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Floral Biology of the Persea Drymifolia (Mexican Avocado) Cultivated in San Remo, Italy

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The flower behavior of the "Persea Americana Mill" (Guatemalan Avocado), was studied in California by B. S. Nirody and by A. B. Stout of New York at the request of the California Avocado Association.

This association was concerned about the fact that the fruit setting was very irregular. Some mature, vigorous, flowering trees were altogether sterile: whereas others of the same variety yielded abundant crops.

According to Nirody and Stout the sterility of the avocado is due to pronounced dichogamy, this is, during the receptive period of the stigma, the anthers are not open and, when later the pollen is shed, the stigma is already shriveled. However, as there are certain varieties that open their flowers in the morning and others whose flowers open in the afternoon, it happens that when the stigma of one variety is receptive it is fertilized by pollen of another variety whose flowers opened the day before. Apparently flowers which open in the afternoon, and are receptive only at that period become fertilized if pollen of another variety is available.

On the basis of this phenomenon avocado varieties in California were divided into two groups: Those whose flowers are receptive in the morning (type A) and those whose flowers are receptive in the afternoon (type B). It is recommended to plant varieties of the two groups to insure pollination.

Ecological Observations On Avocados Cultivated At San Remo

At San Remo, fruit setting of the avocado is very irregular. There are isolated trees 3 to 4 years of age which yield some fruit and others 10 to 15 years are completely sterile. But sometimes isolated trees of the latter type yield a good crop. Since this behavior cannot be explained on the basis of dichogamy, I decided to make an investigation.

The avocados cultivated in the orchards of San Remo and environs (some hundred trees) are not "Persea Americana Mill" (Guatamalan), but are "Persea Drymifolia Cham, and Schlecht", (Mexican).

Most of these trees were grown from seeds shipped from Mexico by Prof. Mario Calvino, and one of these trees belonging to M. Giancinto Gandini is outstanding. Its trunk measures 1.24 meters in circumference, is 9 meters high and bears an annual crop of about a thousand fruits. It was planted in an olive orchard and began to bear when a few years old. Three trees approximately 50 meters away are vigorous and they

regularly produce an abundance of flowers, but began to bear only a few years ago. The yield has been small.

Of four specimens cultivated at the "Villa Meridiana," from 5 to 11 years old, only one specimen bears fruit, it is in a spot well protected by neighboring buildings and plants. However, very close by stands another specimen which so far has been sterile.

A third group of three specimens from 6 to 7 years old, is cultivated on the property of Gio Bernardo Calvino, in the locality of S. Giovanni, 350 meters above sea level. Two of these are four meters distant from each other and belong to different varieties. One is an avocado tree from Mexico and is bearing fruit. The other comes from the seed of the avocado of Mexico (Guatemala), a variety that produces, in Guatemala, fruits weighing 3 Kg. This specimen is sterile. The third specimen is approximately 100 meters away and bears fruit. The two trees which bear fruit are sheltered by buildings and olive trees more than the third specimen which does not bear fruit.

On the property of Mr. Proudoni there are two large trees of "Persea Drymifolia" (Mexican): one of them—the older one—bears fruit every year, and it began to bear before the others were planted. The younger tree has been sterile. The older tree is close to an olive and other trees; the second specimen has its foliage exposed almost completely to the sun.

On the property of Merlo an eight year old tree has been bearing fruit for three years. The position of this specimen is particularly interesting owing to the nearness of a large uncovered reservoir which is constantly filled with water. Approximately one-half of its foliage hangs over the reservoir and is therefore benefited by the water vapor. The fruits numbering about forty are borne mostly on the north side adjacent to the reservoir.

One tree has another special position in the garden of the estate owned by the Vigo-Martini brothers. It is about ten years old and bears many fruits. On the south side there are several very tall palms. Thus the tree is completely sheltered from high winds. The fruits, about 400, weighing from 150 to 160 gr., are distributed mostly toward the side of the building and the south, i.e. on the most protected sides. In the same garden there are about ten other trees all sterile, some of them already quite high; all are completely exposed to the sun.

On the property of De Bernardi are two trees, one fertile, the other sterile. The former has about fifty fruits this year, unevenly distributed; they are somewhat more numerous on the north side and where the branches are close to the sterile tree. These two trees are not uniformly watered; the fruit bearing specimen receives the seepage from a ditch one meter away, while the sterile specimen receives only rain water.

Conclusion: Fruit setting of the avocados at San Remo is limited to specimens standing in localities protected from winds, and to that portion of the tree which suffers least from atmosphere dryness.

Dichogamy of Avocados Cultivated at San Remo

Imperfect dichogamy. It was interesting to ascertain whether dichogamy would occur in avocados cultivated at San Remo, and if so, what relation would it have to irregular fruit setting. The result of my observations show that, although dichogamy is a factor, there are various other important influences.

The first anthesis occurs in March and in some years (1938), during the last days of February; the last anthesis takes place in the third week of May. In order to study all of the phases of the development of the flowers, I attached to each bud a tag on which I marked hourly the state of the floral organs from anthesis to the falling of the flowers. About 30 flowers on each of about 10 specimens were studied, especially from March to May of 1937 and 1938.

In this way I was able to establish the fact that the developmental cycle of the flower of "Persea Drymifolia" (which is protogynous) lasts five days. In certain plants it develops as follows:

First day, at 8 o'clock—first anthesis, female phase, faded stigma: second day 8 o'clock—flower closed. Third day at 8 o'clock Idem, at 3 to 4 o'clock—flower closed. Fourth day at 10 to 4 o'clock—second anthesis, male phase. Fifth day at 10 to 12 o'clock, the conditions of the previous day prevailed. Idem, at 4 o'clock, flower definitely closed.

These observations show that the first anthesis or female phase of the flower lasts only a few hours and is followed by a period of two days during which time the flower remains closed. The second anthesis or male phase lasts two days and then the flower closes definitely.

However, in the plants of this group, the first anthesis may start toward the late afternoon (at about six o'clock) and extend until the following morning, or in other plants, the first anthesis may occur in the afternoon, from 2 to 6 o'clock, the flower then closes and remains closed for 2 days, then it reopens (second anthesis) at 8 o'clock in the morning and remains open another day after which is closes definitely. When the second anthesis occurs the anthers are still closed. The opening begins about half an hour after and is complete at about 3 o'clock. In this case the floral cycle is as follows:

First day at 2 o'clock—first anthesis, female phase. Idem, at 6 o'clock, stigma faded. Second day, at 8 o'clock, flower closed. Third day—flower closed. Fourth day, at 8 o'clock, second anthesis, male phase. Fifth day, at 8 o'clock, flower closed.

As already stated this alternation is not regular. Exceptionally, the first anthesis may extend until 10 or 12 o'clock of the following day; hence one may find in the same plant and at the same time, several flowers in the phase of first anthesis, namely, with receptive stigma, and many in the phase of second anthesis, polliniferous.

There is a third type of dichogamy in plants, where the first anthesis occurs on the same day. In some flowers in the morning (from 6 to 9 o'clock) with the peak between 7 and 8 o'clock; in others in the afternoon (from 12 to 6 o'clock) with the peak between 2 and 4 o'clock. In these plants the change of the phases between the two periods is very pronounced, and for this reason there are, as a rule, at the same time flowers in the female phase and flowers in the male phase. To this type belongs the one plant of the "Villa Meridiana" which has fruited.

Another case of imperfect dichogamy is the simultaneous presence, in the same flower, of dehiscent anthers and of receptive stigma. Frequently, self-pollination is performed by anther of the internal series piercing the stigma with one of its valves.

The withering of the stigma coincides mostly with the dehiscence of the last anthers.

There are 9 others, namely, 6 external and 3 internal; between the ripening of the first and that of the last anthers, from 5 to 10 hours will elapse, (in exceptional cases a shorter period). Usually the internal anthers open first and, often as the stigma at this time is still receptive, self-pollination is possible.

In one specimen of "Persea drymifolia", I observed a phase much shorter than the first anthesis. The stigma was receptive only between 8 and 11 o'clock, and the flower closed at about 12 o'clock, opening only at 3 o'clock of the third day with anthers still closed, but about to open.

Stimulated dichogamy, I observed that dichogamy is stimulated in certain cases as:

I. Morphological anomalies of the stigma were often observed in a plant where the stigmas were thin and ending in a point, perhaps bifid and already curved at the first antithesis or a short time afterward.

II. Pronounced scarcity of pollen. In the first case the flowers were practically males owing to the abortion of the stigma; in the second case they were females on account of the deficiency of pollen.

Comparison with the Floral Cycle of the Avocados in America

Stout and Robinson report that the female phase of the flower of "Persea Americana" lasts only 3 to 4 hours and that the anthers begin to open and dehisce within half an hour to one hour. The flowers opening for the first time in the morning (type A) will close at about 12 o'clock, and reopen only in the afternoon of the following day in order to emit the pollen. The flowers opening for the first time in the afternoon (type B) will reopen either in the following morning or in the morning of the second day.

On the other hand in the specimens of "Persea drymifolia" cultivated at San Remo, the biological cycle of the flowers is much longer—totaling 4 to 5 days, of which almost two are taken up by the flower to complete the maturation of the anthers. The female phase is always much shorter than the male; it lasts generally from 3 to 4 hours, and rarely extends beyond 5 or 6 hours. Afterwards the flower closes and remains closed for two days (in exceptional cases one day and in such a case the anthers do not dehisce simultaneously with the second anthesis). In the third phase, the stigma of the flower, opening for the second time, has faded and the anthers are still closed; their opening is not simultaneous, starting after 1 to 2 hours and lasting, as a rule, from 5 to 12 hours. This male phase lasts about 2 days.

The longer floral cycle of the avocados cultivated at San Remo may be due either to a specific difference ("Persea drymoifolia" in comparison with "Persea Americana") or the climatic differences, and above all to the lower temperature.

Trials with Artificial Pollination

Numerous trials with artificial cross-pollination carried out in 1937 and 1938 between varieties of type A and type B have always given negative results. Negative results were also obtained by Dr. R. Jerry Desloges, who owns about 20 avocado trees of the following varieties: Fuerte (B)—Puebla (A)—Northrop (B) and nurseries of Mexican avocados at Villa Africa in Menton, Garavan, Prance. (Letter of Desloges 16, V. 937). One should note that the specimens of types A and B are planted very close together

and cross their branches. At the Villa Africa the variety "Puebla" bears fruit often, though very intermittently, whereas the variety "Fuerte" rarely bears. The contrary is the case in another garden of Mr. Desloges, where the variety "Fuerte" bears fruits while the "Puebla" is sterile. The facts cannot be explained by dichogamy.

Morphology and Floral Biology

The flowers of the "Persea drymifolia" are produced in apical racemes, whose characters vary noticeably in the plants obtained from seeds; dense inflorescence almost globular in some plants, poor in inflorescence with hermaphroditic, actinomorphous, apetatous, six pubescent sepals in two series, 9 stamens in 3 series, 6 external opposite the sepals and 3 internal; pubescent filaments, continuous anthers with filament, dehiscent valves, with four valves (rarely 5), 2 ventral and 2 lateral. In the anthers of the internal series the two frontal valves are at the bottom, in the external series they are at the top. The dehiscence from the bottom toward the top is extrorsal in the internal series, and introrsal in the external series. In some cases the extrorsal anthers have the two lateral valves a little curved toward the interior, so that the lid can brush against the stigma and effect the pollination. Indeed, it is frequently seen that a lid of the anthers of the internal series pierces the stigma and deposits the pollen. There are nine (9) staminodes, orange yellow, in 3 series; one consisting of 3 staminodes, alternating with the internal stamens and two external series alternate with the sepals, each of 3 staminodes. The external staminodes thus alternate also with the stamens of the external series. They are supported by a short, rough and hairy filament, formed like a spear head; those of the internal series are pointed and those of the external series are blunt.

There are not always 9 staminodes. In the flowers of each specimen of "Persea Drymifolia", I observed, besides the staminodes alternating with the anthers, a pair supporting the sepals of the internal series. A total of 12 staminodes which make these flowers much more attractive for the insects.

Superior ovary, one-celled, yellow in some specimens, rose crimson in others; simple terminal style; bilable stigma (rarely bifid), single ovule, pendulous.

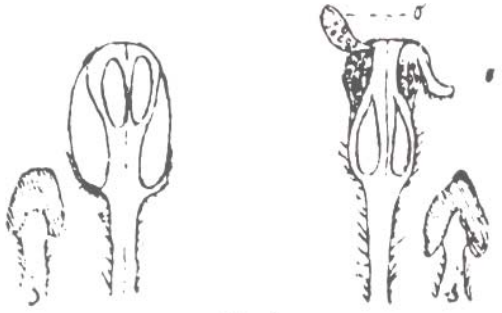

Fig. 9

Entomophilous Pollination

The specimens of "Persea Drymifolia" cultivated at San Remo, 4 to 5 years of age, produce generally a very large quantity of flowers. The occasionally low temperatures (4 to 6 degrees C. below zero for 3 or 4 nights in succession) which occurred during the first days of January 1938, did not in the least damage the growing buds.

The first anthesis occurs in certain years at the beginning of March (occasionally during the latter part of February); in other years at the end of March; the last anthesis occurs about the 20th of May, rarely lasting until the 30th.

The racemes are profuse with flowers and are beautiful; in color they are shaded in yellow and green. Owing to the strong odor of the pollen which emanates when the anthers are open, many insects are attracted. The bees are the most frequent visitors and they suck the plentiful nectar during the warm hours of the day. At San Remo, the Argentine ant **(Iridomyrmet humilis)** has been observed reguarly. Other insects attracted are diptera **(Musca domestica, Sryphus sp. Dasiphorasp. Pollenia sp.)** which remain for sometime and suck the nectar; as also Thrips, Centoniella irta **(Tropinota hirta).**

In Cuba, "Persea Americana" and "Persea drymifolia" bloom from January to February. In addition I observed that the flowers were visited by the bees in large numbers, just as much as the flowers of Cinnamomum Zeylanicum. It is, therefore, certain that in most, if not all members of the Lauraceae, the pollination is entomophilous. According to R Wettstein's "Systematic Botany" volume II—1927, Page 163, the mode of pollination of the Lauraceae is little known.

It is interesting to observe the respective position of the anthers (especially those of the internal series) and of the gynaeceum in the two successive anthesis in the same flower. At the beginning of the first anthesis (female phase) the gynaeceum is completely isolated, but toward the end of this period the anthers of the internal series approach the stigma and touch it. Furthermore, the filament between the first to the second phase period doubles in length and it is this lengthening which enables the anthers to reach the stigma in the second phase. This situation would of course have no effect on pollination if the stigma were not receptive in the second phase.

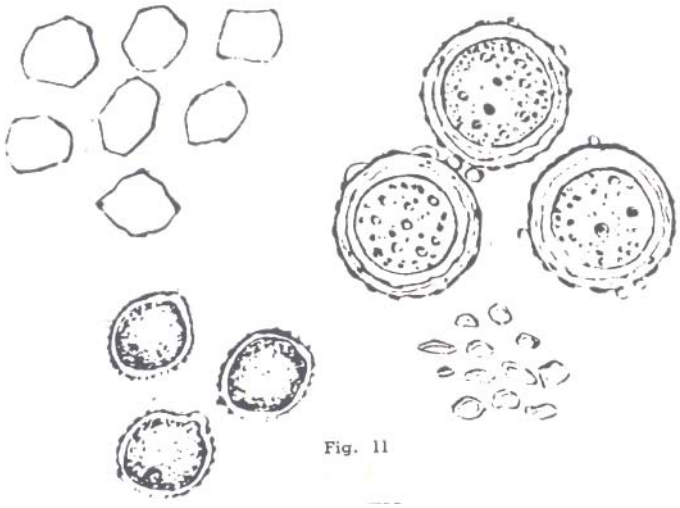

Fig. 11

Pollen

Observations made in Cuba (at the Agronomical Experiment Station of Santiago de las Vegas) on the pollen of avocado trees gave the following results:

Persea gratissima Gaertn (P. Americana Mill) spherical pollen, 36-42 microns, covered with small protuberances. It contains starch before anthesis and fat after anthesis.

Pollen of "Persea drymifolia" Cham, and Schlecht is similar but slightly larger (42-52 microns).

Pollen of the "Persea drymifolia" at San Remo varied from 40-48 microns. The pollen contains spherical or polyhedral grains, probably erythro-amylose, because they change to red mahogany when treated with a solution of iodine. This coloring persists in heat. Later on, in the more developed protuberances containing erythro-amylose, other substances are found which-turn blue with iodine and hence may be amyl-amylose.

At this stage also a widely distributed fatty substance appears. Shortly before the dehiscence of the anthers one can observe in the same anther the three reserve substances (fat, erythro-amylose, amylamylose). Finally, the mature pollen has a distinct covering.

Reflorescence

In October of this year I observed for the first time the reflorescence of "Persea drymifolia".

The fruit bearing specimen on the property of Merlo, showed, since the middle of October, well developed floral clusters. The first flowers opened at the end of October. This plant (according to the owner) flowered also last year and yielded about ten fruits, which fell off in the month of January owing to the exceptionally long frost.

Several other specimens of avocados, so far sterile, flowered this year beginning at the end of October and are still blooming at the end of January. It will be interesting to observe whether this fall and winter flowering will result in setting of fruit.

Shedding of the Flowers

The flowers will fall off 8-12 days after anthesis, sometimes not until 20 days. In some cases shedding is caused by Gleosporium Persea-drymifoliae, which attacks the peduncles, however, in the majority of cases it is due to lack of fertilization.

According to Nirody and Stout fertilization is assured by planting varieties whose anthesis occurs in different hours. However, my observations prove that dichogamy alone is not sufficient to explain the sterility or the scarcity of fruiting of some specimens.

I will sum up the reasons as follows:

I. Dichogamy is invariably imperfect; indeed it is easy to find on the same tree flowers with receptive stigma and flowers with ripe anthers. For this reason dichogamy does not explain absolute sterility.

II. There are occasional anomalies in the floral structure which render the fertilization almost impossible, as I observed in some "Persea drymifolia" cultivated at San Remo, namely: a. deformation of the stigma (ending in a point having the form of a bud, or rather bifid) which is short lived and withers a few minutes after the anthesis. b. scarcity of pollen, c. abnormal pollen.

In a seedling of "Persea drymifolia", 4 to 5 years of age, with many flowers, I found both these anomalies in the stigma and in the pollen. Up to the present this specimen has not produced any fruits and all artificial fertilization tried with the few apparently normal stigmas did not give any result. It will be interesting to see whether it remains sterile.

III. Wind and ensuing dry atmosphere favors shedding of flowers; this condition is quite prevalent along the coast in March and August.

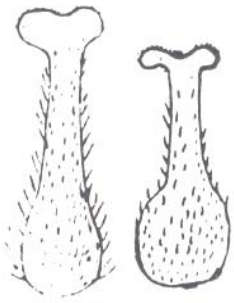

Fig. 10

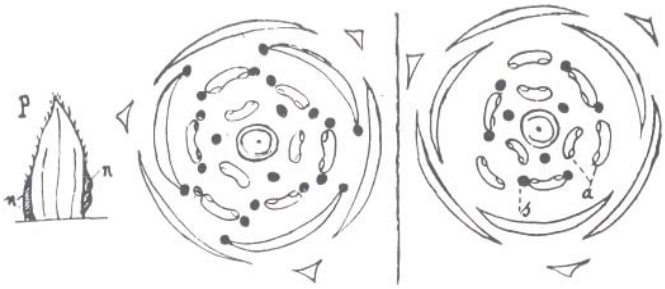

Fig. 8

This hypothesis is supported by the fact that bearing trees (cultivated at San Remo) are all among olive trees or near them, or are protected by buildings from winds and sun. These conditions, limiting the dryness of the air, favor the setting of the fruits. One can also note everywhere that the avocados of San Remo bear more fruits on the north side or on the side which is most protected by neighboring plants. This leads one to conclude that fruit setting is favored by high atmospheric humidity. Indeed, it is well to remember that the avocados bear abundantly in tropical localities where the surrounding conditions, with respect to the atmospheric humidity, are very different from ours. And this explains why the phenomenon of the scarce fruiting occurs also in California where the atmospheric humidity is lower than in the tropics.

In order to prove that the dryness of the air exerts an influence on setting of fruit, I sprinkled four avocado trees during the hot hours of April and May of this year. The result was the production of 80 nice fruits, weighing from 120 to 160 gr, by a tree which, up to this time, had only yielded from 3 to 7 fruits per year. At the same time 2 trees exposed to dry atmosphere set (11 and 5 years) only 13 fruits, which fell off during summer.

The effect of sprinkling of the foliage will be studied again during the coming spring and summer.

Summary

At San Remo, as in California, avocados set fruit very irregularly. Although in California this has been attributed to dichogamy, this investigation has shown that dichogamy is not the sole factor for the following reasons:

I. A study of more than 300 flowers show imperfect dichogamy.

II. Isolated individuals fruited after a few years from time of planting, whereas specimens of types A and B planted close together do not fruit, or produce only a few fruits.

The irregular fruit setting of the avocados at San Remo is attributed instead to the action of the winds and consequent atmospheric dryness.

The favorable conditions are: close proximity of a building, olive trees or other close-by plants in special cases the nearness of uncovered reservoirs.

By sprinkling the foliage of some trees during the hot hours in the months of April and May an abundant set was obtained on a tree which formerly was practically sterile.

Further studies are being made on the morphology and floral biology of the "Persea drymifolia." Comparative studies are being made of pollen from a tropical climate (Cuba) and from San Remo. Observations will also be made on falling flowers and shedding of flowers.

Bibliography

Nirody B. S. Investigations in Avocado Breeding. (California Avocado Ass. Report 1921-22. page 65-78).

Mameli Calvino Eva. Biological studies on the pollen. (Memoirs of the Poey Society, Havana. Januuary 1922).

Stout A. B. A study in cross-pollination of Avocados in Southern California. (Calif. Avocado Ass. Report 1922-23 pgs. 29-45. Oct. 1923).

Clark O. I. Avocado Pollination and Bees (Calif. Avocado Ass. Yearbook 1922-23, pgs. 57-52).

Stout A. B. and Savage E. M. The flower behavior of Avocados with special reference to interplanting (Proc. Fla. Hort. Soc. 1925, pgs. 80-89).

T. Ralph Robinson. Pollen sterility in the Collinson Avocado. (Journal of Heredity, Jan. 1930, pgs. 35-38).

Stout A. B. The pollination of Avocados. (Bull. 257, Agric. Exper. Station Gainsville Florida) March, 1933.

Galang F. G., Morava E. K. Flower Behavior of Avocado Varieties. (The Philippine Journal of Agric. Manila, 1935. Vol. 6 n.3, pgs. 231-268).

Torres J. P. Some notes on Avocado flowers. (The Philippine Journal of Agric. 1936. Vol. 7. n.2, PRS. 207-227).