain other hours of that

* Avocados or alligator pears are evergreen trees of the laurel family (Lauraceae) indigenous to tropical America. Those in cultivation at the present time embrace at least three somewhat distinct races derived evidently from what has been considered as two somewhat closely related species of the genus *Persea*. Apparently avocados were grown during early pre-Columbian time as an important food crop in Central America and Mexico with later introduction into portions of South America and the West Indies. More recently their culture has spread into various tropical countries of the Old World and particularly has their culture become an important horticultural industry in Florida and California, with promise of much further development.

same day. This alternation of the sexes for the entire tree continues day after day with a regularity that greatly limits or even entirely prevents both the self-pollination of individual flowers and pollination from one flower to another (close-pollination) on the same tree or on different trees of the same clonal variety.

But what is still more remarkable, certain plants (individual seedlings and clonal varieties as such) are female during the hours of the day when other plants are male and then there is a reversal of sex in each for other hours of that same day. These reciprocating changes in sex provide chances for mutual cross-pollination between certain plants.

The flowers are perfect, relatively simple, and very uniform in structure throughout the species or group of species represented in the cultivated avocados. The adaptation for cross-pollination is accomplished by physiological regulation. The daily rhythmic alternation of sexes (synchronous dichogamy) for the entire plant and the reciprocation of these changes in certain groups of plants reach a perfection of physiological regulation in avocados that is unapproached, as far as is now known, in any other group of plants.

How synchronous dichogamy is achieved in avocados

The manner in which synchronous dichogamy is accomplished in avocados may be explained by tracing the events in the behavior of the flowers of a single tree throughout an entire day during a period of favorable weather. For this purpose a tree of the Taylor variety (a clonal variety) may be selected.

In the hours of early morning no flowers are open anywhere on the tree but during the early forenoon flowers begin to open here and there in the various clusters of flower buds all over the tree. In the opening of a flower, 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 these stand nearly at right angles to the main axis of the pistil as seen in the open flowers shown in PLATE 24. This leaves the pistil standing erect, alone, conspicuous and fully exposed, with the slightly enlarged end (the stigma) white, fresh and soon

ready to receive pollen. Nectar appears as a glistening film over the surface of the inner set of three nectaries, which stand from between the inner set of stamens. Now bees and other insects seeking nectar can scarcely fail to brush against the stigma of the pistil. 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 this tree of the Taylor variety during this forenoon, one finds that all the flowers are in the same condition as the flower just described. No flowers are shedding pollen. All the flowers have the pistils ready for pollination. The entire tree functions as a female only and this condition continues throughout the entire forenoon.

About midday this set of flowers closes without having shed pollen. In doing this the perianth segments fold inward over the pistil until the flower is completely and tightly closed (see at 3 in PLATES 25 and 26. Thus an entire set of flowers, numbering for a large tree in the maximum of blooming more than a thousand, 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.

During the hours of midday and while the flowers which were open during the forenoon are in the final processes 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. In fact unless individual flowers are tagged for identification in further observation the complete midday shift of sets of flowers would probably not be discovered even under rather close observation. In the only observations on flower behavior in avocados published previously to those of the writer (Nirody, 1922) this shift of sets of flowers was not observed for any of the varieties that have the same daily sequence as the Taylor variety.

The flowers of the set opening for the afternoon are distinctly different in appearance from the set open during the forenoon (see PLATE 25). The stamens are noticeably larger and somewhat longer. The inner three stand erect in the middle of the flower around and overtopping the pistil. The end of the pistil

is frequently dark colored and sometimes it is shriveled and dead. The outer set of six stamens stand at an angle of about 45°. Not long after these flowers are 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 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 (see 4 in PLATES 25 and 26). 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 dry caked mass which then soon falls to the ground.

A careful census of the many flowers open on the Taylor tree during the afternoon will reveal that they are all in the same condition. They all shed pollen, the maximum of shedding being some time during the afternoon. Late in the afternoon these flowers close never to open again.

Thus, during the hours of daylight of a single day, two different sets of flowers open and close on a tree of the Taylor variety. The flowers which are open during the forenoon function only as females, those open during the afternoon function as males.

The differences in these two sets of flowers, and their relations to each other, become clear when the normal life-history or cycle of a single set is traced. The set which is open during the forenoon closes around midday and remains closed during that afternoon, the night following, and the next forenoon. In normal flower-behavior a set of flowers is open for the first or female opening during the forenoon of each day and is open for the

second or male opening on the afternoon of the following day. There are two distinct and separate periods of anthesis, a condition which may be designated as *dianthesis*. Between the two periods of opening the set is closed for an interval of about twenty-four hours and the entire time from the beginning of the first opening to the end of the second opening (the cycle of dianthesis of the set) covers slightly less than thirty-six hours.

The sequence of sets continues regularly under favorable weather conditions and brings two different sets into opening each day. The forenoon set is open for the first or female opening and will open again on the afternoon of the following day to shed pollen. The afternoon set has had the first opening during the forenoon of the day before. Each flower is perfect, it has two distinct periods of being open, it is female during the first opening and male during the second opening. The physiological regulation is seen first in the development of the two sexes in each flower at different times (dichogamy) and second in the coördination of this development among entire sets of flowers so that the dichogamy is synchronous for the tree as a whole.

The two types of daily sequence in the alternation of sexes

A general survey of many seedlings and many named clonal varieties of avocados, including Guatemalan, Mexican, and West Indian types and hybrids between these, growing in California and in Florida, indicates that they may all be grouped into two main classes with respect to the daily changes of sex in the flowers. About half of them behave similarly to the trees of the Taylor variety described above and these may be grouped together and designated as Class *A*. In the other group of seedlings and varieties (Class *B*) the sequence in the daily alternation of two sets of flowers is the *reverse* of that of Class *A*. For these the second-period or male opening of sets of flowers is, normally, in the forenoon, and their first-period or female opening is in the afternoon.

The relative flower behavior of the two groups may be shown by comparing flowers of two varieties such as Taylor and Panchoy.

In 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 photo of PLATE 26). Trees of Panchoy are shedding pollen during the forenoon while the flowers of trees of Taylor are most ready to be pollinated. During midday an alternation or change in sets occurs for each and then *in the afternoon* the flowers 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 (see lower photo of PLATE 26). These two varieties are, therefore, reciprocating in their daily alternations of sex. Taylor is female while Panchoy is male and then while Taylor is male Panchoy is female—all during the hours of a single day.

Extending the observation to trees of other varieties growing side by side one finds that the daily behavior of flowers is either like that of Taylor or similar to that of Panchoy. This is readily revealed when the daily sequence in the flower behavior of a number of varieties (all clonal varieties) is shown diagramatically as in CHART 1. The observations there recorded are for trees growing in the same orchard or in a nearby one and are all for the same day, which was one of a series of warm sunny days on which the flower behavior may be considered as most nearly normal.

It may be stated that in obtaining such records as are shown in the various charts accompanying this report observations were made from tree to tree as quickly as possible, especially during the midday shift of sets. These were checked on squared paper for fifteen-minute intervals. If, for example, flowers were not open on a tree at 8:05 but were open rather abundantly at a next visit at 8:25 the start of opening was credited to 8:15. If at 12:20 first-period flowers were rapidly closing and at 12:40 they were all closed the time of closing was checked for 12:30. Thus in the charts there is rarely an error of 15 minutes, and for the majority of cases the start of opening and the end of closing of sets is given within five minutes of the correct time.

This record (see explanation of chart for symbols used) is typical of that which may be obtained day after day during favorable weather (see also CHARTS 2, 3, and 4). Such records

reveal the general rules of the normal flower-behavior during the hours between sunrise and sunset in a single day.

1. For all varieties there are two different sets of flowers open during the day. The flowers of one set function as females, those of the other as males. Each set opens and closes in unison and the two sets are open during different hours of the day. While there is frequently a short interval of overlap of the two sets during the shift in midday, the rule is that no pollen is shed while flowers in the female condition are open. Pollen is lacking for a time after flowers open for the second period and then it is scant for a time. Later the maximum of pollen shedding is reached after which pollen again becomes increasingly scarce. Unless pollen is carried away by insects the masses of pollen harden and become dried into little balls that fall to the ground. It 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 a line representing their most receptive condition would be much shorter than is shown in the various charts. But considering the entire periods of opening, in every case the synchronous alternation of sex most decidedly limits self- and close-pollination.

2. The varieties fall into two groups which reciprocate with respect to the relative sequence of the daily alternation in the development of the two sexes. The members of one group are female in the forenoon and male in the afternoon while the members of the other group are male in the forenoon and female in the afternoon.

List of the most important varieties according to the daily sequence of dianthesis

A. Varieties that 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	Butler	Challenge	Dickey
Baker	Cantel	Clower	El Presidente
Baldwin	California	Colorado	Family
Benik	Trapp	Dickinson	Gottfried

Grande	Murrietta Green	Richardson	Taft
Hawaii	Murrietta 2 lb.	Sharpless	Taylor
Kanan	Perfecto	Simmonds	Ultimate
Kashlan	Pinelli	Sinaloa	Wagner
Lulu	Popenoe No. 3	Solano	Waldin
Manik	Puebla	Spinks	Wester
Mayapan			

B. Varieties that 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	Fuerte	Mattair	Rey
Butternut	Fulford	McClure	Rolfs (old)
Cabnal	Ganter	McDonald	San Sebastian
Cardinal	Golden, Taft's	Meserve	Schmidt
Champion	Hanson	Montezuma	Stephen's Choice
Colla	Hardee	Nabal	Surprise
Collins	Harmon	Nimlioh	Tertoh
Cook	Ishim	Nimliohson	Trapp
Dorothea	Itzamna	Northrup	Tucker
Eagle Rock	Knight	Nutmeg	Tumin
Earle's Late	Lamat	Panchoy	Verde
El Oro	Linda	Pollock	Walker
Estelle	Lyon	Queen	Winslow
			Winslowson

One or more trees of each of the above-named varieties have been observed in flower by the writer either in California or in Florida. For most varieties observations of normal flower behavior were made for a number of trees and on a number of days. In a few cases the tree or trees studied may have come to the grower wrongly named or the identity may otherwise have been given incorrectly. A tree called El Oro studied in California was *A* in behavior and a tree of this name in Mr. Krome's orchard in Florida was *B*. A tree studied in California under the name Ishkal was *B* in flower behavior; one of this name observed by Mr. T. Ralph Robinson (reported to the writer by letter) at Lucerne Park, Florida, was *A* in flower behavior. The normal daily sequence of sets of flowers is, of course, the same for all trees of any of the clonal varieties of the avocados whether grown in California or in Florida.

The number of varieties having the *A* behavior is nearly equal to the number having *B* behavior. There is no definite evidence regarding the heredity of flower behavior further than the fact that the two main classes *A* and *B* seem to exist in nearly equal numbers.

THE CYCLES OF DIANTHESIS OF THE SETS OF FLOWERS

The entire time from the first opening to the final closing of a flower or of sets of flowers, which includes the two periods of opening and the interval of closing between them, may be called the complete cycle of dianthesis, the flowering cycle, or merely "the cycle" of a flower or of a set of flowers.

The striking difference in the *daily* behavior of the flowers of the two main classes of avocados is that the sequence of the two sets is reversed. This involves and is accomplished by decided differences in the flowering cycle of the sets of flowers with reference to the time of the day when the two periods of anthesis occur and in respect to the length and the time of the interval during which the flowers are closed between the two separate openings. This is revealed by "tagging" some of the flowers and tracing their behavior throughout the following day. This method was used very generally throughout the investigations both in California and in Florida.

The main types of flowering cycles thus revealed for sets of flowers may be shown by the diagrams in CHART 5.

For the *A* varieties (of which Taylor, described above, is typical) daily a set of flowers opens for the first or female opening in the forenoon and then closes about noon to remain closed for 24 hours (until the following afternoon) before opening for the second or male opening. The cycle of a set covers about 36 hours. During the hours of sunlight each day two different sets of flowers are in action. During the hours of darkness one set is in the interval between the two openings (see A in CHART 5).

For all *B* varieties, in normal behavior, daily a set of flowers opens for the first or female opening in the afternoon and closes late in the afternoon. But in respect to the further history of the sets, there is a decided diversity.

For certain *B* varieties the rule is for each set to open for the second time during the next forenoon after an interval of about 12 hours. For such sets the complete cycle is about 24 hours. In this case but *one* set is in some stage of the cycle at a time (see B1 in CHART 5) and it completes its flowering cycle alone and while every other set is inactive. The studies indicate that this behavior is characteristic of certain West Indian varieties of which Trapp may be mentioned as fairly typical. In Florida in 1925 the weather during February and March was unusually warm and the 24-hour cycle was usual for sets of flowers on many of the *B* varieties.

For certain of the *B* varieties, however, sets of flowers opening for the first time in the afternoon may remain closed for two nights and one day (of daylight). The interval between the two openings is 36 hours and the entire cycle covers 48 hours as shown in B 2 of CHART 5. Under such behavior three different sets of flowers, including the set in the interval, are in some stage of action during each period of daylight. During the hours of darkness two different sets are in the interval. In California, throughout nearly all of the period of study in 1923, this was the regular rule of sequence for *B* varieties under observation when there was a normal daily alternation. The nights were, however, much cooler than in Florida. Nothing like the Florida conditions of March 1925 were experienced in California in 1923 where studies were made, until very late in May when the blooming of avocados was mostly over.

On trees of certain varieties the cycle of sets of flowers may shift from 48 to 24 hours, or *vice versa* in response to certain changes in weather. It is to be noted, however, that at times when the 48-hour schedule gives normal daily alternation of two sets for these varieties, certain other varieties of the *B* group, such as Trapp, may be blooming on the 24-hour schedule. None of the tender West Indian varieties which in Florida rather persistently bloom on the 24-hour cycle were available to the writer for study in California.

It was frequently observed, especially of the Harmon and Fuerte varieties, that a single set of flowers opening and closing in unison for the first period will divide into two groups; part of

the flowers will open to shed pollen the next forenoon (interval of 12 hours) and the others will remain closed for an interval of 36 hours (see B 3 in CHART 5). Then, on any given forenoon, part of the flowers of two different sets shed pollen. Those of the older set (of 36-hour interval) begin shedding pollen somewhat the earlier. The three types of behavior (B 1, B 2, and B 3) may all be observed in a single day for different varieties growing side by side in the same grove.

In considering the sequence of complete cycles of sets of flowers, the varieties of the *B* group show the greatest diversity. The simplest sequence seen among avocados is that with the 24-hour cycle and the 12-hour interval (see B 1) and the most complex is in the splitting of single sets into groups having 24-hour and 48-hour cycles.

It would seem that marked changes in the cycles of sets such as are described above must have a profound influence on the ability of flowers to function in fruit-setting entirely independently of pollination.

No attempt is here made to indicate cycles of anthesis during periods when off stride and irregular blooming breaks the normal daily alternation and its regular sequence.

INDIVIDUAL OF VARIETAL DIFFERENCES IN FLOWER BEHAVIOR

The various charts recording normal daily alternation of sets (CHARTS 1–4) reveal that noticeable variations exist among different varieties of each group *A* and *B* regarding the particular hours in the day when the sets of flowers are open.

Thus, for the *A* varieties studied on February 24 (CHART 1), there was a difference of two hours in the time when the different sets of first-period flowers began to open. The length of time these sets were open also varied; for Atlixco the time was from 9:00 A. M. to 2:00 P. M., while for Pinelli the period was from 11:00 A. M. to 2:15 P. M., a difference of nearly two hours.

Even more marked differences are seen for the sets of first-period flowers among varieties of the *B* group. For some varieties, such as Queen and Meserve, the first-period flowers begin to open early in the afternoon, for others this set starts to open late in the afternoon.

Similar differences exist in the performance of sets open for the second period. As a rule the periods for the two sets normally opening on any one day are closely coördinated in sequence, especially for *A* varieties. But in the *B* varieties the sets of second-period flowers are rather uniform throughout as to their hours of shedding pollen, while marked differences exist as to the sets of firsts. Thus, for example, the seconds on Meserve and Trapp (CHART 1) act quite alike but their sets of firsts for the same day behave very different as to time of opening.

Thus, for some varieties and particularly the *A* varieties, there is normally a short *period of overlap* or a time when one set is closing and another set is opening. A period of overlap (for a reverse order of sequence) exists for some of the *B* varieties but for several of these, Pollock, Hardee, Trapp, Estelle, and Taft's Golden, there is normally no overlap but a decided *lapse between openings.* After the set of seconds which is open in the forenoon is fully closed, there is a period of as long as three hours before the day's set of firsts starts to open during which no flowers are open. Nirody (1922) observed and reported this condition for the varieties Fuerte, Linda, Pollock, Queen, Trapp, and McDonald, and for all but the last named he noted that the flowers which open late in the afternoon are from "fresh buds" and that they close for the night without shedding pollen. Evidently Nirody considered that this was merely a closing for the night, which in these varieties is indeed the case. In none of the *A* varieties did he discover the closing of sets of first-period flowers at midday and he considered that for these the same flowers were open throughout the day for only one continuous opening.

In the various charts (1 to 4) the records are arranged with the varieties listed in order according to the time when the first-period flowers start to open. This arrangement brings out the differences that exist among varieties as to the precise time in the same day when the two sets are open, and as to the extent and the particular time of the period of overlap and of the period of lapse between sets.

A comparison of the charts for different days shows clearly that these relative differences are rather constant characteristics

of varieties. The varieties standing first or last in the two groups of *A* and *B* remain thus day after day with decided uniformity.

Irregular and abnormal flower-behavior

The particular behavior of sets of avocado flowers, as to precise time of opening, duration of the opening, period of overlap and lapse between sets, 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.

When the temperatures tend to be low the hours of opening are comparatively late in the day (CHART 3). With higher day and night temperatures and with increasing hours of daylight the hours are earlier (see CHART 4). Thus the "clock" hours for opening tend to be later during the earlier part of the season of bloom (January and February) and earlier in the day during April and May. This general trend to earlier hours is shown when the daily performance of a single variety is charted for an entire season of bloom (see CHART 9).

A change to a lower temperature at night will frequently result in the differences recorded in CHARTS 3 and 4. Here the relative behavior of the two sets of flowers for each variety, the relative behavior for different varieties as such, and the relative performance of the *A* and of most of the *B* groups remain quite uniform. The hours of opening for all merely shift to later clock hours.

With an increasing severity of changes in temperature, flower behavior becomes correspondingly more abnormal until the daily sequence of sets is thrown out of stride and the flowers belonging to one or more sets respond with marked irregularity.

Even under slight lowering of temperatures, for such varieties as Trapp and Taft's Golden, the first or female opening may be omitted by an entire set or a part of a set (see in CHART 3). Such flowers really open but once. They may then shed no pollen at all, they may shed pollen poorly, or they may shed pollen freely and quite fully, depending on conditions of weather.

The first anthesis of sets of flowers may be delayed from forenoon to afternoon (in *A* varieties) and from afternoon to the fol-

lowing forenoon (in *B* varieties) and the second opening of the sets following may be correspondingly delayed. On days when this occurs there will be a very general and complete reversal in the *daily* alternation normal to the varieties (see record for May 17 in CHART 8). Flowers in the first period of opening may be held in this condition for some time, even continuing thus over night from one day to another.

Sets of flowers subjected to sudden lower temperatures while in the interval exhibit irregular behavior in the second opening. This may be delayed, prolonged, or even omitted. The various flowers of a single set may behave quite differently.

A decided change from a period of cold inclement weather, during which there was much delay in the opening of sets of flowers, to warmer weather favorable to normal flower-behavior sometimes brings three different sets of flowers into opening between sunrise and sunset (see record for May 19 in CHART 8).

In response to decided changes in temperature the blooming of all varieties is thrown off-stride and marked irregularities appear in nearly every aspect of flower behavior. The records of CHARTS 6 and 7 (see explanation with charts) are fairly typical of such behavior.

Comparing the season of bloom of 1925 in Florida with that of 1923 in California for the orchards in which the writer made observations, it can be said that in California there were many more days of irregular behavior.

Varieties differ in the degree and the type of irregularity which they exhibit. The observations both in California and Florida indicate that the varieties of the *B* class exhibit the greatest irregularity and off-stride behavior under unfavorable weather conditions. Weather which merely delays the opening of the two sets on varieties of the *A* group will often cause various varieties of the *B* group to continue a set of firsts open over night and into the next day, or to skip a set of firsts, or to have them open for a period during the night. See especially the records here given for March 4 and 5 in CHART 6.

Frequently during irregular and off-stride blooming there is an overlapping of different sets and first-period flowers may be open at the time second-period flowers are shedding pollen.

There is then an opportunity for close-pollination. When a set of flowers skips the first period and has a single opening during which pollen is shed, there would seem to be opportunity for self-fertilization of individual flowers provided the pistils have remained receptive to the pollen. There is, however, some question as to what extent off-stride flowers can function in fertilization and fruit-setting.

The variations in blooming due to influences of weather and the time of the season no doubt have an effect on pollination relations and on the efficiency of pollinations in the setting of fruit. Growers frequently state that often the fruit borne by avocados is set late in the period of bloom.

The regulation of the flower mechanism

It seems evident that the principal external stimuli affecting the flower mechanism of avocados are light and temperature. The rule is that during normal action the flowers are open only during the hours of daylight. Changes in temperature, however, produce marked irregularities in the action of the flowers irrespective of light.

The influence of low temperatures was tested by submitting branches with flowers to the cool temperatures of an ice-box. Under such treatment flowers that were fully open remained thus for hours after flowers of the same set left on the trees had closed. Meanwhile flowers in the interval between the two openings remained closed while those of the same set left on the tree opened normally. Low temperatures seem to inhibit changes in flowers as may be expected from the observations on off-stride and irregular behavior.

Clusters of flowers were placed in an ice-box during the mid-day shift of sets when first-period flowers were in process of closing and when second-period flowers were about halfway open. In several instances the action of these two sets was stopped and reversed. The first-period flowers returned to the condition of being widely open and the second-period flowers returned to the fully closed condition. An extension of such studies would no doubt reveal much regarding the influence of

temperature on the flower mechanism and the time relations of the reactions.

It would appear from observing the action of the flowers that the movements of the parts involve chiefly changes in turgor with perhaps some actual growth of certain parts. The coördinated action of sets of flowers does not necessarily imply that there is a regulation by internal stimuli. It may only involve an identity in the constitution and condition of the many flowers which mature in each set. But in the repeated synchronous maturity of sets there would seem to be a very fundamental coördination in the growth and development of flowers throughout the entire plant.

Each flower normally exhibits two different actions. The mechanism of the first opening and the mechanism of the second opening operate under different external stimuli. The same stamens which reflex strongly in the first anthesis stand nearly erect in the second anthesis, but in the interval between they grow noticeably. The same segments of the perianth open and close in quite the same manner in both openings but they reflex more strongly and for most varieties close more tightly in the first opening. The pistil evidently usually matures during the period of the first opening, which is when the inner set of nectaries excrete nectar. The outer set of nectaries functions at the time pollen is shed. The two sets of nectaries are, however, quite different in appearance. Those of the inner set resemble aborted stamens; those of the outer set are shorter and more rounded and dome-shaped.

In both groups of varieties (*A* and *B*), the flowers are apparently identical in general morphology and in the mechanism of each of the two openings. Yet the conditions of light, temperature, and humidity of the forenoon or of the preceding hours bring into simultaneous opening first-period flowers on *A* varieties and second-period flowers on *B* varieties and the midday brings a shift of sets in each in the reverse order. Such decided and specific differences in action can only be due to differences in the inherent constitution of the two groups of varieties.

Evidence bearing on the evolution of dianthesis and synchronous dichogamy in avocados

The flower behavior of avocados exhibits an advance in development beyond the dichogamy generally seen in other plants in at least three important particulars.

First there is a definite and pronounced interval between two distinct openings of each flower. Except for general periodic closing such as night closings, the dichogamous flowers of other species (as far as known) have one continuous period of opening and the flowers have what amounts to a single opening.

This is closely approached or perhaps realized in certain of the *B* varieties which have the shortest cycle in the action of sets of flowers (see CHART 5) and in which the interval of closing is for one night only. From this rather simple and short cycle the complexity increases to cycles having longer intervals, giving flowering cycles of 36 hours and 48 hours.

Furthermore, certain changes in temperature may cause flowers or sets of flowers to skip the first opening and to open only for a single opening. And the varieties with the shortest interval are most liable to behave thus. All this may be taken as evidence that the extended cycle of the avocado flower with its two periods of opening has evolved from a simpler cycle of only one anthesis. A study of flower behavior in the close relatives of the avocados may reveal evidence on this matter.

So far as is known, in other plants dichogamy is not exclusively synchronous for the entire plant. For certain species having monoecious flowers, there is a tendency for female flowers to ripen before the male flowers, giving somewhat of a seasonal alternation in the sex of the entire plant. In pecans, for example (see Bulletin No. 124, Georgia Experiment Station, by H. P. Stuckey) this condition is so fully developed for certain clonal varieties that they are decidedly self-fruitless. But for plants with perfect but dichogamous flowers the rule is that some flowers will be shedding pollen while others are ready for pollination. Unless there be but one flower open at a time there is chance for close-pollination. For avocados this condition is frequently seen when there is overlap of sets during off-stride

and irregular behavior. The ease with which this occurs may indicate that this was the general condition from which evolved the perfection in the daily and synchronous alternation of sexes now seen in avocados.

In avocados the climax in the adaptation of dichogamy for cross-pollination is seen in the reciprocation of the daily sequence. Nothing approaching this condition is known for any other group of plants. There are two classes of individuals, apparently nearly equal in number, and the daily sequence of one is the reverse of the other. This indicates an inherent organization with hereditary values and determination.

But the precise behavior is far from uniform among the individuals of either group. In respect to time of the opening of flowers, the duration of the periods of opening, the length of the interval and the period of overlap, there are wide differences characteristic of individual seedlings and clonal varieties.

When the behavior of varieties is arranged in sequence for the time of first opening there are many gradations from the earliest of the *A* varieties to the latest of the *B* varieties (see CHARTS 1 to 4). The hereditary basis involved in the differentiation of the two groups can scarcely be considered as due to a few simple units of uniform value and as achieved in one step by a single change in heredity.

The male sterility of the Collinson variety[1]

The Collinson variety is an exception among cultivated varieties of avocados in that it is completely sterile as a pollen parent. The flowers have two periods of opening and the second opening is normally in the afternoon but the anthers remain closed and no pollen is shed (see in PLATE 27). Sections properly prepared for microscopic study reveal that the stamens are mere masses of sterile tissue.

The writer has made observations on the flowers of the original tree of the Collinson (a seedling from open-pollinated fruit collected at the Miami Station for Plant Introduction), of

[1] The writer did not see any trees of this variety in California. The facts regarding the male sterility of Collinson were first determined in 1925 through the joint observations of Mr. E. M. Savage and the writer.

some of the first trees propagated from its buds, and on about thirty Collinson trees of blooming age in grove plantings. For some of these trees observations were continued day after day over a period of more than two weeks. In two instances a single anther valve was found lifted but no pollen was present.

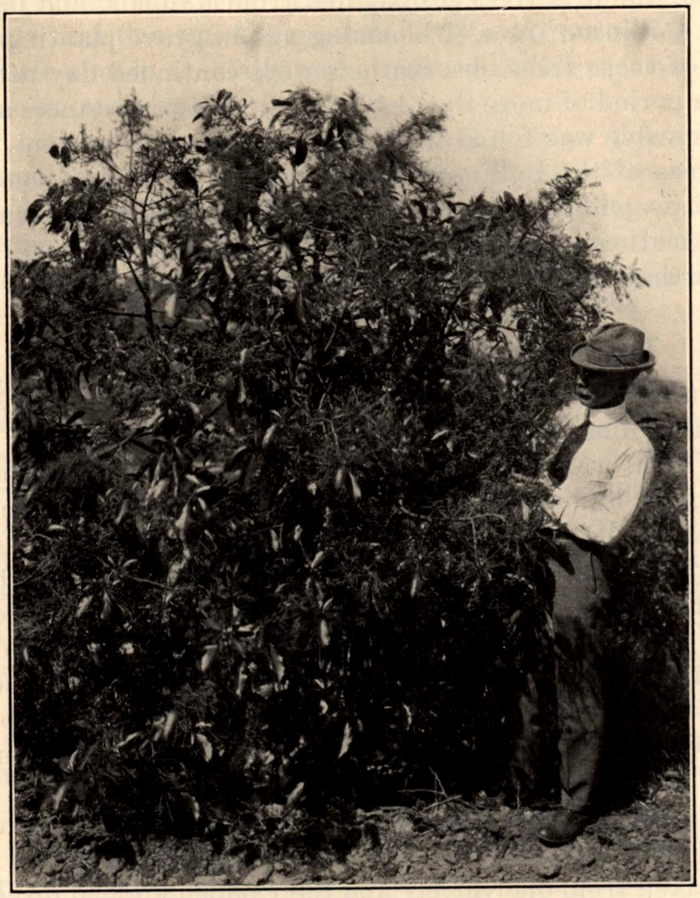
Trees of the Collinson variety appear to be completely impotent as pollen parents. Their flowers shed no pollen. The fruits maturing on them are all the results of cross-pollination unless they develop without any pollination.

The results of pollinations made by hand

Fruit is not readily obtained on avocados even by the most careful pollinations made by hand.

In California several thousand self- and close-pollinations were made by hand and in Florida several hundred were made. The self-pollinations were necessarily for flowers shedding pollen either in their second period of opening or when the first period had been skipped. The close-pollinations were, of course, made at times when there was an overlap of first-period and second-period flowers on the same tree. These are precisely the kind of pollinations possible when a tree is grown in isolation, or is tented, or when a solid block of one variety is grown. Not one of the flowers thus pollinated set a fruit.

But relatively few cross-pollinations succeed. In making such pollinations flowers which were in the height of shedding pollen were taken from one variety and their pollen applied directly by rubbing the pollen masses over the stigmas of flowers of another variety open for the first time. These are the pollinations which flower behavior indicates are most likely to be most proper. With the assistance of various students of Pomona College and particularly of Mr. Howard Lorbeer, the writer made 3,430 such pollinations in California. These involved chiefly the varieties Dickinson, Puebla, and Taft of the *A* varieties and Fuerte, Harmon, and Northrop of the *B* varieties. In February 500 of these pollinations were made, in March 1,280, in April 885 and in May 765. Most of them were made while there was much delayed action in flower behavior and while very little fruit was setting



EXPLANATION OF TEXT FIGURE 1

Many varieties of avocados bloom so profusely that a small tree, such as of the Dickinson variety here shown, will produce many thousands of flowers. Day after day sets of flowers come into bloom. It is a physical impossibility for the tree to hold and mature fruits for even one per cent. of all the flowers. But for most varieties few fruits set even where insects may visit the flowers abundantly. One may make careful cross-pollinations only to have most of the flowers fall promptly. Possibly many of the flowers, especially when in off-stride or irregular action, are unable to yield fruits to any sort of pollination. In the end there may be few or even no fruits on the tree.

From the flower behavior of avocados it is clear that there is a decided adaptation for reciprocal cross-pollination between certain varieties. An increase in proper cross-pollination is liable to give increased yields of fruit.

in the orchards. On June 8th at the last census which the writer was able to make, a total of 173 fruits were setting and some of them were nearly an inch in diameter. A heavy wind storm during the summer stripped most of the fruit from the orchard of Mr. Thomas Sheddon in which many of the fruits were. The pollinations were chiefly made in six rather widely separated orchards and the writer was unable to secure data as to the number of fruits that did mature. On June 8th fruit was developing to 5 per cent. of the flowers cross-pollinated.

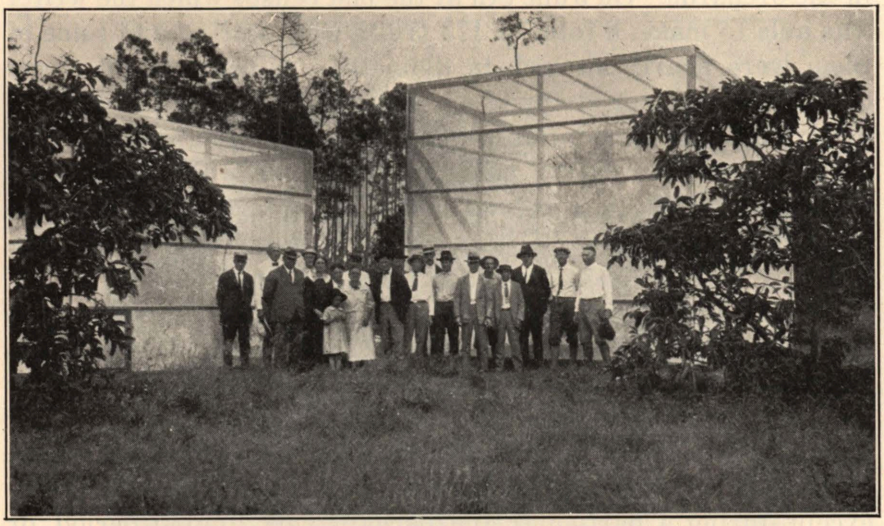
The results of the hand pollinations clearly indicate that the relations of pollination to fruit setting are not readily to be determined for avocados by hand pollinations as they may be for many other types of plants. The percentages of sets thus far obtained by this method are too low to be of much significance. Either the pistils, or pollen, or both can not be used with success except during a particular and perhaps very limited period, or the pollinations are not made in the way necessary to success, or it may be *that a large majority of the flowers produced are not able to set and mature fruit to any kind of pollination!*

Fruit-setting by tented trees with bees enclosed

The extent to which avocado trees are able to produce fruit without cross-pollination may, it would seem, be determined by enclosing an entire tree in a cheesecloth house or tent during the entire period of flowering and supplying a hive of bees to make the pollinations. This was done during the season of 1925 in the orchard of Mr. W. J. Krome at Homestead, Florida. The data on the fruit setting were secured by Mr. Savage after the writer had left Florida.

A tree of each of the varieties Linda, Panchoy, Taft, and Trapp were tented. The selection of these particular varieties was fortunate in that it allowed tests for several different types of flower behavior.

On May 29th, about eight weeks after the close of the blooming season the Taft tree which had been tented had seven fruits. Two other Taft trees of about the same size standing close by and subjected to open orchard pollination bore 44 and 68 fruits



EXPLANATION OF TEXT FIGURE 2

In the tenting experiments entire trees were enclosed in a cheesecloth tent throughout the period of bloom. The strips of cheesecloth were overlapped and nailed under laths to a frame so insects could neither leave the tent nor enter from without. A hive of bees was placed within each tent. The bees worked among the flowers most industriously on most days throughout the entire period of flowering. Under the forced insect pollination each of the four trees tented did mature some fruit. The largest number of fruits for any tree was 22. The results indicate that trees of these varieties are not able to yield full crops to self-pollination only.

respectively. The Panchoy tree which had been tented bore two fruits, while the one other tree of this variety in the same grove bore 12 fruits. The tented tree of Linda had 22 fruits while nine other trees of this variety no larger than the tented tree subjected to open orchard pollination had fruit as follows: 23, 30, 41, 55, 56, 62, 64, 88, and 138. The tree of the Trapp variety bore 18 fruits. On nine other trees of this variety, quite similar in size and standing in the vicinity of the tented tree, there were fruit as follows: 3, 6, 7, 8, 12, 12, 23, 24, and 64.

Each of the tented trees did set some fruit. The yields were low for Panchoy and Taft. The tented tree of Trapp seemed to do as well as about half of the trees of the variety around it. The highest yield on a tented tree, 22 for the Linda, was decidedly lower than that of other trees of this variety.

It should be noted that the tented trees received a highly forced pollination. Day after day the bees worked most industriously among the flowers. On most days every flower was probably visited many times. Obviously flowers in the second opening had pollen liberally distributed over the pistils as soon as pollen was shed. Whenever there was an overlap the pistils of flowers in the first opening had an excellent chance to be close-pollinated not once as in hand pollinations, but many times. For Linda and Panchoy second-period flowers normally shed pollen in the forenoon and possibly bees may have carried pollen on their bodies from late forenoon until the time in the afternoon when first-period flowers were open. For the Taft there would be no such chance as this but only direct and almost immediate self-pollination of second-period flowers or of close-pollination when there was overlap, which the season's record (CHART 9) shows rarely occurred in 1925.

For the Trapp with its first-period flowers opening late in the afternoon (see CHARTS 3, 4, and 10) it would seem that the best chance for fruit-setting when tented would be to self-pollination of flowers that had opened late on the afternoon of the previous day or had skipped this period of opening as is frequent for the variety.

It would seem also from flower behavior that there is very little opportunity for the first-period flowers of Trapp to be cross-pollinated. They open so late that there is scarcely any pollen available from *A* varieties. On account of this the chances for fruit-setting in the Trapp may be fully as good for a tented tree as for trees in the orchard, or even much better when the tented tree is given a hive of bees.

On the basis of flower behavior one might predict that the flowers of Taft with their 36-hour cycle (*A* in CHART 5) and scarcely any overlap (see CHART 9) would set very few fruits without cross-pollination and also that Trapp with a short cycle and frequent skipping of the first opening would be most liable to set fruit to self-pollination accomplished during the second period of flower opening.

There is no question that the flowers of the tented trees received bee visitations far in excess of what flowers of any

orchard tree is likely ever to receive. If trees of these varieties readily set fruit without cross-pollination, the tented trees should have borne heavy crops.

Here the comparisons of yields are between tented trees with abundant and almost complete enforced self- and close-pollination and trees submitted to open pollination. Honey bees were not kept in the vicinity of Mr. Krome's orchard and they were rarely seen in it. The orchard pollination was accomplished by wild insects and chiefly, it would appear, by certain flies and wasps. Proper cross-pollination between *A* and *B* varieties may have been frequent or scant. For an adequate comparison, the results obtained for tented trees should be checked against those obtained when there is repeated and abundant cross-pollination between varieties reciprocating in flower behavior. No such data were obtained and such data would be difficult to obtain. Even when two trees of different and reciprocating varieties are enclosed in one tent, *individual bees* may not freely make the cross-visitations necessary to proper pollination. Further matters concerning the relations of insects to pollination of avocados has been discussed in considerable detail elsewhere (Stout, 1924 c, and 1925).

Some results of tenting experiments with avocados conducted at Point Loma, California (Clark, 1923, 1924), indicate that under certain conditions some varieties may set considerable fruit or perhaps yield good crops to enforced self- and close-pollination by bees. The daily sequence of blooming reported for Point Loma by Clark as "usual" for Fuerte and Spinks is the irregular and off-stride and exactly the reverse of the normal for these varieties. Possibly at the Point Loma location proximity to the ocean may very generally give an off-stride blooming that may somewhat favor fruit-setting to self- and close-pollination.

A few varieties of avocados will frequently set fruits for nearly every flower. They will do this when the flowers are enclosed in a paper bag so that all cross-pollination is impossible and all insects visitations are prevented. As many of these fruits apparently contain no embryos, they evidently set without pollination and fertilization. Usually these fruits soon fall. In

some varieties, however, seedless fruits frequently develop to maturity on the trees. It seems highly probable that when fruits do set in abundance many start to develop without proper pollination and that the fruits that do remain to maturity and develop to proper size are those whose embryos are the products of most proper pollination and fertilization.

There is little direct evidence, experimental or otherwise, as to the exact kind of pollination which is responsible for the fruit that does mature on avocado trees. There is a long period of bloom with a large number of flowers open day after day. A very low percentage of the flowers mature fruit or in most cases even set fruit. The percentage still remains low when one makes most careful hand pollinations, so this method has thus far given no very conclusive data. Possibly, when flowers are fully functional and insects are working most effectively, a few insects make all the pollinations responsible for a full crop in a few minutes, but what these conditions are and when they occur remain to be determined. It is most probable that these conditions are different for different varieties.

Remarks on the interplanting of avocados

It is obvious that the flower behavior of avocados greatly limits the chances for proper self- and close-pollination. If a tree stands alone with no tree of *another* and *reciprocating* variety within insect range, there is little chance that many of the flowers will be pollinated at the proper time.

As avocados are propagated vegetatively, the varieties are all clonal varieties. The many trees of the variety are merely branches derived from one original seedling and when standing together they daily exhibit the same action of flowers. There is no question but that the proper interplanting of different varieties of avocados on the basis of their relative flower-behavior will greatly increase the chances for proper pollination and thereby make possible more abundant and more uniform yields of fruit.

It has been noted that certain avocado trees grown in apparent isolation may yield fair crops of fruit. But it is also well known that many such trees have borne few or even no fruits

year after year when all conditions, except opportunity for cross-pollination, were highly favorable to fruit production. Varieties like Harmon, Taft, and Fuerte have very generally been shy bearers when grown alone or in solid blocks. Yet the Trapp is one variety that has the reputation of being a rather consistent bearer. Differences among varieties in ability to produce fruit to pollination within the variety are to be expected from the marked differences seen in flower behavior. Local conditions of weather may decidedly affect fruit-setting through influencing flower behavior and this may vary considerably in different years. But the general experience has been that for most varieties yields of fruit are frequently low whenever trees of one variety are planted in solid blocks.

The sole aim in interplanting avocados is to increase the yields of fruit beyond that obtained or possible in solid block plantings of single varieties. It can do this only to the extent that it corrects faulty or inadequate pollination and to accomplish this at least three conditions must be satisfied.[3]

1. The interplanting must provide opportunity for an increase in the number of proper pollinations that are possible. This opportunity is provided for when trees that are normally female in the morning are interplanted with trees that are male in the forenoon, provided, of course, that they bloom together for a considerable span of calendar dates. A further selection may be necessary in those cases in which the daily periods are characteristically early or late (see CHARTS 1–4).

2. Means for effecting pollination must be provided and must be in operation year after year. Insects are without doubt the natural agents for the pollination of avocados. Honey bees are fond of avocado nectar, they freely visit the flowers during both periods of their opening, and when their hives are in the vicinity of avocado trees they are frequently seen in great numbers working among avocado flowers. But for an insect to effect cross-pollination it must repeatedly fly back and forth from one variety whose flowers are shedding pollen to another whose

[3] A more complete discussion of interplanting has previously been printed (Stout, 1925) and also reprinted in a later paper (Stout and Savage, 1925). This matter will therefore only be briefly summarized here.

flowers are in the first or female opening. Observations indicate that individual honey bees may not do this freely.

3. The pollinations when made must result in fertilization if there is to be setting of fruit. There seems to be some evidence from field plantings which suggests that certain varieties cross-fertilize more readily than others but whether this involves merely increased cross-pollinations or affinities in fertilization is not now known.

At the present time there is no rule of thumb for the interplanting of avocados that will insure unqualified success. On the basis of flower behavior alone, the orchardist makes no mistake to interplant every variety and to choose one or more pairs for the interplanting whose reciprocating flower behavior provides chances for abundant cross-pollination.

Any interplanting on this basis is better than none at all. The grower may not immediately hit upon the best combination which (1) provides the best opportunity for abundant cross-pollination, (2) encourages and facilitates cross-visitations by insects, and (3) involves strong affinities in fertilization, but he will be no worse off than if solid blocks are planted and he stands a good chance to increase fruit production.

It is to be emphasized that interplanting aims only to correct fruitlessness that is due to faulty or inadequate pollination. The many environmental and cultural conditions that affect or determine production of fruit must be met. They exist quite apart from, independently of, and in addition to the problems of proper pollination and they very frequently limit production of fruit when all the conditions for proper pollination are fully satisfied.

While environmental conditions and cultural treatment greatly influence the holding and the maturing of fruit, the setting of fruits most likely to mature depends without a doubt on proper pollination. That an increase in proper pollinations is to be accomplished through cross-pollination is obvious. That this is to be promoted through proper interplanting with consideration of flower behavior is also fully obvious.

Acknowledgment

This is a report of investigations which the writer made in California in 1923 and in Florida in 1925. The studies in California were made under the auspices of Pomona College and in coöperation with the officers and various members of the California Avocado Association. Those in Florida were conducted under the auspices and with the financial support of The New York Botanical Garden and the Farm Bureau of Dade County, Florida. This coöperation was accomplished chiefly through the keen interest of Mr. T. Ralph Robinson of the Bureau of Plant Industry, of Mr. Wm. J. Krome, of Homestead, Florida, in whose orchards most of the studies were made, and of Mr. J. S. Rainey, County Agent of Dade County. During most of the period of study in Florida Mr. E. M. Savage of the Bureau of Plant Industry participated in the investigations as did also Mr. T. Ralph Robinson for a part of the time. The writer is pleased to acknowledge the assistance and coöperation rendered by all these persons and also by other officers and members of the Florida and the California Avocado associations not here mentioned by name.

In this report the aim is to present in one paper the most important facts thus far determined regarding flower behavior in avocados, together with more ample illustration by photographs and charts than has hitherto been possible. While this report includes many new data obtained in Florida for varieties not available in California, there is necessarily some repetition from papers previously published. But for the most part these papers are in publications not readily available in botanical libraries.

Literature Bearing on Flower Behavior of Avocados

Clark, Orange I., 1923. Avocado pollination and bees. Ann. Rep. Calif. Avocado Association, **1922–1923**: 57–62.

————, 1924. Avocado pollination tests. Ann. Rep. Calif. Avocado Association, **1923–1924**: 16–22.

Nirody, B. S., 1922. Investigations in avocado breeding. Ann. Rep. , Calif. Avocado Association, **1921–1922**: 65–78.

Stout, A. B., 1923, a. Avocado studies: pollination and setting of fruit. Farm and Tractor Section, Los Angeles Sunday Times, April 29, 1923. Reprinted in The Florida Grower, Jan. 24, 1925.

————, 1923, b. Pollination of avocados. California Cultivator **61**: 522.
————, 1923, c. Clocking the avocado. A study in cross-pollination. Farm and Tractor Section, Los Angeles Sunday Times, July 8, 1923.
————, 1923, d. A study in cross-pollination of avocados in southern California. Ann. Rep. Calif. Avocado Association, **1922–1923**: 29–45. Contrib. N. Y. Bot. Gard. no. 251.
————, 1924, a. Sightseeing among avocado flowers. Calif. Cultivator **62**: 3 and 15.
————, 1924, b. The flower mechanism of avocados with reference to pollination and the production of fruit. Jour. N. Y. Bot. Gard. **25**: 1–9.
————, 1924, c. Consider an avocado fruit. Calif. Cultivator **62**: 256.
————, 1924, d. Comments on avocados. Calif. Cultivator **62**: 324–325.
————, 1924, e. Let the bees do the work. Calif. Cultivator **62**: 392.
————, 1925. On interplanting avocados. Calif. Cultivator **63**: 264.
Stout, A. B., and **Savage, E. M.**, 1925. The flower behavior of avocados with special reference to interplanting. Proc. Florida Hort. Soc. **1925**: 80–89.

Note. After this volume of the Memoirs of The New York Botanical Garden was fully paged by the printers, a publication "Pollination of the Avocado," Department Circular 387 of the U. S. Department of Agriculture, by T. Ralph Robinson and E. M. Savage, was received (October 26, 1926.)—A. B. Stout.

EXPLANATION OF PLATE 24

During normal flower-behavior each avocado flower opens for two different periods. The appearance during the *first* anthesis is shown here (enlarged about 2 times). The stamens do not shed pollen but stand away from the pistil, leaving it exposed and in a position to be pollinated. As shown in the insert, the stigmatic end of the pistil is white and evidently in a condition for pollination. The shape and size of the stigma differ for different varieties and its structure is rather intricate and delicate. During this first opening the flower functions only as a female.

The flowers here shown are of the Taylor variety and the picture was taken at 10:00 A. M. In this variety a set of flowers is open in the first or female opening for several hours each forenoon. These flowers close during midday and open for the second or male opening during the afternoon of the following day.

The male and female organs in each flower develop at different times (a condition known as dichogamy). This limits or prevents self-pollination of individual flowers.

At *a* is shown a pistil with fresh stigmatic surface as it appears in the first anthesis.

STOUT: THE FLOWER BEHAVIOR IN AVOCADOS

COCKAYNE BOSTON

EXPLANATION OF PLATE 25

In the second or male anthesis, avocado flowers are as shown here. The contrast to their appearance in the first opening is marked (compare with PLATE 24). Now the stamens are larger and they are more erect. Part of them stand above and closely about the pistil, which is often discolored and shriveled, as shown in the upper insert. During the second opening pollen is shed by uplifted valves shown here and in the lower insert. In its second opening the flower functions as a male.

The principal stages in the cycle of dianthesis typical of each flower of any avocado tree may be traced in the PLATES 25 and 26 as follows:

No. 1. Flower bud not yet old enough to open.

No. 2. Flower in the first or female opening.

No. 3. Flowers that have been open for the first period and are now closed in the interval before it is time to open for their second period.

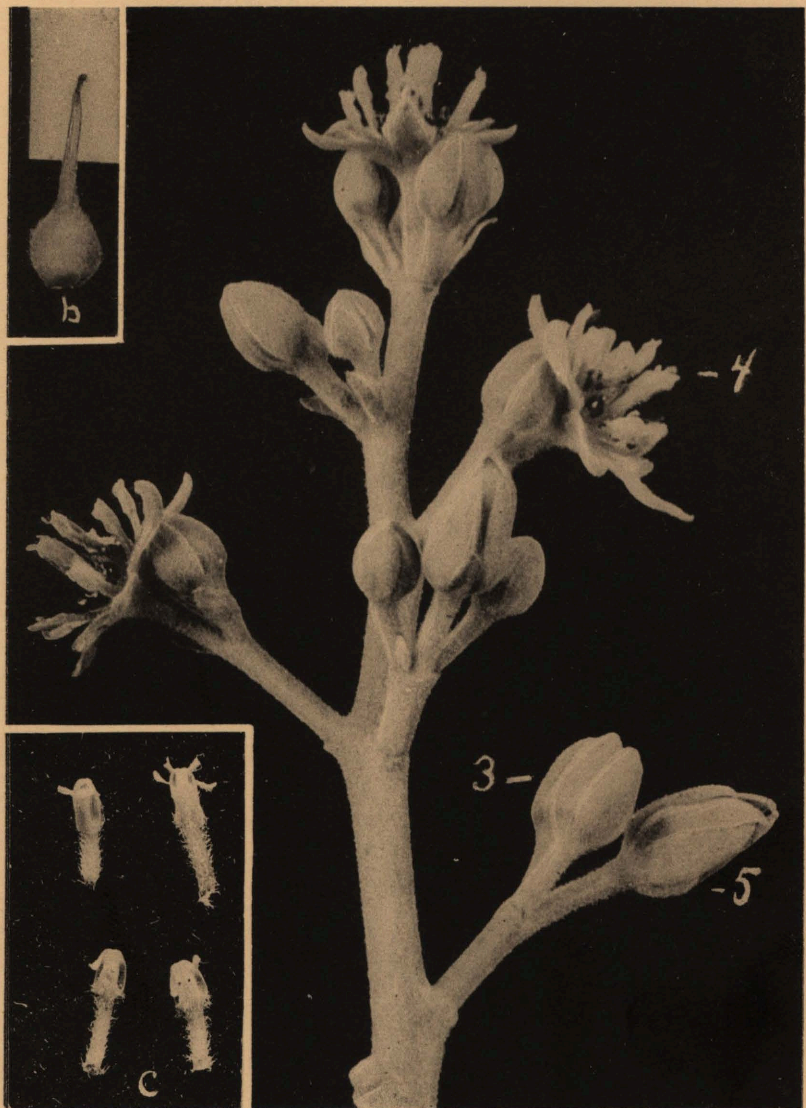
No. 4. Flowers open for the second or male opening.

No. 5. Flowers closed after the second opening. The cycle of flower behavior is complete.

The flowers (except the inserts) here shown are of the Taylor variety and the picture was taken at 3:00 P. M. In this variety normally all the flowers open in the afternoon are those open for the second time. The entire tree functions only as a male in the afternoon. The dichogamy is synchronous. This condition greatly limits or even prevents pollination between flowers of the same tree or of trees of the same clonal variety.

At *b* is shown a pistil at the time of the second anthesis, exhibiting the dead and shriveled tip as it frequently appears at this time.

At *c* are shown several stamens with uplifted valves on which pollen is exposed.



STOUT: THE FLOWER BEHAVIOR IN AVOCADOS

EXPLANATION OF PLATE 26

The reciprocal alternations in the development of sexes as they normally occur each day in the two main groups of avocados are here well shown.

Flowers of Taylor, typical of the *A* varieties, are shown at the right. Flowers of Panchoy, representative of the *B* varieties, are shown at the left. The upper photo is typical for the forenoon, the lower typical for the afternoon. In each photo the two branches were photographed together at the same moment.

In the forenoon, on trees of Panchoy, only flowers in the second or male opening are open and on trees of Taylor only flowers in the first or female opening are open. During midday a shift of sets occurs in each and then in the afternoon the trees of Taylor become male while those of Panchoy become female.

The daily sequence of sets of flowers for Taylor is the reverse of that for Panchoy. In general and under normal flower action the daily sequence of sexes in avocados is either as here shown for Panchoy or as for Taylor. The reciprocating alternations of sex provide for cross-pollination between members of the two groups.

STOUT: THE FLOWER BEHAVIOR IN AVOCADOS

COCKAYNE BOSTON

EXPLANATION OF PLATE 27

Upper photo. Flowers of the Trapp variety for which the normal cycle of dianthesis of each flower and the daily sequence of sets are as follows:

A set of flowers begins to open for the first time late in the afternoon —usually not earlier than 3:00 P. M. Then they appear as shown at 2′ on the branch at the left. An hour or so later the flowers are as seen at 2 on the branch in the middle. These flowers close during the night and then the same flowers open for their second or male opening the following forenoon, when they are as at 4 on branch to the right. Only one set of flowers is in action at a time and there is no overlap of sets with opportunity for close-pollination. The opening for the first time late in the afternoon almost prohibits cross-pollination from any of the *A* varieties (see CHARTS 1 to 4) throughout most of the blooming season. But the cycle of sets of flowers is much shorter than that of *A* varieties and of some *B* varieties (see B 1, CHART 5) so it seems highly probable that fruit may set on Trapp to self-pollination while flowers are shedding pollen.

Lower photo. The flowers of the Collinson variety have two periods of opening quite as in other varieties. Stamens are present but they shed no pollen.

At the left is a flowering branch of this variety with four flowers fully open for the second opening. At the right is shown somewhat enlarged a flower of Collinson (left) by the side of a second-period flower of Taylor (right) as the two appear in the afternoon. The uplifted valves carrying out pollen may be seen as finger-like projections from anthers of the Taylor flower. No such valves open from anthers of flowers of Collinson. The anthers remain intact and studies of their structure show them to be merely masses of sterile tissue. The Collinson variety is male sterile.

STOUT: THE FLOWER BEHAVIOR IN AVOCADOS

COCKAYNE BOSTON

EXPLANATION OF PLATE 28

1. During irregular flower-behavior, flowers are frequently shedding pollen (flower at lower left) while others on the same branch are open for the first or female opening (see flowers at apex of branch). Then there is chance for close-pollination. Such pollinations do not necessarily insure setting of fruit.

2. For some varieties fruits often start to mature to nearly every flower, but most of these fruits soon fall and at the harvest the crop may be scant. This condition has led many growers of avocados to believe that the main problem in avocado growing is to provide cultural conditions which enable trees to hold and mature fruit. This may often be the case. The flower behavior of these varieties is *A* or *B* as for other varieties and is as fully dichogamous. In certain tests, the fruits set when the flowers had been enclosed in bags. Further tests are needed to determine if in these varieties fruit will start to develop without pollination or with only self-pollination and whether adequate yields may be had without cross-pollination.

3 and 4. The flowers of avocados are borne on lateral branches. After yielding flowers for a time, the main axis may produce a few leaves and then resume flowering, as shown here. When the flowering period is over, nearly always an end bud emerges as a vegetative bud, as shown at 4. The fruit therefore hangs from main stems which are leafy at their tips.

The cluster of flowering branches may continue to bloom for several weeks or even months. If as many as two fruits mature in each cluster, the tree bears a large crop. An increase in the number of flowers that are properly cross-pollinated will without a doubt lead to greater setting of fruit.

STOUT: THE FLOWER BEHAVIOR IN AVOCADOS

COCKAYNE BOSTON

EXPLANATION OF CHART 1

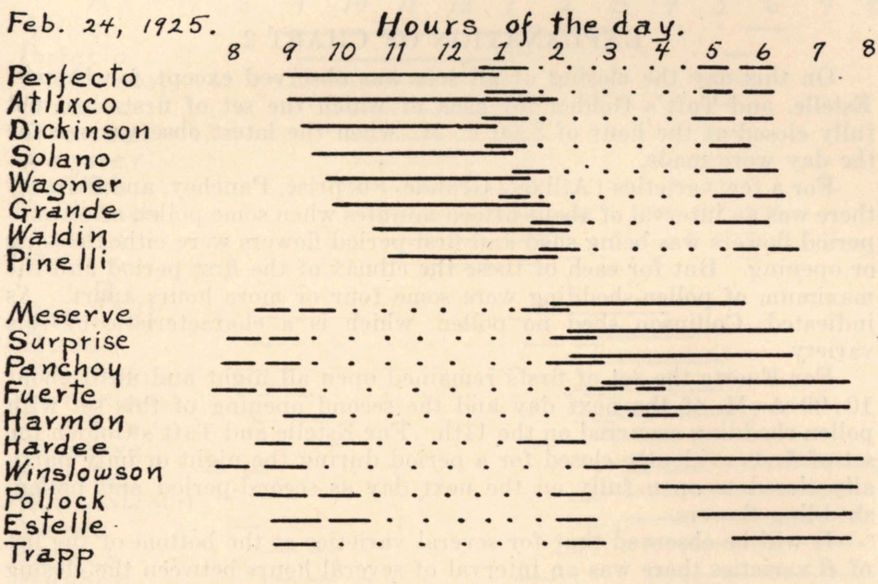
In this chart, as in those following, the continuous line indicates for each variety the *entire* time when flowers were open for the *first* period. The dots indicate the time during which flowers of the *second* period of opening were shedding pollen and the dashes show the intervals of opening and closing before and after pollen was being shed. As a rule the pollen was being shed most abundantly near the middle of the period covered by the dots.

This chart is a record of the flower behavior of 18 varieties for one and the same day. After a minimum of 57° during the preceding night and an early morning fog the day was clear and breezy with a maximum temperature of 85° reached sometime after noon. This record is typical for days of good weather during February, 1925, in Florida.

Every variety studied on this day had two sets of flowers open as indicated. For Perfecto, Grande, and Harmon, there was a short interval when pollen was being shed while first-period flowers were slightly open, otherwise there was no overlap of first-period flowers open while second-period flowers were open and shedding pollen, and no opportunity for self or close-pollination. Thus in avocados, the normal flower-behavior greatly limits self-fruitfulness.

The varieties fall into two groups. Those of one group (*A*) are female in the forenoon and male in the afternoon. The others (Group *B*) are male in the forenoon and female in the afternoon. There is thus a most decided adaptation for reciprocal cross-pollination between certain varieties of the two groups.

CHART 1



A TYPICAL RECORD OF FLOWER BEHAVIOR FOR A DAY OF RATHER FAVORABLE WEATHER RATHER EARLY IN THE SEASON OF BLOOM

EXPLANATION OF CHART 2

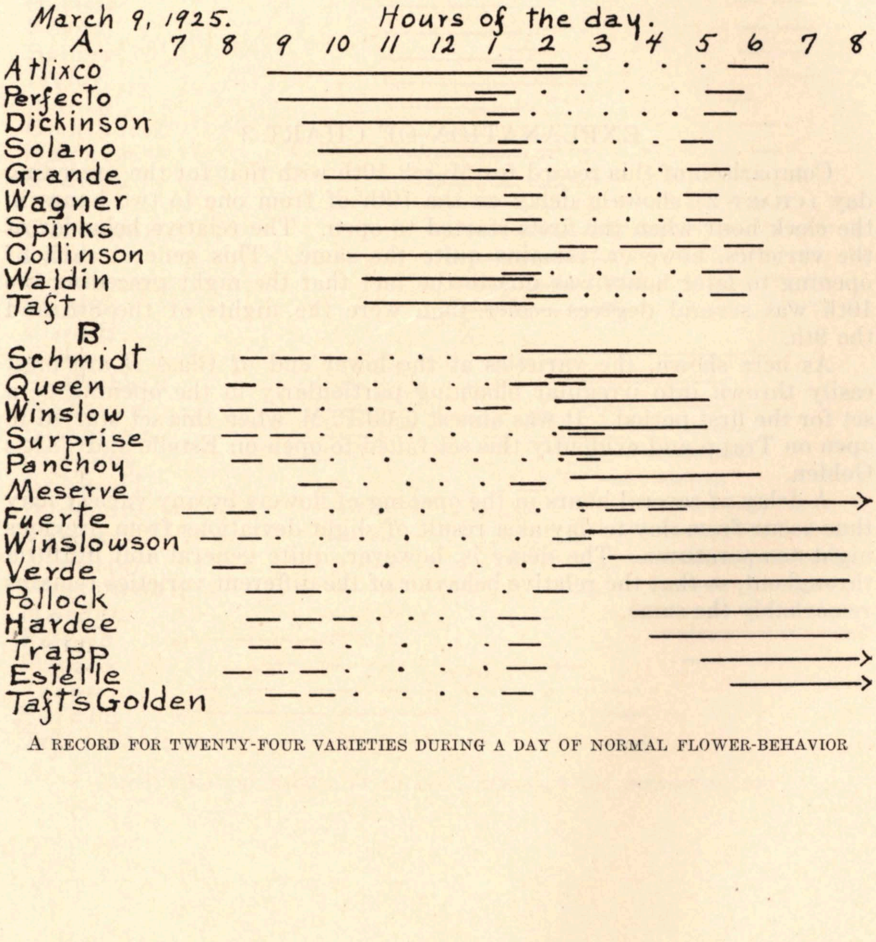
On this day the closing of all sets was observed except for Fuerte, Estelle, and Taft's Golden for each of which the set of firsts had not fully closed at the hour of 8:00 P. M., when the latest observations for the day were made.

For a few varieties (Atlixco, Grande, Surprise, Panchoy, and Fuerte) there was an interval of about fifteen minutes when some pollen of second-period flowers was being shed and first-period flowers were either closing or opening. But for each of these the climax of the first period and the maximum of pollen-shedding were some four or more hours apart. As indicated, Collinson shed no pollen, which is a characteristic of this variety.

For Fuerte the set of firsts remained open all night and until about 10:00 A. M. of the next day and the second opening of this set with pollen-shedding occurred on the 11th. For Estelle and Taft's Golden the set of firsts evidently closed for a period during the night or only partially closed to open fully on the next day as second-period and pollen-shedding flowers.

It will be observed that for several varieties at the bottom of the list of *B* varieties there was an interval of several hours between the closing of the set open in the forenoon and the opening of the afternoon set. This is a marked and normal characteristic of these varieties.

CHART 2



A RECORD FOR TWENTY-FOUR VARIETIES DURING A DAY OF NORMAL FLOWER-BEHAVIOR

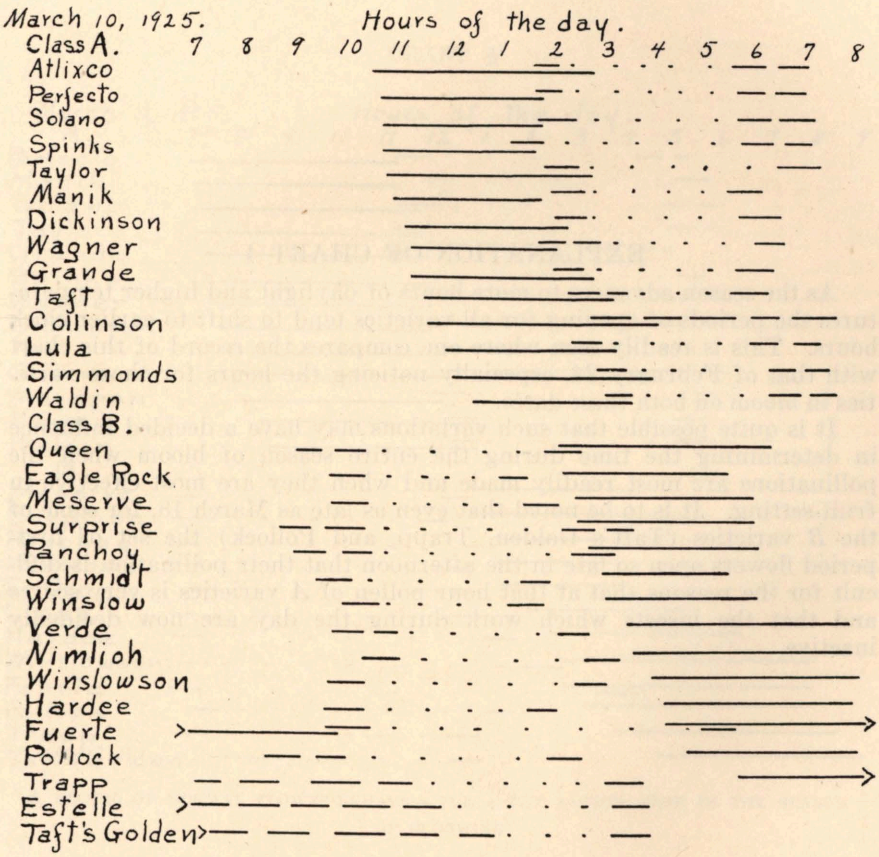
EXPLANATION OF CHART 3

Comparison of this record for March 10th with that for the preceding day (CHART 2) shows a delay on the 10th of from one to two hours in the clock hour when the firsts started to open. The relative behavior of the varieties, however, remains quite the same. This general shift of opening to later hours was due to the fact that the night preceding the 10th was several degrees cooler than were the nights of the 8th and the 9th.

As here shown, the varieties at the lower end of Class *B* are most easily thrown into irregular blooming particularly in the opening of a set for the first period. It was almost 6:00 P. M. when this set started to open on Trapp and evidently this set failed to open on Estelle and Taft's Golden.

A delay of several hours in the opening of flowers by any variety may thus occur from day to day as a result of slight deviations from previous night temperatures. The delay is, however, quite general and uniform throughout, so that the relative behavior of the different varieties remains remarkably the same.

CHART 3



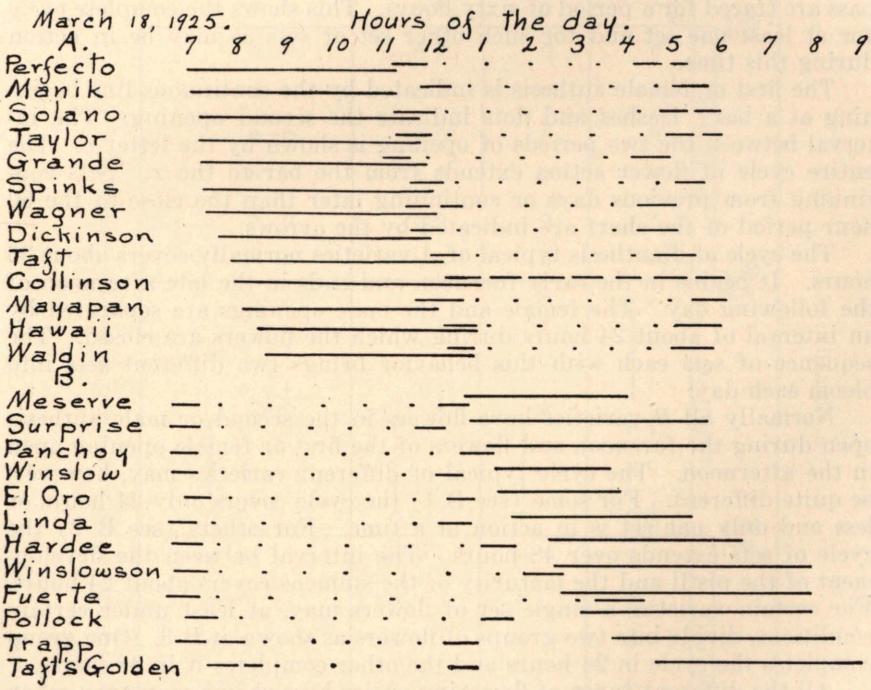
CONTINUING THE RECORD OF CHART 2 THROUGH THE FOLLOWING DAY

EXPLANATION OF CHART 4

As the season advances to more hours of daylight and higher temperatures the periods of opening for all varieties tend to shift to earlier clock hours. This is readily seen where one compares the record of this chart with that of February 24, especially noticing the hours for those varieties in bloom on both these dates.

It is quite possible that such variations may have a decided influence in determining the time during the entire season of bloom when the pollinations are most readily made and when they are most effective in fruit-setting. It is to be noted that even as late as March 18, for some of the *B* varieties (Taft's Golden, Trapp, and Pollock) the set of first-period flowers open so late in the afternoon that their pollination is difficult for the reasons that at that hour pollen of *A* varieties is very scarce and that the insects which work during the day are now decidedly inactive.

CHART 4



A RECORD OF NORMAL FLOWER-BEHAVIOR FOR A DAY RATHER LATE IN THE SEASON OF BLOOMING

EXPLANATION OF CHART 5

Different types of flowering cycles for avocado flowers are here shown diagramatically. The different conditions through which sets of flowers pass are traced for a period of sixty hours. This shows the complete cycle for at least one set and for such other set or sets as may be in action during this time.

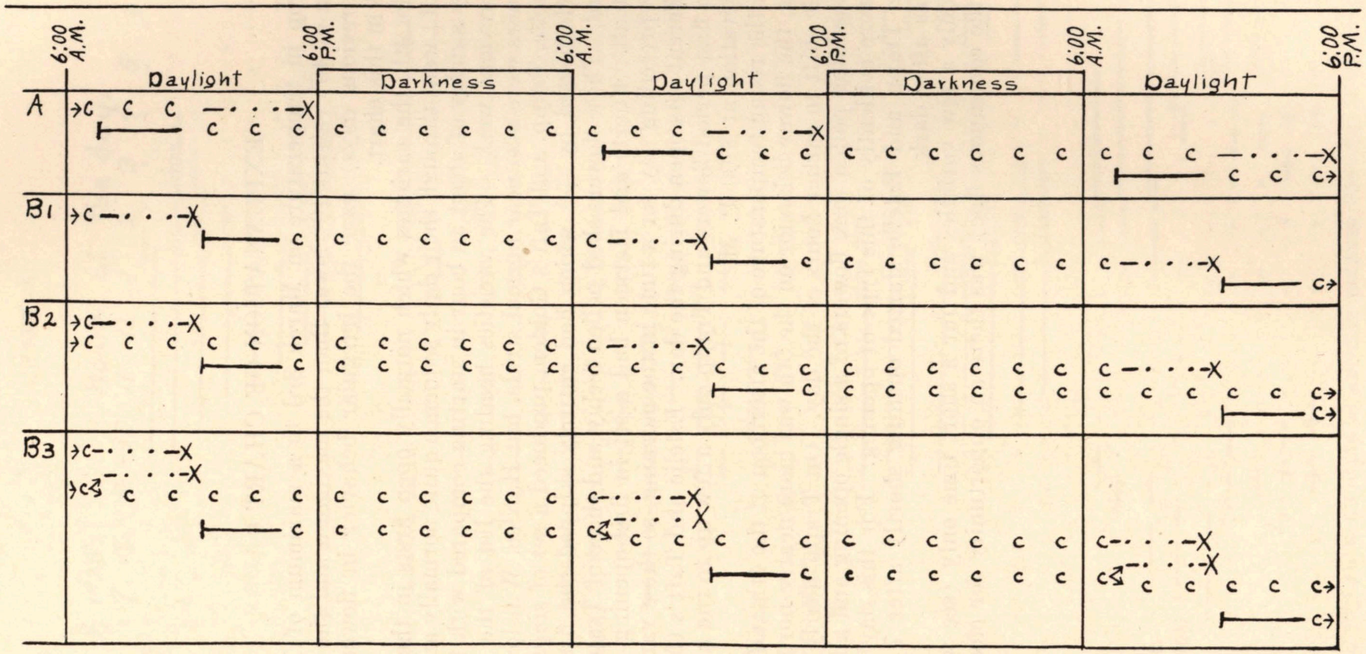
The first or female anthesis is indicated by the continuous line beginning at a bar. Dashes and dots indicate the second opening. The interval between the two periods of opening is shown by the letter *c*. The entire cycle of flower action extends from the bar to the *x*. Sets continuing from previous days or continuing later than the close of the 60 hour period of the chart are indicated by the arrows.

The cycle of dianthesis typical of *A* varieties normally covers about 36 hours. It begins in the early forenoon and ends in the late afternoon of the following day. The female and the male openings are separated by an interval of about 24 hours during which the flowers are closed. The sequence of sets each with this behavior brings two different sets into bloom each day.

Normally all *B* varieties have flowers in the second or male anthesis open during the forenoon and flowers of the first or female opening open in the afternoon. The cycle typical of different varieties may, however, be quite different. For some (see B 1) the cycle covers only 24 hours or less and only one set is in action at a time. For others (see B 2) the cycle of sets extends over 48 hours. The interval between the development of the pistil and the maturity of the stamens covers about 24 hours. For certain varieties a single set of flowers may, at least under certain conditions, divide into two groups of flowers as shown at B 3. One group completes the cycle in 24 hours and the other completes it in 48 hours.

All the different types of flowering cycles here shown may exist when the daily alternation of all the varieties is quite normal. Under abnormal and off-stride blooming the cycles of sets are, of course, also very irregular.

CHART 5



TYPES OF CYCLES OF DIANTHESIS FOR SETS OF AVOCADO FLOWERS

EXPLANATION OF CHART 6

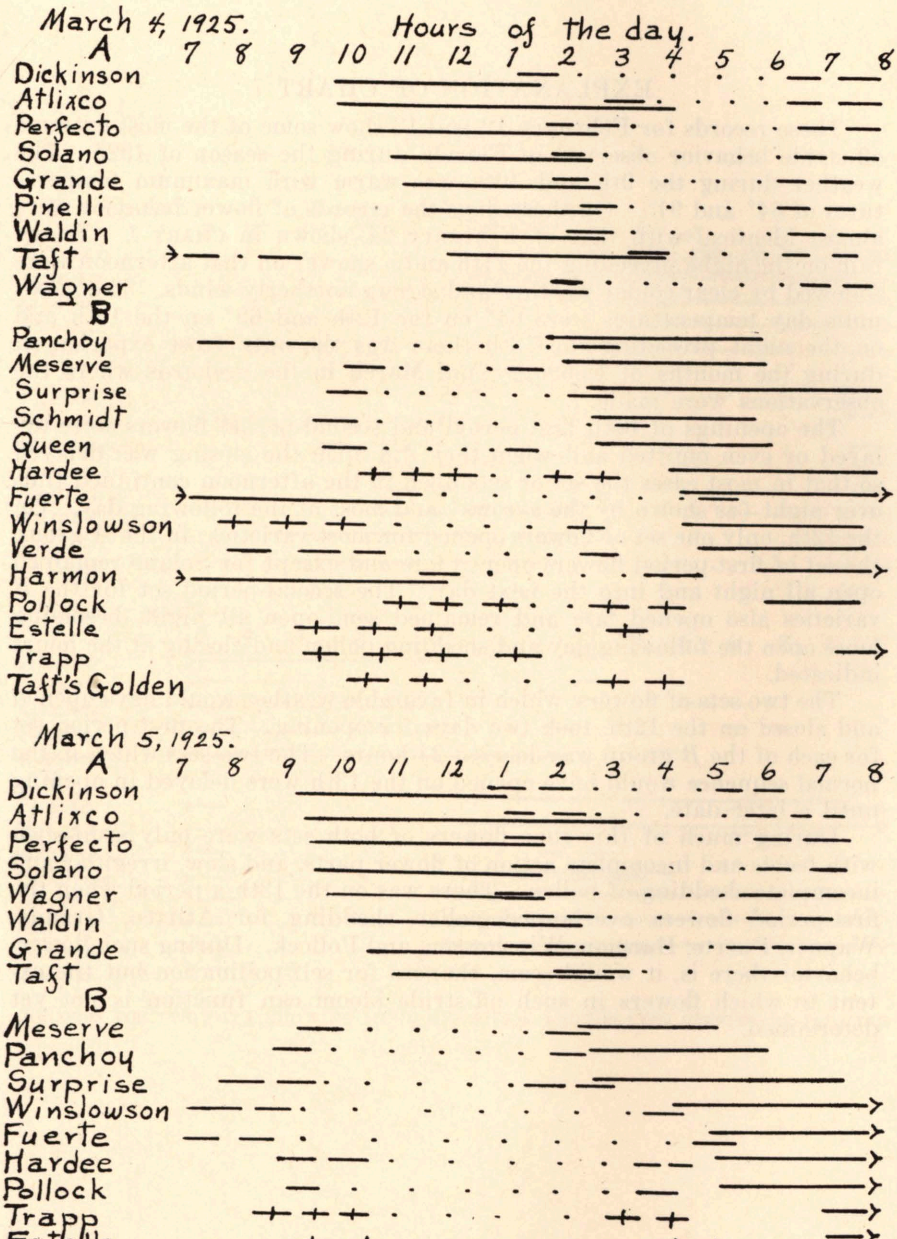
A drop in temperature on March 3rd to a maximum of 77° and a minimum of 46° (about 10° lower than the maximum and the minimum of the previous days) gave the irregular behavior in flower opening recorded in this chart.

On the 4th, the varieties which normally open firsts in the forenoon (Group *A*) went through their daily sequence quite normally and quickly with only a delay of about an hour in starting compared with the record of the previous week. The varieties heading the list of the afternoon first-openers were also near normal stride, but Hardee, Winslowson, Pollock, Estelle, Trapp, and Taft's Golden, produced a set of *single-opening* flowers (indicated by +) which had entirely skipped the first-opening on the 3rd. These flowers shed pollen feebly and those of Trapp shed no pollen at all. Fuerte and Harmon had a set in first-opening continued from the preceding day for a time in the morning, so these varieties had three different sets open during the day. Estelle and Taft's Golden produced no first-period flowers and Trapp only a few up to the hour of the last observation at 8:00 P. M.

With the rising temperature of the afternoon of the 4th and the night following, the flower behavior on the 5th was more nearly normal with a noticeable shift to earlier hours of the day. On Trapp nearly all of the flowers shedding pollen were flowers of a single opening and all those for Estelle were evidently of this type of opening. For this day the set of firsts for Trapp and Estelle started opening shortly after 7:00 P. M. which was after dark.

For only a few varieties and for a short time only (see where dots overlap the continuous line) was there an opportunity for close-pollination.

CHART 6



RECORDS FOR TWO DAYS SHOWING SOMEWHAT DELAYED OPENING, A SKIPPING OF THE FIRST OPENING BY CERTAIN SETS AND SINGLE OPENING

EXPLANATION OF CHART 7

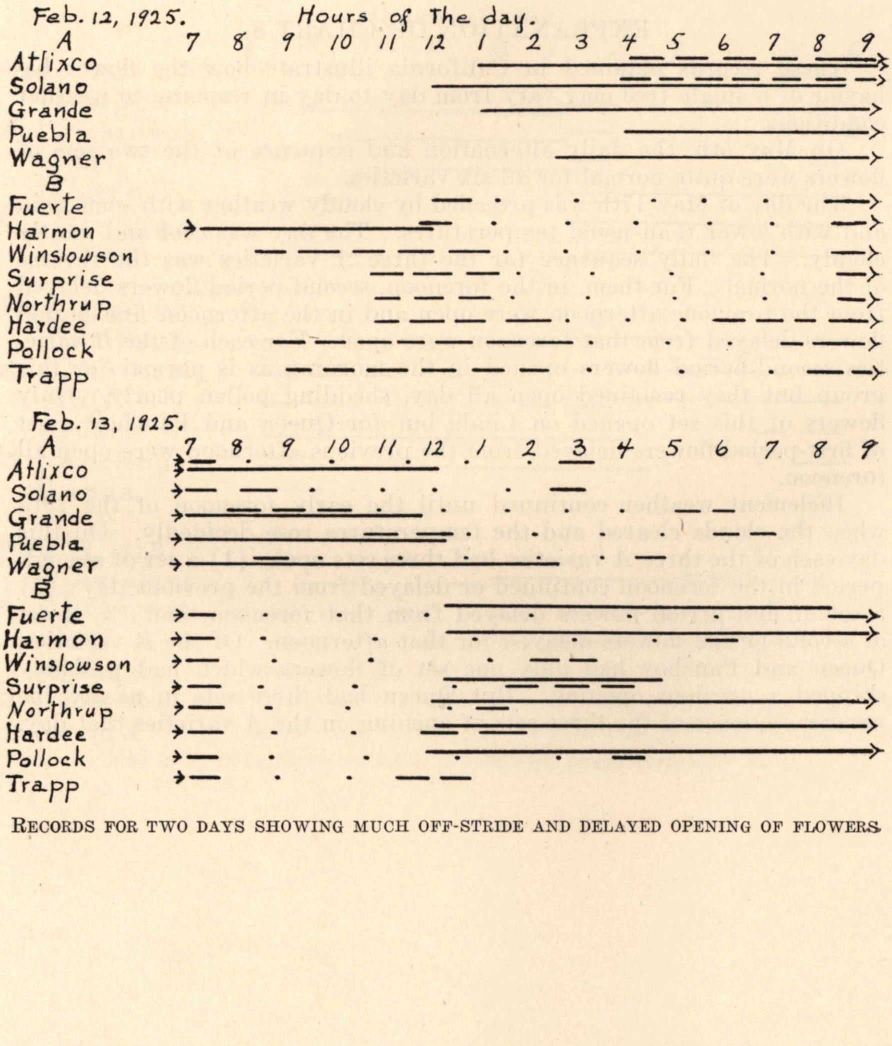
These records for February 12 and 13 show some of the most extreme off-stride behavior observed in Florida during the season of 1925. The weather during the 9th and 10th was warm with maximum temperatures of 84° and 91°. On these days the records of flower behavior were almost identical with that of February 24, shown in CHART 1. Heavy rain on the night preceding the 11th and a shower on that afternoon were followed by clear colder weather and strong northerly winds. The maximum day temperatures were 64° on the 12th and 69° on the 13th and on the night preceding the 13th there was the only frost experienced during the months of February and March in the orchards where the observations were made.

The openings of both first-period and second-period flowers were delayed or even omitted and when they did open the closing was delayed so that in most cases the set or sets open in the afternoon continued thus over night (as shown by the arrows) and most of the following day. On the 12th, only one set of flowers opened for most varieties; in the *A* group the set of first-period flowers opened late and except for Solano remained open all night and into the next day. The second-period set for the *B* varieties also opened late and remained semi-open all night, becoming more open the following day and shedding pollen and closing at the hours indicated.

The two sets of flowers, which in favorable weather would have opened and closed on the 12th, took two days for opening. The first-period set for each of the *B* group was delayed 24 hours. The two sets which in the normal sequence would have opened on the 13th were delayed in opening until a later date.

During much of this time flowers of both sets were only semi-open with feeble and incomplete action of flower parts, and slow, irregular and incomplete shedding of pollen. There was on the 13th a period when the first-period flowers overlapped pollen shedding for Atlixco, Grande, Wagner, Fuerte, Harmon, Winslowson, and Pollock. During such flower-behavior there is, it would seem, chances for self-pollination but the extent to which flowers in such off-stride bloom can function is not yet determined.

CHART 7



RECORDS FOR TWO DAYS SHOWING MUCH OFF-STRIDE AND DELAYED OPENING OF FLOWERS

EXPLANATION OF CHART 8

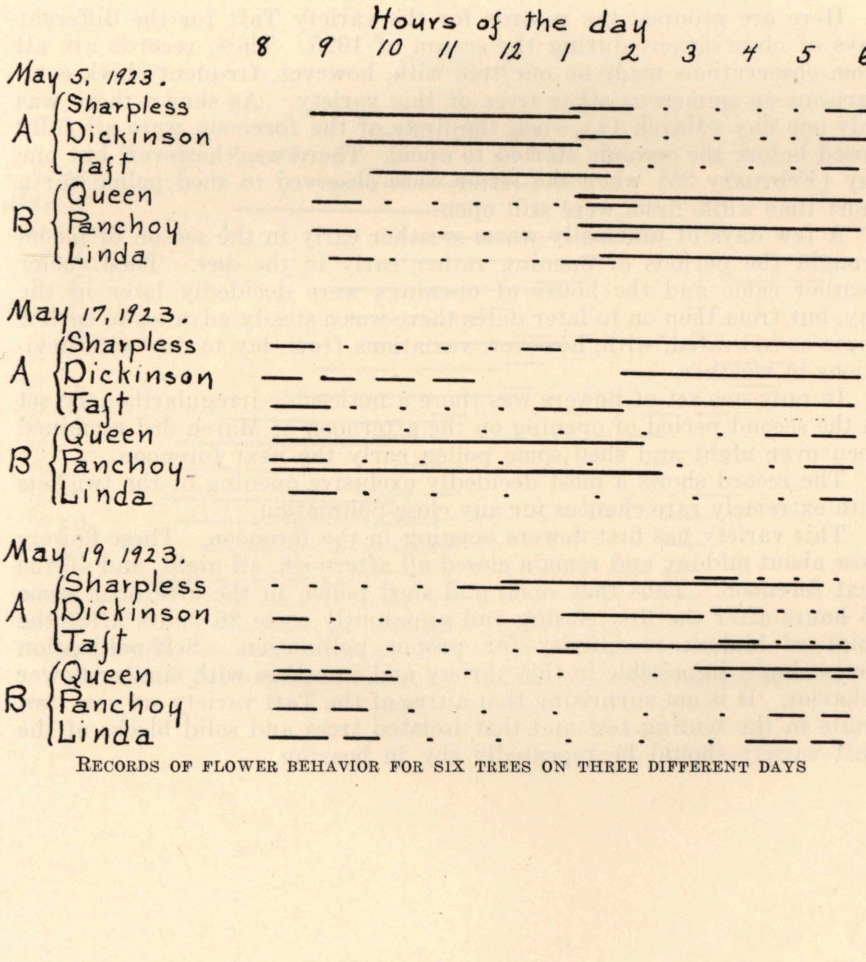
These records obtained in California illustrate how the flower behavior of a single tree may vary from day to day in response to weather conditions.

On May 5th, the daily alternation and sequence of the two sets of flowers were quite normal for all six varieties.

The day of May 17th was preceded by cloudy weather with some rain and with lower than usual temperatures. The day was cool and mostly cloudy. The daily sequence for the three *A* varieties was the reverse of the normal. For them, in the forenoon, second-period flowers delayed from the previous afternoon were open and in the afternoon first-period flowers delayed from that forenoon were open. For each of the *B* varieties second-period flowers opened in the morning as is normal for this group but they remained open all day, shedding pollen poorly. Only flowers of this set opened on Linda but for Queen and Panchoy a set of first-period flowers delayed from the previous afternoon were open all forenoon.

Inclement weather continued until the early forenoon of the 19th when the clouds cleared and the temperatures rose decidedly. On this day each of the three *A* varieties had three sets open; (1) a set of second-period in the forenoon continued or delayed from the previous day; (2) a set of first-period flowers delayed from that forenoon, and (3) a set of second-period flowers delayed for that afternoon. Of the *B* varieties, Queen and Panchoy had only one set of flowers which had probably skipped a previous opening. But Queen had three sets in nearly the reverse sequence of the three sets of opening on the *A* varieties that day.

CHART 8



RECORDS OF FLOWER BEHAVIOR FOR SIX TREES ON THREE DIFFERENT DAYS

EXPLANATION OF CHART 9

Here are grouped the records for the variety Taft for the different days of observations during the season of 1925. These records are all from observations made on one tree with, however, frequent check comparisons on numerous other trees of this variety. As shown there was only one day (March 11) when the firsts of the forenoon were all fully closed before the seconds started to open. There was, however, but one day (February 25) when the latter were observed to shed pollen for a short time while firsts were still open.

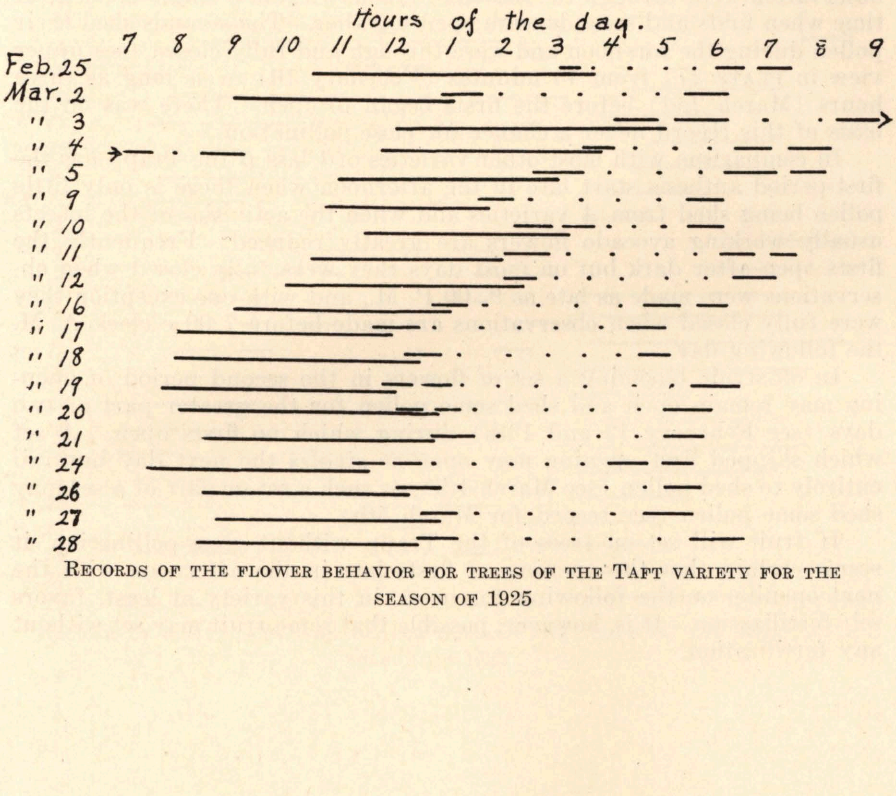
A few days of unusually warm weather early in the season of bloom brought the periods of opening rather early in the day. Then cooler weather came and the hours of openings were decidedly later in the day, but from then on to later dates there was a steady advance to earlier hours as indicated, with, however, variations from day to day with deviations in weather.

In only one set of flowers was there a noticeable irregularity; the set in the second period of opening on the afternoon of March 3rd remained open over night and shed some pollen early the next forenoon.

The record shows a most decidedly exclusive opening of the two sets with extremely rare chances for any close-pollination.

This variety has first-flowers opening in the forenoon. These flowers close about midday and remain closed all afternoon, all night, and all the next forenoon. Thus they open and shed pollen in the afternoon some 25 hours after the first closing and apparently some 26 hours after the point of highest receptivity for proper pollination. Self-pollination seems almost impossible in this variety and in others with similar flower behavior. It is not surprising that a tree of the Taft variety set very few fruits in the tenting test and that isolated trees and solid blocks of the Taft variety should be repeatedly shy in bearing.

CHART 9



RECORDS OF THE FLOWER BEHAVIOR FOR TREES OF THE TAFT VARIETY FOR THE SEASON OF 1925

EXPLANATION OF CHART 10

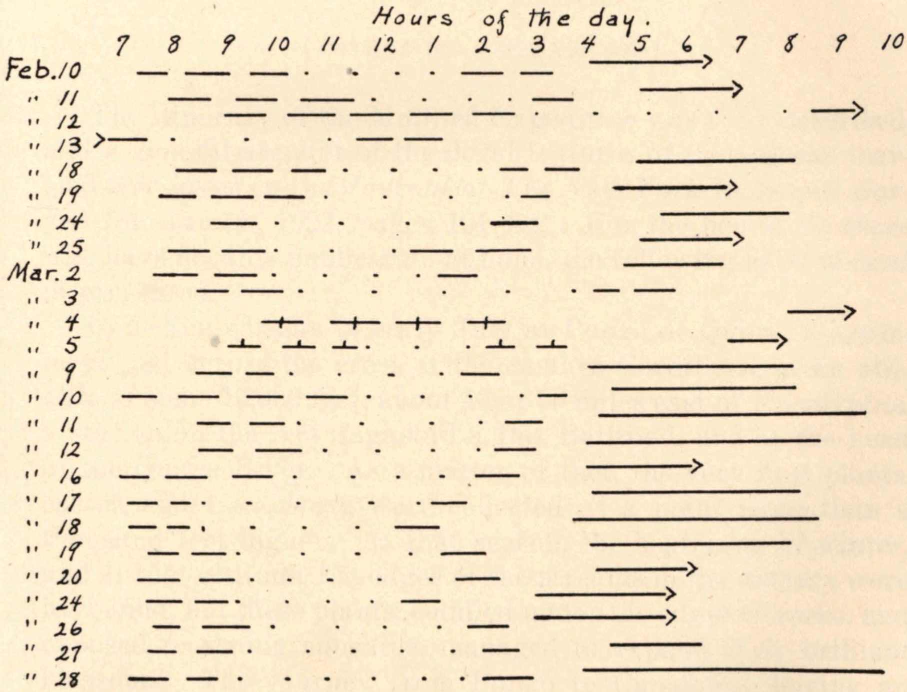
As shown here in this record for the season, the trees of Trapp under observation went through the season of bloom without a single moment of time when firsts and seconds were open together. The seconds shed their pollen during the forenoon and were through and fully closed (see upper view in PLATE 27) from 45 minutes (February 10) to as long as three hours (March 2nd) before the firsts began to open. There was on the basis of this record never a chance for close-pollination.

In comparison with most other varieties of Class *B* the Trapp has the first-period anthesis start late in the afternoon when there is only little pollen being shed from *A* varieties and when the activities of the insects usually working avocado flowers are greatly reduced. Frequently the firsts open after dark but on most days they were fully closed when observations were made as late as 9 : 00 P. M., and with one exception they were fully closed when observations are made before 7 :00 o'clock A. M. the following day.

In off-stride blooming a set of flowers in the second period of opening may remain open and shed some pollen for the greater part of two days (see February 12 and 13th) during which no firsts open. A set which skipped first opening may open as *singles* the next day but fail entirely to shed pollen (see March 4th), or such a set or part of a set may shed some pollen (see record for March 5th).

If fruit will set on trees of the Trapp without cross-pollination, it seems certain that the opening of firsts late in the afternoon with the next opening on the following forenoon, in this variety at least, favors self-fertilization. It is, however, possible that some fruit may set without any fertilization.

CHART 10



RECORDS OF THE FLOWER BEHAVIOR FOR TREES OF THE TRAPP VARIETY FOR THE SEASON OF 1925