California Avocado Society 1976 Yearbook 60: 106-152

Some Aspects of the Flower Behavior, Pollination and Fruit Set of Avocado (Persea Americana Mill.) in Trinidad

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Abstract

In studies conducted on avocado at the Field Station of the University of the West Indies pollination was found to be essential for crop production. Insects were necessary for pollination and the common "wasp" appeared to be the most important pollinating agent. Exclusion of insects almost entirely prevented fruit set. In order to increase the probability of pollination the desirability of mixing A-type and B-type cultivars in an orchard was recognized.

The two periods of flower opening, the protogynous dichogamy and the classification of cultivars into two types (A and B) were confirmed. In the A-type cultivars overlapping of the two sets of flowers occurred. Most of the flowers of the cultivar 'Fujikawa' shed pollen during the end of their first period of opening.

1. Introduction

The range of crops grown on a commercial scale in Trinidad has been mainly limited to such crops as sugar cane, cocoa, coconuts, citrus and coffee. With increasing uncertainty in marketing of these crops, however, an interest has arisen in diversifying production. The supply and sales of avocado locally and in the European Economic Community at the present are relatively low; also, the prospects of supplying South and North American countries with off-season avocados are good. Since satisfactory conditions for avocado culture exist in Trinidad and the possibilities for development of an export trade of this fruit are considerable (Storey, 1968; Tai, 1969, 1972), an interest has developed in commercial production.

Within the last fifty years attention has been given to the flowering and fruiting habits of avocado in the United States of America, particularly to flower behaviour and its effect on pollination and subsequent fruit setting (Nirody, 1922; Stout, 1923; Clark, 1923, 1924).

Although the avocado has perfect flowers, there are pollination peculiarities. Avocado flowers are generally protogynous *i.e.* the stigmas mature before the stamens are ready to shed pollen. Each flower, therefore, behaves as if it were first only a female flower and later as if it were only a male flower. In addition, each individual flower has two periods of opening with an interval between these openings varying in length according to the cultivar. Weather conditions may greatly affect these flower movements (Stout, 1933; Bringhurst, 1951; Lesley and Bringhurst, 1951).

According to the manner in which the flower parts function, cultivars are classified into two distinct groups. In group A are those cultivars on which flowers function as pistillates in the morning (first period of opening) and as staminates in the afternoon of the following day (second period of opening). In group B are those cultivars on which flowers function *as* females in the afternoon (first period of opening) and as males in the morning, either of the following day or of the second day (second period of opening) (Stout, 1933). Consequently, under certain conditions *e.g.* isolation of plants or localized planting of single cultivars or cultivars of the same group, fruit set might be substantially reduced or even absent. In some cultivars overlapping of the male and female stages occurs.

Various methods have been suggested to accomplish effective pollination, the most common and widely used being the interplanting of A and B cultivars (Wolfe, Toy and Stahl, 1946; Gustafson, 1967).

Up to the present time, avocado flower behavior has not been studied in Trinidad; however, some work has been done on fruit drop problem (Barnell, 1939). For this reason, a study of various aspects of avocado flower behaviour, pollination and fruit set was carried out under the Tropical-Lowland climatic conditions at the University Field Station, Valsayn, Trinidad.

2. Materials and Methods

All phases of the investigations reported here were performed on a block of avocado trees situated at the Field Station of the University of the West Indies, St. Augustine. The trees were four to six years old and consisted of sexually and asexually propagated individuals. Selections used were of local, Jamaican, Grenadian and Costa Rican sources, although the majority originated from lines grown in the United States of America (California, Hawaii, Florida).

2.1. Flower Behaviour

2.1.1. Flowering Season

Studies on the limits of and duration of flowering season were made on 11 and 87 trees, respectively, in the 1971-1972 and 1972-1973 seasons. Trees were observed at the middle and end of each month and the length of flowering period recorded for each tree. In addition, information on fruit maturity was recorded.

2.1.2. Flower Movements

Flower movements were recorded by tagging 20 flowers on each of 79 selected trees and making observations at hourly intervals, from early morning until night (5 a.m.-7p.m.) for five days. Flowers were observed for their opening and closing, receptivity of stigmas and anther dehiscence. This procedure was repeated to give two sets of observations for each of the above characters under study.

2.1.3. Time of Opening, Closing and Dehiscence of Anthers of the Flowers

The possibility of daily variation in the time of opening, closing and pollen shedding of flowers was investigated by tagging six new inflorescences on each of seven selected trees daily, for six or seven days. Four flowers in each inflorescence were marked and observed at hourly intervals from early morning until night (12:30 a.m.-7 p.m.). On trees

R_5T_{27}, R_0T_{29} and R_8T_{18}, stage I and stage II flowers were observed for seven and six days respectively; stage I and stage II flowers of the trees R_7T_{20}, R_7T_{28}, R_7T_{29} and $R_{10}T_{22}$ were observed for six and five days, respectively.

In cultivars 'Simmonds' and 'Pollock' all the flowers on six selected inflorescences were studied in a similar way for two consecutive days. Twelve different inflorescences were, therefore, marked on each cultivar. This was done in order to determine if there was any overlapping of the two sets of flowers.

More detailed measurements were made by observing flowers at 15 minute intervals from early morning until night (3 a.m.-7 p.m.), on each of 27 trees. The time of opening and closing of stage I and stage II flowers and the time of pollen shedding were recorded.

2.2. Insects Visiting the Avocado Flowers

During the two flowering seasons, 1972 and 1973, observations were carried out on the insects visiting the avocado flowers. A number of insects were taken to the laboratory and identified. In addition, insects were examined microscopically for the presence of avocado pollen grains.

2.3. Hand Cross—and Self—Pollination of the Stage I Flowers

As the avocado flower mechanism appears to be complex, there were several important points which had to be taken into consideration. These were:

- The selection of inflorescences
- Removal of the unwanted parts of inflorescences
- Bagging of inflorescences of the female parent
- Emasculation of flowers
- Bagging of inflorescences of the male parent
- Collection and storage of pollen
- Application of pollen

2.3.1. The Selection of Infloresences

No evidence of wind pollination was found in tests by Furon (1963) using a greased plate technique. However, pollination by gravity is possible when pollen grains remain on inflorescences, leaves or other parts of the tree. For this reason care was always taken to ensure that marked inflorescences were not beneath branches either of the same or any other tree. Care was also taken to select healthy inflorescences and branches which were convenient to work on.

2.3.2. Removal of the Unwanted Parts of Inflorescences

On each avocado inflorescence, a number of new flowers open and close every day, so that flower buds, open flowers, closed flowers and fruits can be seen simultaneously. Therefore, it was necessary to remove unwanted parts of the inflorescence. This was done one or two days before pollination using a pair of fine scissors. By doing this, only flowers which open for their first period remained on the inflorescences during the day of pollination.

2.3.3. Bagging of Inflorescences of the Female Parent

In order to prevent insects from visiting flowers, the selected inflorescences were bagged a day before opening of the flowers. Each bag *(ca.* 60x75 cm.) was made of fine-mesh, nylon mosquito net.

2.3.4. Emasculation of Flowers

This was done at the beginning of the first period of opening of the flowers. The stamens were cut using a nail clipper at any point along the filament, usually near the middle, so that the anther and part of the filament were removed. Care was taken to prevent injury to any other part of the flower.

2.3.5. Bagging of Inflorescences of the Male Parent

This was always done a day before the first opening of flowers, in order to avoid pollen contamination.

2.3.6. Collection and Storage of Pollen

Pollen was obtained from trees during anther dehiscence. Petri dishes were used for collection. The bottom of each dish was lined with a sheet of black paper so that the pollen was more visible.

The system of crossing and selfing used was as follows:

(i) A-type (female) x B-type (male)
(ii) B-type (female) x A-type (male)
(iii) B-type (female) x Different B-type cultivar (male)
(iv) B-type (female) x Same B-type cultivar (male)

In (i) the pollen was collected and immediately applied to the stigmas as the female and male stage of the A and B-type trees coincide, respectively. In (ii) the pollen was stored for a few hours, as the pollen shedding in the A-type trees started a few hours before the opening of the stage I flowers of the B-type trees. In (iii) and (iv) the pollen was stored from morning until afternoon. A cool room held at 55°F (12.8°C) was used for storage, as pollen retains its viability when stored under these conditions (Schroeder, 1942).

2.3.7. Application of Pollen

As soon as the flower were emasculated the pollen was applied to their stigmas. The stigmatic surface was dabbed onto the pollen grains in the petri dishes used for collection. In this way, pollen was transferred onto the stigma.

In all the trees which were cross-and/or self pollinated by hand, a number of flowers were used as controls. Pollination was prevented using methods already described (selection and bagging of inflorescences, removel of unwanted parts, emasculation of flowers).

2.4. Hand Cross-Pollination of the Stage II Flowers

Two B-type trees (R_2T_{30} and R_2T_{32}) were selected for this study. In most of the flowers on these trees the stigmas remained receptive during the second period of opening. Preliminary work indicated that it was necessary to emasculate the flowers at the beginning of the second period of opening, before the dehiscence of anther, for the following reasons:

(a) Once the flowers were emasculated during the first period of opening, the stigmas remained receptive in only a few cases during the second period of opening.

(b) Emasculation during the first period of opening delayed flower movements on the B-type trees. On the trees R_2T_{30} and R_2T_{32} flowers opened in the afternoon instead of the morning of the following day for their second period. On other B-type trees the second opening of the flowers was either in the afternoon of the following day or in the morning of the second day; some flowers did not open at all for their second period. In the A-type trees there was no such effect.

The rest of the work was carried out as previously described. Flowers of these trees were then hand cross-pollinated during their second opening and observed for fruit set.

2.5. Fruit Set Without Pollination

In addition to the flowers used as controls, a number of flowers on the trees R_2T_{30}, R_2T_{32}, R_8T_{14} and $R_{10}T_{22}$ were used for this work. In the latter, the stigma of each flower was removed and the cut surface covered with 4 per cent celloidin. The flowers were then observed for fruit set.

2.6. Mature Parthenocarpic Avocados

That avocados produce parthenocarpic fruits is a widely known fact and reported by several investigators (Clark, 1924; Stout, 1933; Gustafson, 1942; Stewart and Hield, 1951; Chandler, 1958; Umali and Bernando, 1958; Ticho, 1966; Camacho, 1970). This phenomenon was observed in 1972 during the course of this study. With a view to estimating the extent of parthenocarpy, an investigation was undertaken in 1973. Five trees of different cultivars were selected and the seeded and seedless fruits of these trees counted. The percentage of "cukes" (parthenocarpic avocados) was determined for each tree.

2.7. Fruit Set When Insects Are Excluded

The purpose of this study was to determine the extent to which fruit can set and develop to maturity without insects as pollinating agents. Four trees, one from each of the cultivars 'Simmonds,' 'Nishikawa H.,' 'Nishikawa C.,' and 'Fujikawa' were used. Inflorescences were bagged before the first opening of the flowers after removal of the unwanted parts. The flowers were then observed for fruit set and fruit development.

3. Results And Discussion

3.1. Flower Behaviour

3.1.1. Flowering Season*

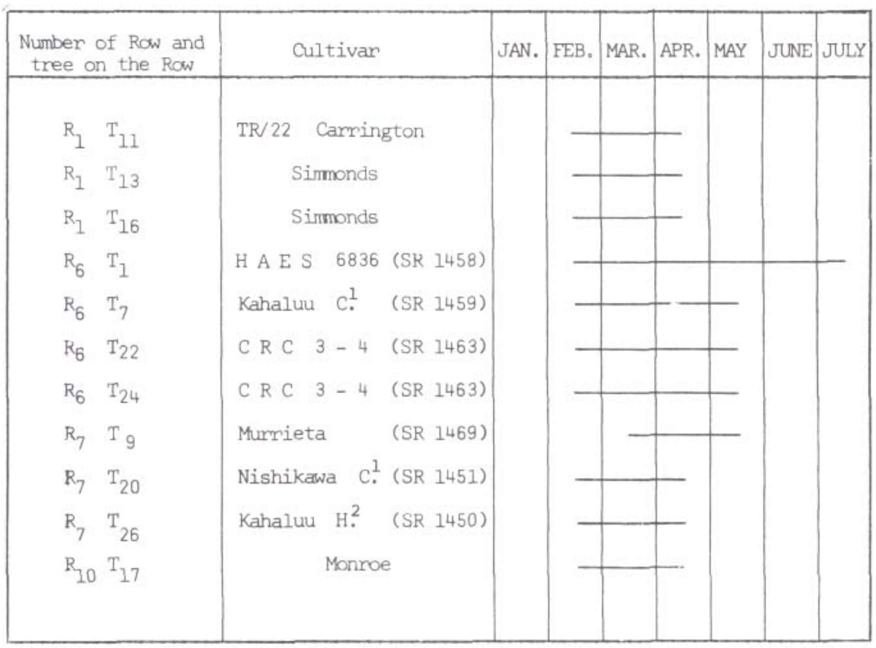
The period and duration of flowering of the trees studied are presented in Figs. 1 and 2. The results indicated that time of flowering varied between cultivars. Also great variations in duration of flowering were noticed. Some cultivars were in flower for seven to eight months, while others only one to two months; but for the majority of the cultivars the duration of flowering was two to three months. For example, cultivar 'SR 1402-127' (Fig. 2) began flowering as early as November and continued until May and the cultivar 'CRC 4-16' flowered from December to April and from July to September; the cultivar

'RC 16' began flowering in May and continued only until June. The majority of the culitvars had their first blooms during January, February or March and their last in May. Flowering in flushes was observed in the cultivars 'SR 1402-96,' 'Esparta,' 'HAES 6836,' 'CRC 3-6,' 'CRC 4-16,' 'Nishikawa C.,' 'C-154,' 'Monroe' and the tree $R_{11}T_{17}$. The amount of bloom varied greatly among trees of different cultivar.

Some mature fruits were available from June in certain cultivars *i.e.* 'Simmonds,' 'C-154' and 'C-184.' However, in the majority of cultivars fruit did not mature until July-August. The time from opening of the flowers to maturity of fruit was approximately four and one half months for the cultivar 'Simmonds' and approximately five and one half months for the cultivar 'CRC 4-16.'

* *There was an unusually long dry season in 1973 but not in 1972.*

FIGURE 1. FLOWERING SEASON OF AVOCADO TREES IN 1972.

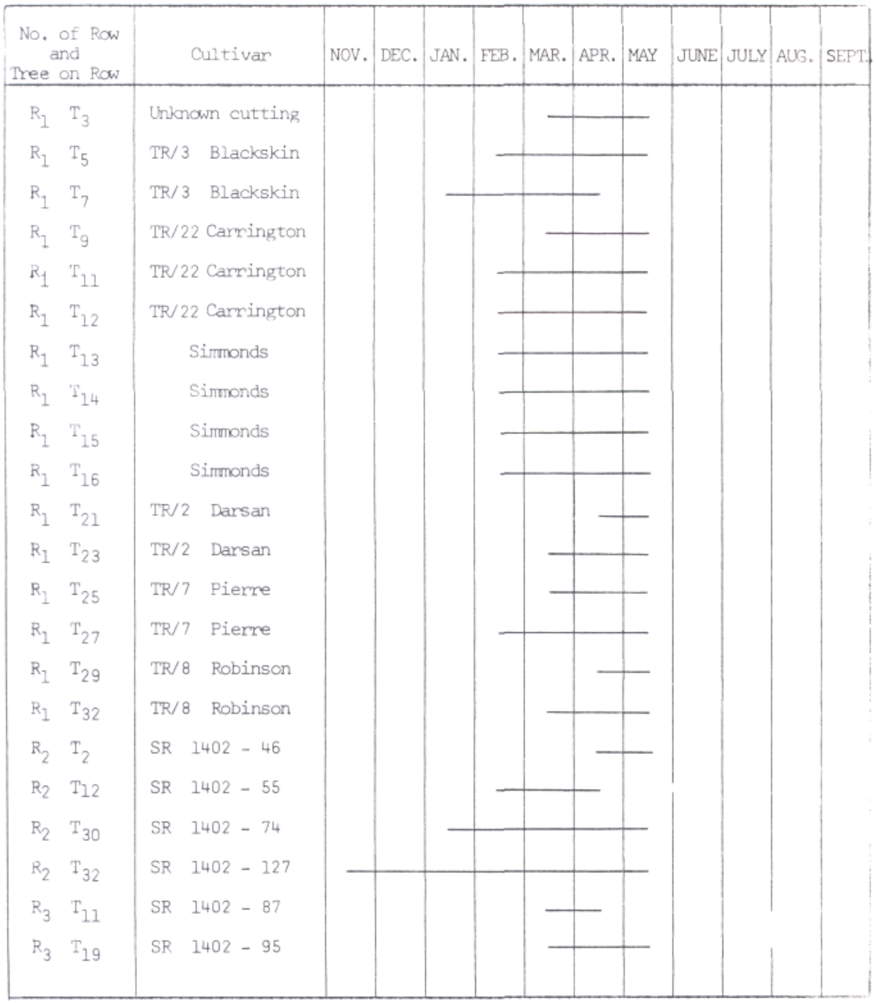


N.B. Each line represents the flowering period. Trees were observed at the middle and end of each month.

[1]*From California*

[2]*From Hawaii*

FIGURE 2. FLOWERING SEASON OF AVOCADO TREES IN 1972-1973



N.B. Each line represents the flowering period. Trees were observed at the middle and end of each month.

FIGURE 2. Continued

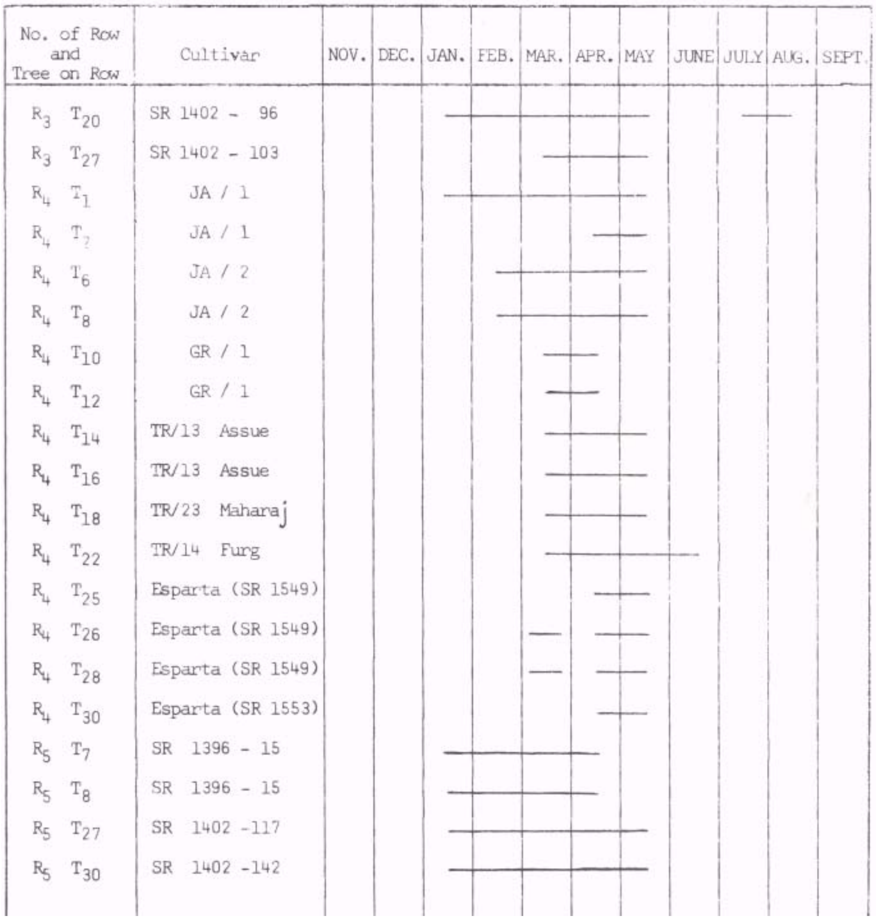
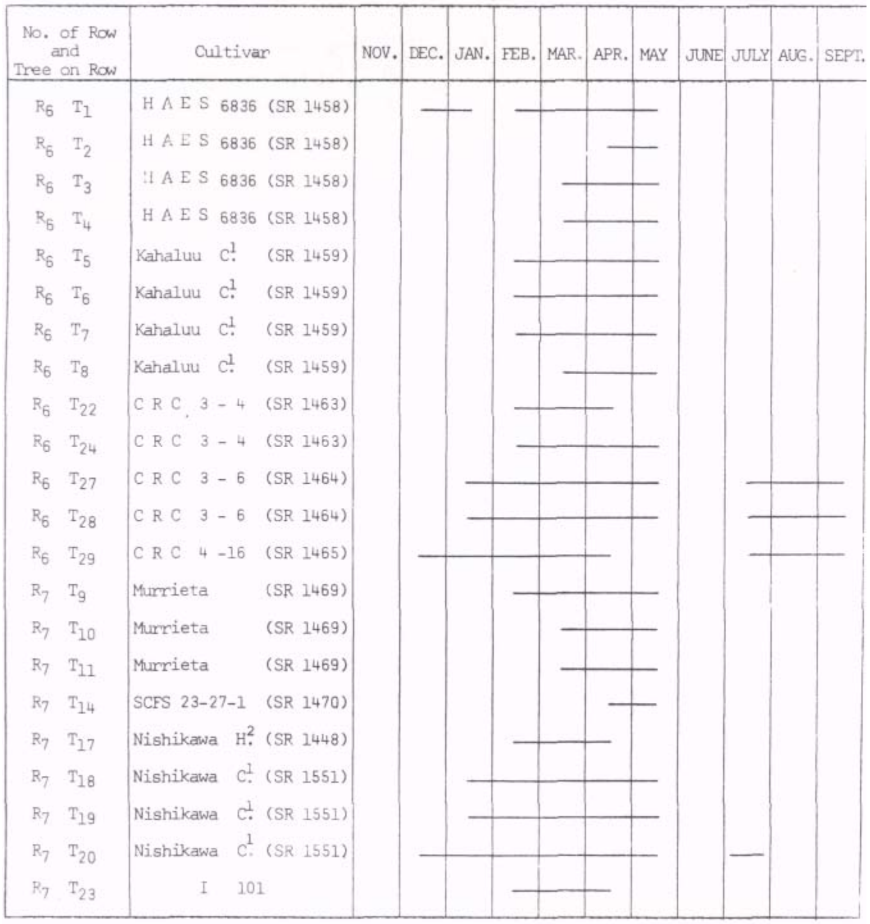


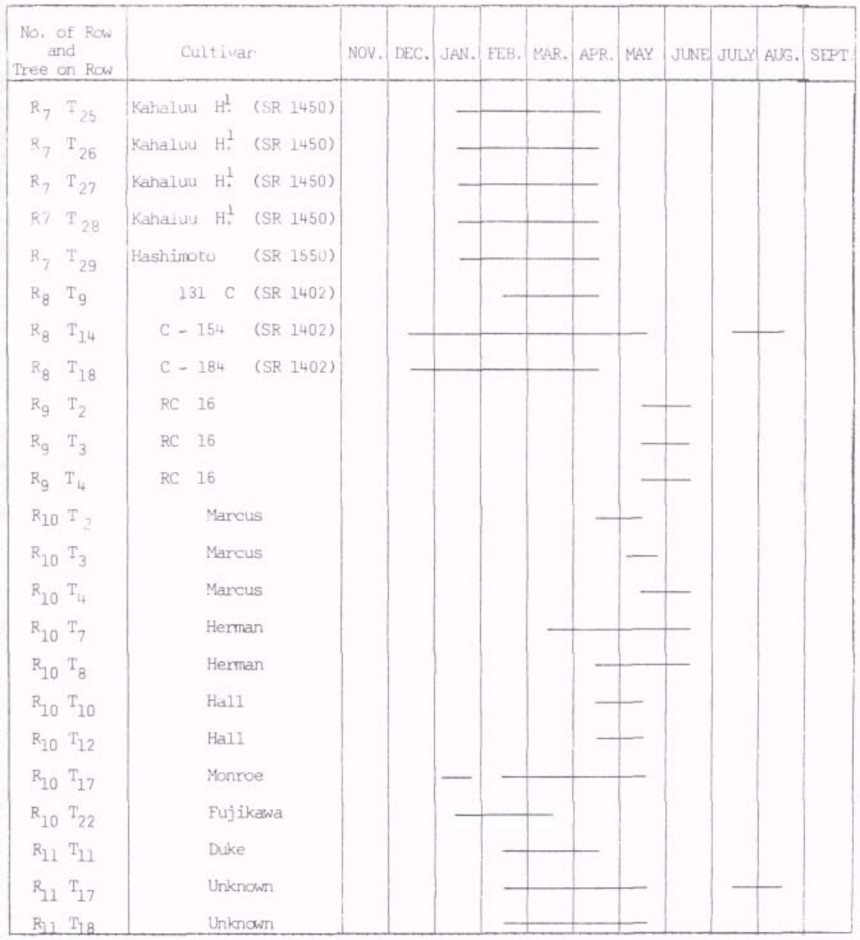
FIGURE 2. Continued



[1]From California

[2]From Hawaii

FIGURE 2. Continued



[1]*From Hawaii*

3.1.2. Flower Movements

All the trees studied had hermaphrodite flowers. The flowers were very similar in structure and appearance. However, abnormalities were observed. These were deviations from the normal number of stamens, pistils and perianth parts, fusion of parts, naked ovules, staminoidy and pistilloidy. Such abnormalities have already been observed, discussed and reported by Schroeder (1940).

3.1.2.1. Two Periods of Flower Opening

There were two distinct, separate periods of opening in each individual flower. The first and second period of opening occurred on different days. The flower opened for its first period then closed and re-opened the following day for the second period after which it closed and never re-opened.

Robinson (1931), Skutch (1932), Stout (1933), Galang and Morada (1935) and Lammerts (1942) have reported single opening of flowers. From the work of Robinson and Stout there is no doubt that this was due to changes in temperature, but in the case of Skutch and Galang and Morada single opening might have been a characteristic of the tree. No explanation was given by Lammerts for the single opening of the flowers of the 'Lyon' cultivar, but Robinson (1931) stated that such single opening of the flowers of this cultivar was due to weather conditions. Furthermore, Stout (1933) found that this cultivar was regular and classified it into Class B. No single opening of flowers was observed during this study.

3.1.2.2. The First Period of Opening

During the first period of opening of any avocado flower the stamens lay flat against the perianth parts and the pistil stood erect and separate. At this stage, the stigma was white and shining, ready to receive pollen (Plate 1 A). Also no pollen was shed, except in the cultivar 'Fujikawa.' The first period of opening may be called stage I or the female stage of the flower.

3.1.2.3. The Second Period of Opening

During the second period of opening the stamens were longer, upright and prominent (Plate 1B). The inner three stood erect in the middle of the flower, around the pistil. The outer six stood at an angle of about 40-50 degrees. At this period the stamens shed pollen, but the stigma was usually no longer receptive. However, it was observed that stigmas remained receptive on some trees during this period. The second period of opening may be called stage II or the male stage of the flower.

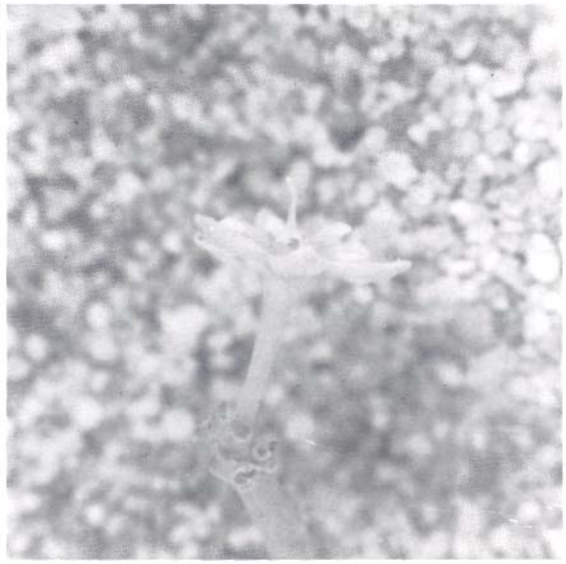
Plate 2 A illustrates avocado flowers in the interval between the first and second opening. Plate 2 B illustrates flowers closed after their second opening; at this stage the flowers are elongated.

3.1.2.4. Receptivity of the Stigma

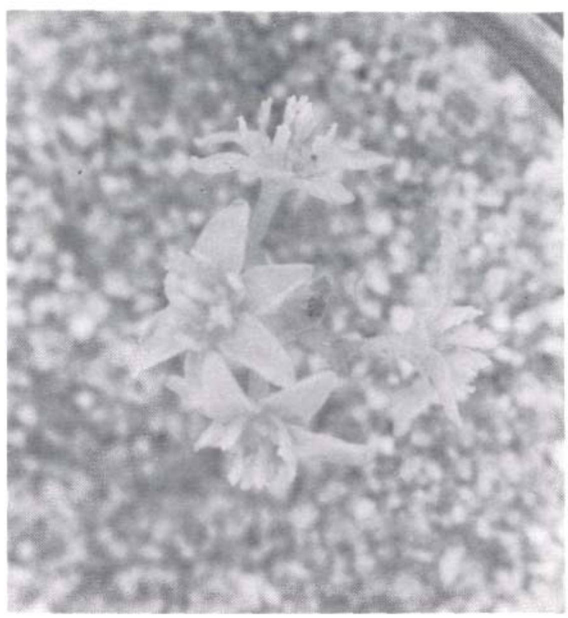
The rule for all the flowers of the trees studied was that the stigma was receptive during the first period of opening. However, stigmas appeared white and fresh during the second period. The percentage of such stigmas depended on the cultivar. In some cultivars no one stigma remained receptive, whilst in others a few or many stigmas remained receptive. Therefore, the percentage of receptive stigmas during the male stage of the flowers varied greatly between cultivars.

Stout and Savage (1925), Robinson and Savage (1926), Robinson (1931), Skutch (1932), Stout (1933), Bijhower (1938), Calvino (1939), Bringhurst (1952) and Peterson (1955b) observed receptive stigmas during the male stage of the flowers and Galang and Morada (1935) reported up to 26.52 per cent of such stigmas. Observations made in this study indicated that the majority of stigmas on the trees R_2T_{30} (cultivar 'SR 1402-74') and R_2T_{32} (cultivar 'SR 1402-127') remained receptive. It was also noted that in trees with very fine stigmas none remained receptive during the male stage of the flowers. Trees with large stigmas always appeared to have receptive ones during this stage. The size of the stigmas seemed to be a characteristic of the cultivar. It would seem that the larger the stigmas the greater percentage that remained receptive during the male stage of the flowers.

PLATE 1

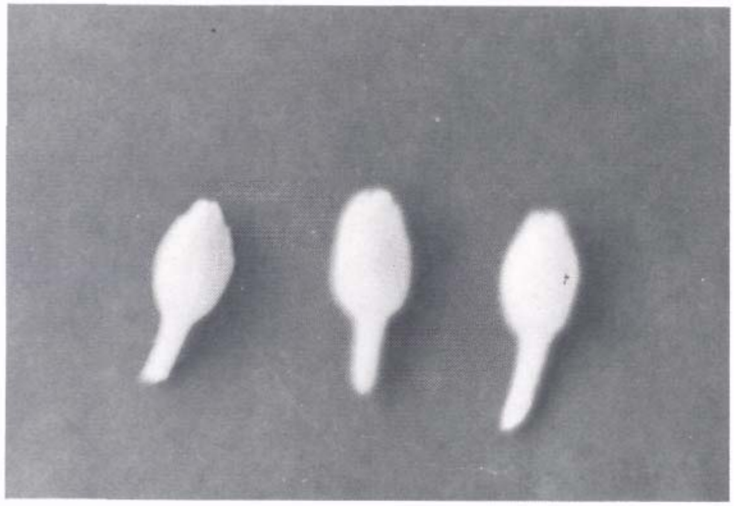


A: Avocado flower in the first period of opening (female stage).

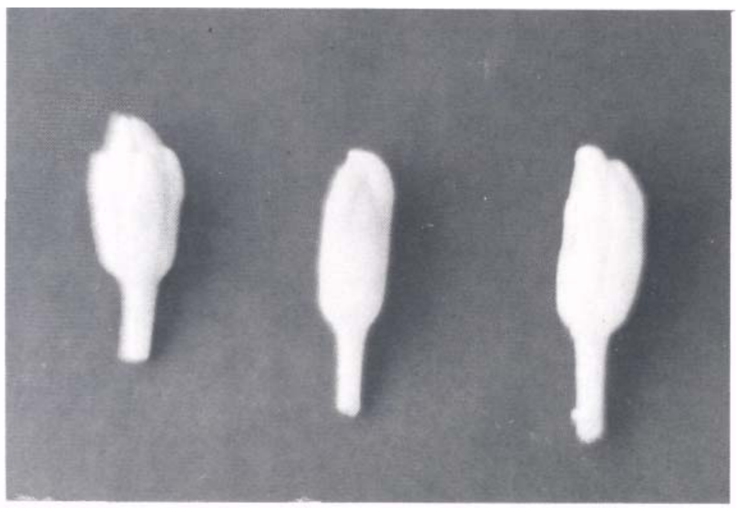


B: Avocado flowers in the second period of opening (male stage).

PLATE 2



A: Flowers in the interval between first and second opening.



B: Flowers closed after the second opening; at this stage the flowers are elongated.

3.1.2.5. Dehiscence of Anthers

With the exception of cultivar 'Fujikawa,' the general rule was that the stamens matured and shed pollen during the second period of opening of the flowers. During the first period no pollen was shed. Occasional pollen shedding during the male stage was observed on the tree R_6T_1 (cultivar 'HAES 6836').

3.1.2.6. Dichogamy

Since the pistil was mature during the first period of opening and that the stamens ripened and shed pollen in the second period only, the avocado flowers observed exhibited dichogamy of a protogynous type. The results of these observations were in agreement with Stout (1933) and others, but did not agree with Garra and Gueit (1948) who found that avocado flowers were not dichogamous.

3.1.2.7. The Two Sets of Flowers and Their Daily Alternation

Avocado flowers opened and closed for their first and second period in sets. The set of flowers, which opened for their first period, closed the same day and re-opened for the second period on the following day. Each individual tree had a succession of sets of flowers that have continuous flowering for several weeks or months. Therefore, two different sets of flowers opened and closed on each tree every day. One set opened for the first or female opening, while the other for the second or male opening. The two sets were open during different hours of the day.

3.1.2.8. Classification of the Studied Trees

In a group of trees which included different cultivars, the first opening of the flowers was in the morning and the second around midday of the following day. In another group of trees the first opening was in the afternoon and the second in the morning of the following day. Therefore, it appeared that the trees studied could be classified into two groups or classes or types, namely A and B as Stout (1923) designated them.

In the A-type trees the flowers had their first opening in the morning and their second opening around midday of the following day. In this case, one set of flowers on each tree functioned as a female in the morning and another set as a male around midday of the same day (Fig. 3).

In the B-type trees the flowers had their first opening in the afternoon and the second opening in the morning of the following day. So, the flowers of one set functioned as males in the morning, while those of the other set as females in the afternoon of the same day (Fig. 4).

It must be pointed out that all trees of the same cultivar belonged to the same group.

As indicated in Fig. 4 the ''Simmonds' (R_1T_{13}, R_1T_{14}, R_1T_{15}, R_1T_{16}) was of B-type, despite the fact that it is known as an A-type (Stout, 1933; Wolfe *et al,* 1946). Also two trees of the same name (TR/8 Robinson) behaved differently; the tree R_1T_{29} (Fig. 3) was A-type, while the tree R_1T_{32} (Fig. 4) B-type. Probably, this was the result of a mistake in budding material. As far as is known, no experimental work has been carried out concerning the change of flower behaviour type of plants when grown from seed or when budded/grafted onto rootstocks of a particular flowering type. Further work is, therefore, required on these aspects.

FIGURE. 3. A-TYPE TREES

No. of Row and Tree on Row	Cultivar	Remarks
R_1 T_9	TR/22 Carrington	Bud from local tree owned by Mr. Carrington
R_1 T_{11}	TR/22 Carrington	" " " " " " " "
R_1 T_{12}	TR/22 Carrington	" " " " " " " "
R_1 T_{29}	TR/8 Robinson	" " " " " " Mr. Robinson
R_2 T_{12}	SR 1402 - 109	Bud from California seedling
R_3 T_{11}	SR 1402 - 87	———
R_3 T_{19}	SR 1402 - 95	———
R_3 T_{20}	SR 1402 - 96	———
R_3 T_{27}	SR 1402 - 103	Wedge graft from California seedling
R_5 T_{27}	SR 1402 - 117	" " " " "
R_6 T_{29}	CRC 4-16 (SR 1465)	Bud from California
R_6 T_{30}	CRC 4-16 (SR 1465)	" " "
R_8 T_9	131 C (SR 1402)	Cutting from California seedling
R_8 T_{14}	C - 154 (SR 1402)	" " " "
R_8 T_{18}	C - 184 (Sr 1402)	" " " "
R_{10} T_7	Herman	Bud from Florida
R_{10} T_8	Herman	" " "
R_{11} T_{11}	Duke	———

FIGURE 4. B-TYPE TREES

No. of Row and Tree on Row	Cultivar	Remarks
R_1 T_5	TR/3 Blackskin	Bud from local selection
R_1 T_7	TR/3 Blackskin	Bud from local selection
R_1 T_{13}	Simmonds	Bud from a tree at the St. Augustine Nursery
R_1 T_{14}	Simmonds	" " " " " " " " "
R_1 T_{15}	Simmonds	" " " " " " " " "
R_1 T_{16}	Simmonds	" " " " " " " " "
R_1 T_{21}	TR/2 Darsan	Bud from a local tree owned by Mr. Darsan
R_1 T_{23}	TR/2 Darsan	" " " " " " " " "
R_1 T_{25}	TR/7 Pierre	" " " " " " " Mr. Pierre
R_1 T_{27}	TR/7 Pierre	" " " " " " " "
R_1 T_{32}	TR/8 Robinson	" " " " " " " Mr. Robinson
R_2 T_{30}	SR 1402 - 74	———
R_2 T_{32}	SR 1402 - 127	———
R_4 T_1	JA / 1	Bud from Jamaica
R_4 T_2	JA / 1	" " "
R_4 T_6	JA / 2	" " "
R_4 T_8	JA / 2	" " "
R_4 T_{10}	GR / 1	Bud from Grenada
R_4 T_{12}	GR / 1	" " "
R_4 T_{14}	TR/13 Assue	Bud from local tree owned by Mrs. Assue

FIGURE 4. Continued

No. of Row and Tree on Row	Cultivar	Remarks
R_4 T_{16}	TR/13 Assue	Bud from local tree owned by Mrs.Assue
R_4 T_{18}	TR/23 Maharaj	" " " " " " Mr.Maharaj
R_4 T_{26}	Esparta (SR 1549)	Bud from Costa Rica
R_4 T_{28}	Esparta (SR 1549)	" " " "
R_6 T_1	HAES 6836 (SR 1458)	Bud from California
R_6 T_3	HAES 6836 (SR 1458)	" " "
R_6 T_4	HAES 6836 (SR 1458)	" " "
R_6 T_5	Kahaluu C.(SR 1459)	Bud from California
R_6 T_6	Kahaluu C.(SR 1459)	" " "
R_6 T_7	Kahaluu C.(SR 1459)	" " "
R_6 T_8	Kahaluu C.(SR 1459)	" " "
R_6 T_{22}	C R C 3-4 (SR 1463)	Bud from California
R_6 T_{24}	C R C 3-4 (SR 1463)	" " "
R_6 T_{27}	C R C 3-6 (SR 1464)	" " "
R_6 T_{28}	C R C 3-6 (SR 1464)	" " "
R_6 T_{29}	C R C 4-16 (SR 1465)	" " "
R_6 T_{30}	C R C 4-16 (SR 1465)	" " "
R_7 T_9	Murrieta (SR 1469)	" " "
R_7 T_{10}	Murrieta (SR 1469)	" " "
R_7 T_{11}	Murrieta (SR 1469)	" " "

FIGURE 4. Continued

No. of Row and Tree on Row	Cultivar	Remarks
R_7 T_{14}	SCFS 23-27-1 (SR 1470)	Bud from California
R_7 T_{17}	Nishikawa H. (SR 1448)	" " Hawaii
R_7 T_{18}	Nishikawa C. (SR 1551)	" " California
R_7 T_{19}	Nishikawa C. (SR 1551)	" " "
R_7 T_{20}	Nishikawa C. (SR 1551)	" " "
R_7 T_{23}	I 101	" " "
R_7 T_{25}	Kahaluu H. (SR 1450)	" " Hawaii
R_7 T_{26}	Kahaluu H. (SR 1450)	" " "
R_7 T_{27}	Kahaluu H. (SR 1450)	" " "
R_7 T_{28}	Kahaluu H. (SR 1450)	" " "
R_7 T_{29}	Hashimoto (SR 1550)	" " California
R_{10} T_2	Marcus	" " Florida
R_{10} T_3	Marcus	" " "
R_{10} T_4	Marcus	" " "
R_{10} T_{10}	Hall	" " "
R_{10} T_{12}	Hall	" " "
R_{10} T_{17}	Monroe	" " "
R_{10} T_{22}	Fujikawa	" " Hawaii
R_{11} T_{17}	Unknown	
R_{11} T_{18}	Unknown	
- - -	Pollock	

3.1.2.9. The Flower Behaviour of the Cultivar 'Fujikawa'

The flowers of this cultivar had two distinct, separate periods of opening as in the case of all the other trees studied but behaved quite differently as regards the dehiscence of anthers. Most of the flowers shed pollen during the end of the first period of opening, which was in the afternoon. The number of stamens which were exposed during this stage varied among individual flowers. In some of them all the stamens shed pollen, while only a few shed pollen in others; the rest of the stamens of these flowers and the flowers without any pollen shedding during this stage, shed pollen either during the interval or the second period of opening. A similar phenomenon has been observed by Lammerts (1942) in the cultivar 'Anaheim.' This worker stated that flowers of this cultivar often shed pollen a few hours after the first opening, especially during warm weather.

Indirect autogamy or geitonogamy are quite possible during the stage I, but direct autogamy may occur as well during the closing of the stage I flowers. Such flower behaviour may be of considerable interest in the avocado industry. This is because cultivars or single trees may stand alone in solid blocks or back yards, without the need for reciprocating cultivars and even without insect visitations, provided that self-incompatibility does not exist.

3.1.3. Time of Opening, Closing and Dehiscence of Anthers of the Flowers

The results of observations on the time of opening and closing of the flowers are presented in Tables 1, 2, 3, 4, 5, 6, 7, 8, 9 and Figs. 5a and 5b. Figs. 5a and 5b also show the beginning of pollen shedding for each tree. These tables and figures summarize various characteristics of flower behaviour of the several cultivars studied.

3.1.3.1. Two Sets of Flowers on Each Tree

Two different sets of flowers opened and closed every day on each tree. The flowers of each set opened and closed relatively in unison. As the tables indicate most of the flowers of each set started opening within 1 hour and then began closing again within 1 hour. This period might have been less than 1 hour but since the observations were carried out at hourly intervals it was not possible to define the exact period.

From the beginning of opening of the first flowers until the beginning of opening of the last flowers of each set there was an interval of about 2 hours. The same situation existed for the beginning of closing of the first and last flowers.

The first period of opening was always shorter than the second period.

TABLE 1. TIME OF OPENING AND CLOSING OF THE STAGE I AND STAGE II FLOWERS

TREE: R_5T_{27}—CULTIVAR 'SR 1402-117' (A-TYPE)

Opening and closing of the Stage I flowers (first period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers Observed	Time of opening and closing and number of flowers																			
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
8-2-73	6	24								2	20	2	↓ 3	20	1							
9-2-73	6	24								7	17	0	↓ 8	16	0							
10-2-73	6	24								8	15	1	↓ 5	18	1							
11-2-73	6	24								5	18	1	↓ 7	17	0							
12-2-73	6	24								6	17	1	↓ 7	16	1							
13-2-73	6	24								10	13	1	↓16	8	0							
14-2-73	6	24								8	15	1↓8	9	7	0							

Opening and closing of the Stage II flowers (second period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers Observed	Time of opening and closing and number of flowers																			
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
9-2-73	6	24											12	11	1			↓ 6	17	1		
10-2-73	6	24											9	15	0			↓11	13	0		
11-2-73	6	24											11	13	0			↓12	12	0		
12-2-73	6	24											16	8	0			↓13	11	0		
13-2-73	6	24											13	11	0			↓22	2	0		
*14-2-73	6	24											8	15	1			↓ 0	13	11		

↓ = Beginning of the closing of the flowers
1↓8 = One flower begins opening and eight begin closing
* Rain in the afternoon 1-5 p.m.

TABLE 2. TIME OF OPENING AND CLOSING OF THE STAGE I AND STAGE II FLOWERS

TREE: R_6T_{29}—CULTIVAR 'CRC 4-16' (A-TYPE)

Opening and closing of the Stage I flowers (first period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers Observed	Time of opening and closing and number of flowers																				
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
8-2-73	6	24								3	18	3	↓ 3	21	1							
9-2-73	6	24								6	15	3	↓ 7	16	1							
10-2-73	6	24								11	13	0	↓14	9	1							
11-2-73	6	24								7	16	1	↓ 6	18	0							
12-2-73	6	24								2	17	5	↓ 2	19	3							
13-2-73	6	24								16	8	↓2	12	10	0							
14-2-73	6	24								3	13	8	↓ 3	20	1							

Opening and closing of the Stage II flowers (second period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers Observed	Time of opening and closing and number of flowers																				
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
9-2-73	6	24											12	12	0			↓ 8	15	1		
10-2-73	6	24											16	8	0			↓12	12	0		
11-2-73	6	24											15	9	0			↓12	11	1		
12-2-73	6	24											6	17	1			↓ 8	16	0		
13-2-73	6	24											9	15	0			↓14	10	0		
*14-2-73	6	24											2	20	2				↓19	5		

↓ = Beginning of the closing of the flowers

* Rain in the afternoon 1-5 p.m.

TABLE 3. TIME OF OPENING AND CLOSING OF THE STAGE I AND STAGE II FLOWERS

TREE: R_8T_{18}—CULTIVAR 'C-184' (A-TYPE)

Dates of Observations	No. of Inflore-scences	No. of flowers observed	Time of opening and closing and number of flowers																				
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
Opening and closing of the Stage I flowers (first period of opening)																						
8-2-73	6	24								3	14	7	↓ 2	5	27							
9-2-73	6	24								5	16	3	↓ 4	10	10							
10-2-73	6	24								7	15	2	↓ 8	10	6							
11-2-73	6	24								4	15	5	↓ 7	16	1							
12-2-73	6	24								5	17	2	↓ 8	16	0							
13-2-73	6	24							10	12	2	↓13	11	0								
14-2-73	6	24								6	16	2	↓ 7	17								
Opening and closing of the Stage II flowers (second period of opening)																						
			Time of opening and closing and number of flowers																			
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
9-2-73	6	24											15	7	2			↓16	8	0		
10-2-73	6	24											9	11	4			↓11	13	0		
11-2-73	6	24											11	12	1			↓14	10	0		
12-2-73	6	24											8	13	3			↓10	13	1		
13-2-73	6	24										6	18	0				↓20	4	0		
*14-2-73	6	24											22	2	0				↓18	6		

↓ = Beginning of closing of the flowers

* Rain in the afternoon 1-5 p.m.

TABLE 4. TIME OF OPENING AND CLOSING OF THE STAGE I AND STAGE II FLOWERS

TREE: R_7T_{20}—CULTIVAR 'NISHIKAWA C.' (B-TYPE)

Opening and closing of the Stage I flowers (first period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers Observed	Time of opening and closing and number of flowers: A.M. 12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	P.M. 12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
9-2-73	6	24															1	21	2	↓23	1	0
10-2-73	6	24															9	14	1↓2	22	0	
11-2-73	6	24															11	12	1	↓16	8	0
12-2-73	6	24															10	14	↓1	12	11	
13-2-73	6	24															0	21	3	↓13	11	0
*14-2-73	6	24															0	8	16	0	↓24	0

Opening and closing of the Stage II flowers (second period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers Observed	Time of opening and closing and number of flowers: A.M. 12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	P.M. 12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
10-2-73	6	24					14	9	1					↓19	5	0						
11-2-73	6	24					15	8	1					↓ 1	18	5						
12-2-73	6	24					4	16	4					↓ 1	15	8						
13-2-73	6	24				4	13	7						↓14	10	0						
14-2-73	6	24					3	18	3					↓ 2	22	0						

↓ = Beginning of the closing of the flowers
1↓2 = One flower begins opening and two begin closing
* Rain in the afternoon 1-5 p.m.
Nishikawa C. = Nishikawa from California

TABLE 5. TIME OF OPENING AND CLOSING OF THE STAGE I AND STAGE II FLOWERS

TREE: R_7T_{28}—CULTIVAR 'KAHALUU H.' (B-TYPE)

Opening and closing of the Stage I flowers (first period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers Observed	Time of opening and closing and number of flowers																			
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
9-2-73	6	24															0	22	2	↓18	6	
10-2-73	6	24															4	19	1↓4	↓20	0	
11-2-73	6	24															5	17	2	↓16	8	
12-2-73	6	24															0	16	8	↓10	14	
13-2-73	6	24															0	22	2	↓15	9	
*14-2-73	6	24															0	5	19	0	↓24	

Opening and closing of the Stage II flowers (second period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers Observed	Time of opening and closing and number of flowers																			
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
10-2-73	6	24					9	13	2				↓3	19	2							
11-2-73	6	24					10	14	0					↓10	14	0						
12-2-73	6	24					4	9	11					↓ 1	17	6						
13-2-73	6	24					6	14	4					↓ 8	15	1						
14-2-73	6	24					4	16	4					↓ 3	21	0						

↓ = Beginning of the closing of the flowers
1↓4 = One flower begins opening and four begin closing
* Rain in the afternoon 1-5 p.m.
Kahaluu H. = Kahaluu from Hawaii

TABLE 6. TIME OF OPENING AND CLOSING OF THE STAGE I AND STAGE II FLOWERS TREE: R_7T_{29}—CULTIVAR 'HASHIMOTO' (B-TYPE)

Opening and closing of the Stage I flowers (first period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers observed	Time of opening and closing and number of flowers																			
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
9-2-73	6	24													3	20	1	↓ 4	19	1		
10-2-73	6	24													6	16	2	↓23	1	0		
11-2-73	6	24													0	15	9	↓11	11	2		
12-2-73	6	24													0	17	7	↓14	10	0		
13-2-73	6	24													5	18	1	↓12	12	0		
*14-2-73	6	24													0	14	8	2	↓8	16		

Opening and closing of the Stage II flowers (second period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers observed	Time of opening and closing and number of flowers																			
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
10-2-73	6	24		4	16	4						↓10	10	4								
11-2-73	6	24		4	18	2							↓5	16	3							
12-2-73	6	24		5	15	4							↓7	14	3							
13-2-73	6	24		16	8	0						↓21	3	0								
14-2-73	6	24		8	13	3							↓4	15	5							

↓ = Beginning of the closing of the flowers
* Rain in the afternoon 1-5 p.m.

TABLE 7. TIME OF OPENING AND CLOSING OF THE STAGE I AND STAGE II FLOWERS
TREE: $R_{10}T_{22}$—CULTIVAR 'FUJIKAWA'

Opening and closing of the Stage I flowers (first period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers observed	Time of opening and closing and number of flowers																			
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
9-2-73	6	24													8	12	4	↓ 6	17	1		
10-2-73	6	24													3	17	4	↓19	5	0		
11-2-73	6	24													4	14	6	↓14	10	0		
12-2-73	6	24													11	11	2	↓16	8	0		
13-2-73	6	24													9	14	1	↓17	7	0		
*14-2-73	6	24													0	8	14	2	↓8	14	2	

Opening and closing of the Stage II flowers (second period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers observed	Time of opening and closing and number of flowers																			
			A.M.												P.M.							
			12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
10-2-73	6	24					2	17	5				13	11	0							
11-2-73	6	24					0	11	13				6	18	0							
12-2-73	6	24					0	5	15	4			9	15	0							
13-2-73	6	24				8	10	6	0				18	6	0							
14-2-73	6	24					0	7	11	6			0	13	11							

↓ = Beginning of the closing of the flowers
* Rain in the afternoon 1-5 p.m.

TABLE 8. TIME OF OPENING AND CLOSING OF THE STAGE I AND STAGE II FLOWERS
TREE: R_1T_{13}—CULTIVAR 'SIMMONDS' (B-TYPE)

Opening and closing of the Stage I flowers (first period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers observed	Time of opening and closing and number of flowers															
			A.M.								P.M.							
			4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
26-3-73	6	157											114	43	↓56	92	9	
27-3-73	6	135											61	74	↓ 2	128	5	

Opening and closing of the Stage II flowers (second period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers observed	Time of opening and closing and number of flowers															
			A.M.								P.M.							
			4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
26-3-73	6	184		5	106	73				↓21	156	7						
27-3-73	6	157		4	83	70				↓48	109	0						

↓ = Beginning of the closing of the flowers

TABLE 9. TIME OF OPENING AND CLOSING OF THE STAGE I AND STAGE II FLOWERS CULTIVAR 'POLLOCK' (B-TYPE)

Opening and closing of the Stage I flowers (first period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers observed	Time of opening and closing and number of flowers															
			A.M.								P.M							
			4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
26-3-73	6	139											44	85	↓2	106	31	
27-3-73	6	166											50	116	↓1	98	67	

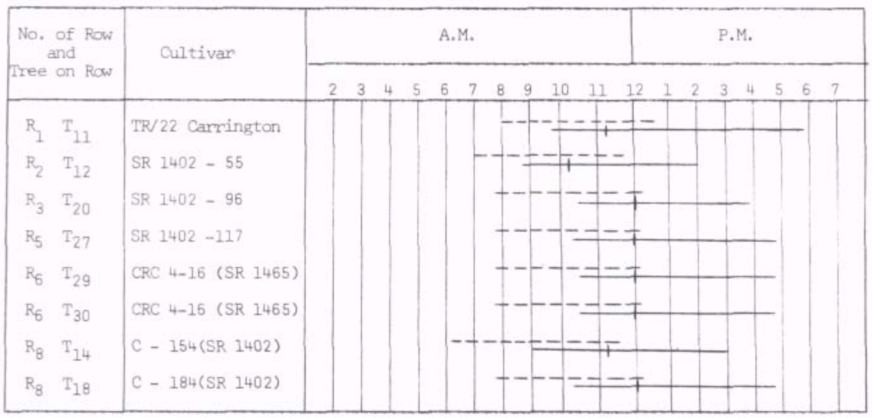
Opening and closing of the Stage II flowers (second period of opening)

Dates of Observations	No. of Inflore-scences	No. of flowers observed	Time of opening and closing and number of flowers															
			A.M.								P.M.							
			4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
26-3-73	6	153		22	96	35				52	90	11						
27-3-73	6	139		31	85	23				11	82	46						

↓ = Beginning of the closing of the flowers

FIGURE 5a. TIME OF OPENING, CLOSING AND ANTHER DEHISCENCE OF THE FLOWERS FOR ONE DAY (APRIL 1st, 1973)

(A-TYPE TREES)



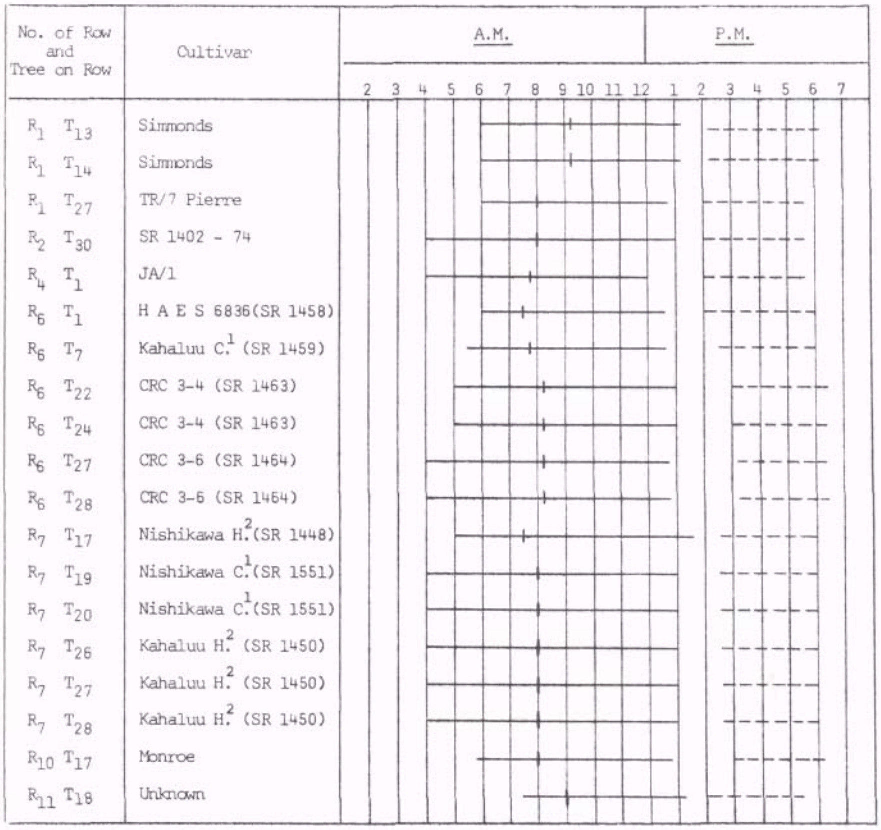
*N.B.** The broken lines indicate the first period of opening of the flowers (stage I). The beginning of the broken line indicates the time when the first flowers start to open, while the end of the broken line indicates the time when the last flowers start to close.

The continuous lines indicate the second period of opening of the flowers (stage II) for each tree. The beginning of the continuous line indicates the time when the first flowers start to open, while the end of the continuous line indicates the time when the last flowers start to close.

The vertical dash indicates the time when the first flowers start to shed pollen.

* Same explanation for the Fig. 5b.

FIGURE 5b. TIME OF OPENING, CLOSING AND ANTHER DEHISCENCE OF THE FLOWERS FOR ONE DAY (APRIL 1st, 1973) (B-TYPE TREES)



[1] *From California*

[2] *From Hawaii*

3.1.3.2. Time of Beginning of Pollen Shedding

The beginning of pollen shedding of the flowers is illustrated in Figs. 5a and 5b. In B-type trees, the period from the beginning of opening of the stage II flowers and the beginning of pollen shedding was usually longer in comparison with A-type trees. The reason for this seemed to be a matter of temperature since the stage II flowers of the B-type trees started opening early in the morning, while those of the A-type trees late in the morning or around midday. It was repeatedly observed that flowers of the cultivar 'Hashimoto' did not shed pollen until 8 a.m. even though flowers of this cultivar started opening early in the morning, 1-2 a.m. (Table 6).

3.1.3.3. Overlapping of the Two Sets

In all the A-type trees studied there was overlapping of the periods in which the two sets of flowers remained open. Because of this overlapping self-pollination was possible. The degree of overlapping differed between trees of different cultivars. As Fig. 5a shows, considerable overlapping occurred in the trees R_1T_{11} and R_2T_{12}. On the trees R_3T_{20}, R_5,T_{27}, R_6T_{29}, R_6T_{30}, R_8T_{14} and R_8T_{18}, when the stage II flowers started pollen shedding, most of the stage I flowers were in the process of closing.

Of the B-type trees only the cultivar 'Hashimoto' exhibited some overlapping. In this cultivar, the closing of the stage II flowers was very slow and so when the stage I flowers were open pollen was available from the half-closed stage II flowers.

These findings were in broad agreement with those of Wolfe *et al* (1946), Robinson and Savage (1926), Stout (1933) and Galang and Morada (1935). It must be mentioned, however, that the cultivars studied (except the cultivar 'Pollock') were different from those studied by these workers, and also that they carried out their observations under different climatic conditions. As regards 'Pollock' the results were in agreement with the previously mentioned observers, but did not agree with Torres (1936) who reported overlapping in this cultivar. In attempting to explain this, he added that it might be due to soil-moisture conditions.

3.1.3.4. Classification of Trees into Two Groups

The trees studied fell into two groups called A and B for convenience. The daily behaviour was typical and representative for the various trees of both groups.

3.1.3.5. Differences within the Groups

Trees of the same cultivar behaved similarly although the precise behaviour was far from uniform among the individuals of either group. With respect to the time of the opening of flowers, the duration of the periods of opening, the length of the interval and the period of overlap there were differences which were characteristic for each cultivar. However, it was observed that the trees R_5,T_{27}, R_6T_{29} and R_8T_{18} had a similar behaviour despite the fact that these trees were different A-type cultivars. Similar behaviour was also observed in the B-type cultivars 'Nishikawa C.' and 'Kahaluu H.'

3.1.3.6. Time of Flower Movements of the Cultivar 'Hashimoto'

As indicated in Table 6 the flowers of this cultivar started to open as early as 1-2 a.m. Despite this, pollen shedding did not occur until about 8 a.m. The stage II flowers remained open for a longer time in comparison with all the other cultivars studied.

Stout (1927) considered that the principal external stimuli controlling flower movements of avocados were light and temperate. He came to this conclusion because during his studies the flowers were open only during the hours of daylight. The fact that the flowers of the cultivar 'Hashimoto' and some other cultivars (Tables 4, 5, 6, 7 and Fig. 5b) opened or started opening during darkness suggested that the role of light in flower opening is doubtful.

3.1.3.7. Steady Flower Behaviour

The flower behaviour of the various trees studied was remarkably constant, day after day, under similar weather conditions. Deviation was observed on the 14th of February, 1973 on the closing of the stage II flowers of the A-type trees R_5T_{27}, R_6T_{20} and R_8T_{18} (Tables 1, 2, 3); also on the closing of the stage I flowers of the B-type trees R_7T_{20}, R_7T_{28}, R_7T_{29} and $R_{10}T_{22}$ (Tables 4, 5, 6, 7). On that day it rained between 1 and 5 p.m. It appeared, therefore, that this rainfall may have delayed the closing of flowers.

3.1.3.8. Reciprocations in Pollination

There was a close relationship between the time of opening of the stage I flowers on the A-type trees and the time of opening of the stage II flowers on the B-type trees. Thus, the female stage of the A-type trees and the male stage of the B-type trees coincided in all the trees which were observed. However, for the male stage of the A-type trees and the female stage of the B-type trees the opening of flowers was not coincidental *e.g.* on trees R_2T_{12} and R_6T_{27} (Figs. 5a and 5b). These observations agreed with those of Stout (1933).

3.2. Insects Visiting the Avocado Flowers

As avocados exhibit dichogamy, an external agent to ensure pollination is required. It is generally recognized that avocados are pollinated by insects and reports have indicated that honey bees are the principal insects visiting the avocado flowers (Nirody, 1922; Clark, 1923; Clark and Clark, 1926; Stout and Savage, 1925; Stout, 1933; Calvino, 1939; Wolfe *et al,* 1946; Lesley and Bringhurst, 1951; Win-slow and Enderud, 1955; Lecomte, 1961; Furon, 1963; Bergh, 1967).

In this study the most abundant species visiting the avocado flowers was *Polistes canadensis* (wasp) of the family *Vespidae.* This insect was quite active throughout the two flowering seasons, frequently moving from flower to flower and from one tree to another. Species of wasps have also frequently been found visiting the avocado flowers in Florida (Stout and Savage, 1925). The next most abundant species was *Metabolybia singulata* of the same family *(Vespidae).*

Honey bees *(Apis mellifera)* were frequent visitors for 2 weeks in 1972 from the middle until the end of March. For the rest of the flowering season honey bees rarely visited the flowers. In 1973, however, only fourteen bees were seen on the flowers after making observations for the entire flowering season. A possible explanation was that the bees were attracted to other areas where plants with more attractive nectar and pollen were growing. Limited visitations by honey bees have been also reported by Robinson and Savage (1926) in certain regions of Florida. In addition, *Musca* sp. and some other flies visited the avocado flowers but only in small numbers.

Microscopic examinations of *Polistes canadensis, Metabolybia singulata* and bees showed that these insects carried avocado pollen on their bodies. It was observed that bees carried more avocado pollen grains than insects of the other two species.

3.3. Hand Cross- and Self-Pollination of the Stage I Flowers

The results of cross- and self-pollination by hand as compared to those of the control are presented in Tables 10, 11 and 12. Hand pollination seems to be effective in avocados. In all cases there was initial fruit set; 10.2 to 44.4 and 13.9 to 46.5 per cent initial fruit set was obtained from cross, and self-pollination, respectively. These results agree with Peterson (1955b).

The initial percentage set decreased gradually during the first 7 weeks. After that period only fruits which attained maturity remained on the trees. Mature fruits were obtained from the 'Simmonds' cultivar crossed with 'Carrington,' 'Nishikawa H.' and the 'Duke' and from the cultivar 'CRC 4-16' crossed with the cultivar 'Fujikawa.' Cultivars 'Simmonds' and 'Carrington' are of West Indian Race, and the cultivar 'Nishikawa H.' appeared to be of Guatemalan Race. All the mature fruits were seeded and normal in size and shape; the percentage varied from 2.04 to 5.81.

Results indicated that there was initial fruit set from flowers of some trees, which were used as control (Table 12). With the exception of the cultivar 'Fujikawa,' the initial percentage fruit set was very low and fruits were on the trees for only a short period (1-2 weeks).

The data obtained suggested that avocados can be used in breeding work, although pollinations by hand seem to be of limited importance in practice, as the percentage set of mature fruits is low (1.5%, if all the flowers cross- and self-pollinated are considered). Such results are in agreement with Nirody (1922), Robinson and Savage (1926), Stout (1933), Lammerts (1942, 1945), Toy (Wolfe *et al,* 1946), Lesley and Bringhurst (1951) and Bergh (1957). In addition to the low percentage fruit set, the whole operation is difficult. Lammerts (1945) commenting on these difficulties stated that he had never worked with a plant that was quite as cantankerous and difficult to handle from all points of view.

TABLE 10. HAND CROSS-POLLINATION OF THE STAGE I FLOWERS

Row and Tree	R_1T_{11}(♀) x R_1T_{15}	R_1T_{15}(♀) x R_1T_{11}	R_1T_{13}(♀) x R_7T_{17}	R_7T_{17}(♀) x R_1T_{13}	R_1T_{13}(♀) x $R_{11}T_{11}$
Cultivar	Carrington (♀) x Simmonds	Simmonds (♀) x Carrington	Simmonds (♀) x Nishikawa H.[1]	Nishikawa H.[1] (♀) x Simmonds	Simmonds (♀) x Duke
No. of flowers hand cross-pollinated	42	41	38	36	49
Initial fruit set	7	5	9	12	5
1 week after	4	3	8	11	4
2 weeks after	3	3	3	8	2
3 " "	1	2	2	0	1
4 " "	1	2	2		1
5 " "	0	2	2		1
6 " "		2	2		1
7 " "		2	2		1
8 " "		2	2		1
9 " "		2	2		1
10 " "		2	2		1
11 " "		2	2		1
12 " "		2	2		1
13 " "		2	2		1
14 " "		2	2		1
15 " "		2	2		1
16 " "		2	2		1
17 " "		2	2		1
18 " "		2	2		1
19 " "					
20 " "					
21 " "					
Initial percentage set	16.7	12.2	23.7	33.3	10.2
percentage set of mature fruits	0	4.88	5.26	0	2.04

From Hawaii

TABLE 10. Continued

Row and Tree	$R_{11}T_{11}$(♀) x R_1T_{13}	R_7T_{17}(♀) x $R_{11}T_{11}$	$R_{11}T_{11}$(♀) x R_7T_{17}	R_6T_{29}(♀) x R_7T_{29}	R_7T_{29}(♀) x R_6T_{29}
Cultivar	Duke (♀) x Simmonds	Nishikawa H.[1] (♀) x Duke	Duke (♀) x Nishikawa H.[1]	CRC 4-16 (♀) x Hashimoto	Hashimoto (♀) x CRC 4-16
No. of flowers hand cross-pollinated	25	40	23	39	36
Initial fruit set	5	9	4	11	16
1 week after	5	8	3	8	8
2 weeks after	3	5	2	6	2
3 " "	1	0	0	6	0
4 " "	1			4	
5 " "	0			2	
6 " "				1	
7 " "				0	
8 " "					
9 " "					
10 " "					
11 " "					
12 " "					
13 " "					
14 " "					
15 " "					
16 " "					
17 " "					
18 " "					
19 " "					
20 " "					
21 " "					
Initial percentage set	20.0	25.5	17.4	28.2	44.4
Percentage set of mature fruits	0	0	0	0	0

[1]From Hawaii

TABLE 10. Continued

Row and Tree	R_6T_{29}(♀) x $R_{10}T_{22}$	$R_{10}T_{22}$(♀) x R_6T_{29}	R_7T_{20}(♀) x R_6T_{29}	R_5T_{27}(♀) x R_7T_{20}
Cultivar	CRC 4-16 (♀) x Fujikawa	Fujikawa (♀) x CRC 4-16	Nishikawa C.[1] (♀) x CRC 4-16	SR 1402-117 (♀) x Nishikawa C.[1]
No. of flowers hand cross-pollinated	86	49	35	41
Initial fruit set	19	21	8	12
1 week after	17	19	6	8
2 weeks after	12	10	3	5
3 " "	9	2	0	2
4 " "	9	0		0
5 " "	8			
6 " "	5			
7 " "	5			
7 " "	5			
8 " "	5			
9 " "	5			
10 " "	5			
11 " "	5			
12 " "	5			
13 " "	5			
14 " "	5			
15 " "	5			
16 " "	5			
17 " "	5			
18 " "	5			
19 " "	5			
20 " "	5			
21 " "	5			
Initial percentage set	22.1	42.9	22.9	29.3
Percentage set of mature fruits	5.81	0	0	0

[1]From California

TABLE 11. HAND SELF-POLLINATION OF THE STAGE I FLOWERS

Row and Tree	R_1T_{13}(♀) x R_1T_{13}	R_7T_{17}(♀) x R_7T_{17}	R_7T_{20}(♀) x R_7T_{20}	$R_{10}T_{22}$(♀) x $R_{10}T_{22}$	R_7T_{29}(♀) x R_7T_{29}
Cultivar	Simmonds (♀) x Simmonds	Nishikawa H:[1] (♀) x Nishikawa H:[1]	Nishikawa C:[2] (♀) x Nishikawa C:[2]	Fujikawa (♀) x Fujikawa	Hashimoto (♀) x Hashimoto
No. of flowers hand self-pollinated	38	64	115	43	38
Initial fruit set	7	15	16	20	14
1 week after	4	10	9	10	7
2 weeks after	1	5	6	5	4
3 " "	1	1	2	0	1
4 " "	0	1	0		0
5 " "		1			
6 " "		0			
7 " "					
Initial percentage set	18.4	23.4	13.9	46.5	36.8
Percentage set of mature fruit	0	0	0	0	0

[1]*From California*
[1]*From Hawaii*

TABLE 12. CONTROL

Row and Tree	R_1T_{13}	R_1T_{15}	R_1T_{11}	R_7T_{17}	$R_{11}T_{11}$	R_6T_{29}	$R_{10}T_{22}$	R_7T_{29}	R_7T_{20}	R_5T_{27}
Cultivar	Simmonds	Simmonds	Carrington	Nishikawa H[1]	Duke	CRC 4-16	Fujikawa	Hashimoto	Nishikawa C[2]	SR 1402-117
Number of flowers used as controls	46	45	53	102	31	128	91	36	133	47
Initial fruit set	2	0	0	0	0	4	30	0	2	0
1 week after	1					1	14		1	
2 weeks after	0					0	7		0	
3 " "							0			
4 " "										
5 " "										
6 " "										
7 " "										
Initial percentage set	4.3	0	0	0	0	3.1	33.0	0	1.5	0
Percentage set of mature fruit	0	0	0	0	0	0	0	0	0	0

[2]*From California*
[1]*From Hawaii*

3.4. Hand Cross Pollination of the Stage Ii Flowers

Bringhurst's (1952) and Peterson's (1955b, unpublished) hand pollinations during the second period of opening of the flowers never resulted in fruit set and Gustafson and Bergh (1966), who reviewed the literature on pollination of avocados, concluded that the egg cell is ready for fertilization for only a limited time.

Results from this study (Table 13) demonstrated that there was fruit set from the trees R_2T_{32} and R_2T_{30}. There was also initial fruit set on the control, but fruits remained on the trees for only a short period. The last two fruits, one from the tree R_2T_{32} and one from the tree R_2T_{30}, which resulted from pollination during the second opening of the flowers, were examined after abscission and were found to contain seeds.

At present there is no proof that apogamy or apospory occur in avocados. Work by Schroeder (1944) showed that there was no evidence of nucellar embryony such as occurs in citrus and mangoes. In view of the evidence presented above, it would seem probable, therefore, that egg cells remain in proper condition for fertilization during the second period of opening of the flowers. However, the number of flowers pollinated was relatively low and more conclusive work is required.

TABLE 13. HAND CROSS-POLLINATION OF THE STAGE II FLOWERS

Row and tree	R_2T_{32}(♀) x R_1T_{13}		R_2T_{30}(♀) x R_7T20	
Cultivar	SR 1402-127(♀) x Simmonds		SR 1402-74(♀) x Nishikawa C[1]	
	Cross-pollination	Control	Cross-pollination	Control
Number of flowers	29	29	38	35
Initial fruit set	6	3	9	3
1 week after	4	2	2	1
2 weeks after	2	0	2	0
3 " "	2		1	
4 " "	1		1	
5 " "	1		1	
6 " "	0		0	
7 " "				
Initial percentage set	20.7	10.3	23.7	8.6
Percentage set of mature fruits	0	0	0	0

'From California

3.5. Fruit Set Without Pollination

As indicated in Tables 12, 13 and 14 there was initial fruit set in seven of the 12 tested cultivars. This fruit set varied between cultivars, *i.e.* 1.5 to 33 per cent in the control (Tables 12 and 13) and 6.5 to 39.4 per cent in flowers in which stigmas had been removed and the cut surfaces covered with celloidin in addition to bagging (Table 14). The initiated fruits were on the trees for only a short period. In view of the results obtained it would seem that autonomous parthenocarpy occurs in avocados.

3.6. Mature Parthenocarpic Avocados

Table 15 indicates the ratio between seeded and seedless fruits on five trees of different cultivars. The percentage of "cukes" (or "cues") varied from 2.3 to 100. It is noteworthy that the 'Esparta' produced only seedless fruits. A similar situation, regarding this cultivar, was found by Camacho (1970) in Costa Rica.

Plate 3 shows seedless fruits from the cultivars studied as compared to the seeded ones. The size of the seedless fruits varied greatly. Some of them were very small and were, therefore, of no commercial importance; others were as large as the seeded fruits (Plate 3F). However, as a general rule from observations made seedless avocados were found to be smaller than seeded ones.

Many of the "cukes" were cut open for observation. Macro inspection of seed cavity showed that in some of them (Plate 3A, E, F) there were rudimentary seeds, which suggested that embryo development started and abortion occurred at a later stage.

3.7. Fruit Set When Insects Are Excluded

The results of this study or given in Table 16.

In cultivars 'Simmonds' and 'Nishikawa H.' there was no fruit set from the bagged inflorescences. These cultivars had no receptive stigmas during the second period of opening of the flowers when pollen was being shed. However, it was found in another study (Table 12), that in the cultivar 'Simmonds' there was some initial fruit set in the control and most probably such fruit set was due to autonomous parthenocarpy.

In the cultivar 'Nishikawa C.' there was initial fruit set. Possible explanations were that the fruit resulted either from autonomous parthenocarpy or from direct autogamy since some stigmas remained receptive during the second opening of the flowers.

In the cultivar 'Fujikawa,' there was initial fruit set and three of the fruits attained maturity. As previously mentioned the flowers of this cultivar shed pollen during their first period of opening when the stigmas were receptive and most probably the fruit resulted from direct autogamy. However, a considerable percentage of the flowers set fruit without any pollination, but those fruits remained on the tree only for a short period.

An anomaly has been observed on the three fruits which attained maturity. These fruits were substantially smaller in comparison with the fruits from open pollinated flowers (plate 4A); also they were seedless (Plate 4B). Pollen germination and pollen tube growth occurred whenever the flowers were self-pollinated. Therefore, either fertilization did not occur, or if it did occur, embryo abortion probably took place. Three fruits from the open pollinated flowers (of the interior of the tree) were similar to these fruits (small and seedless) and probably resulted from self-pollination. All the other fruits from the open pollinated flowers were seeded and normal in size and shape.

Clark and Clark (1926), Lammerts (1942), Lesley and Bringhurst (1951) and Peterson (1955b) found that the exclusion of insects almost entirely prevents fruit setting. The results of this study agreed with their findings, except for the observations on the cultivar ‘Fujikawa’ where pollen was shed during the first opening of the flowers.

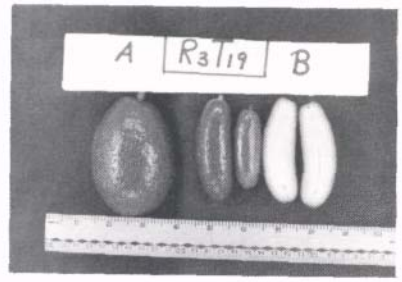
TABLE 14. FRUIT SET WITHOUT ANY POLLINATION

Row and Tree	$R_{10}T_{32}$	R_2T_{32}	R_2T_{30}	R_8T_{14}
Cultivar	Fujikawa	SR1402-127	SR1402-74	C-154
No. of bagged unpollinated flowers	28	44	46	47
Initial fruit set	11	4	3	10
1 week after	2	3	1	2
2 weeks after	0	0	0	0
3 " "				
4 " "				
5 " "				
Initial percentage set	39.4	9.1	6.5	21.3
Percentage set of mature fruits	0	0	0	0

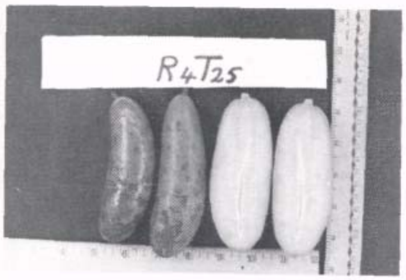
TABLE 15. PERCENTAGE OF PARTHENOCARPIC FRUITS

Row and Tree	Cultivar	No. of mature fruits	No. of seedless fruits	Percentage of seedless fruits
R_1T_{13}	Simmonds	128	3	2.3
R_3T_{19}	SR 1402-95	17	14	82.3
R_4T_{25}	Esparta	23	23	100
R_7T_9	Murrieta	62	14	22.6
$R_{11}T_{18}$	Unknown	37	9	24.3

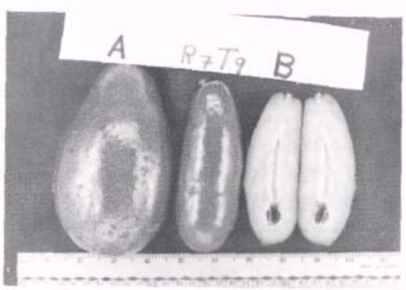
PLATE 3

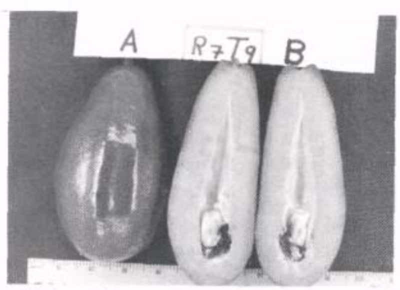


A. Seeded fruit at left. Seedless fruit at right (Cultivar: 'Simmonds'). B. Seeded fruit at left. Seedless fruit at right (Cultivar: 'SR 1402-95).



C. Seedlss fruit from the cultivar 'Esparta.' D. Seeded fruit at left. Seedless fruit at right. (Unknown cultivar).





E. Seeded fruit at left. Seedless fruit at right. (Cultivar: 'Murrieta'). F. Seeded fruit at left. Seedless fruit at right. (Cultivar: 'Murrieta').

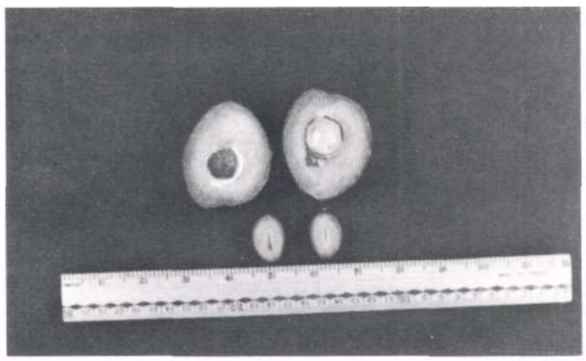
TABLE 16. FRUIT SET WHEN INSECTS ARE EXCLUDED

Row and tree	R_1T_{13}	$R_7\ T_{17}$	$R_{10}T_{22}$	R_7T_{20}
Cultivar	Simmonds	Nishikawa H.[1]	Fujikawa	Nishikawa C.[2]
No. of flowers bagged	138	128	229	148
Initial fruit set	0	0	104.	4
1 week after			42	1
2 weeks after			14	0
3 " "			10	
4 " "			9	
5 " "			9	
6 " "			7	
7 " "			5	
8 " "			5	
9 " "			4	
10 " "			3	
11 " "			3	
12 " "			3	
13 " "			3	
14 " "			3	
15 " "			3	
16 " "			3	
17 " "			3	
18 " "			3	
19 " "			3	
20 " "			3	
21 " "			3	
22 " "			3	
23 " "			3	
24 " "			3	
Initial percentage set	0	0	45.4	2.7
Percentage set of mature fruits	0	0	1.3	0

[1]*From California*
[2]*From Hawaii*

PLATE 4

A: Fruits from the cultivar 'Fujikawa.' Both small and large fruits are of the same age (about six months). The three small fruits resulted, more probably, from self-pollination, while the three large fruits resulted from open-pollinated flowers.



B: Two fruits, one small and one large from the upper photograph A. The small one is seedless and the large one seeded.

4. Summary and Conclusions

1. The duration of flowering varied from 1-2 to 7-8 months between different cultivars. Most of the cultivars flowered for 2-3 months. Certain cultivars had their flowers in flushes. Variations were also observed in the period of flowering. Therefore, when reciprocating cultivars are interplanted their flowering periods must coincide sufficiently.
2. Flowers exhibited two periods of opening and dichogamy of protogynous type. As a general rule stigmas were receptive during the first opening and the pollen was shed during the second opening of the flowers.
3. Two different sets of flowers opened and closed every day on each tree. The flowers of one set opened for their first period while those of the other set for their second period.
4. The flower behaviour of the various trees studied was regular, day after day. Cultivars were classified into two groups, A and B. In group A cultivars, the flowers had their first opening in the morning and their second opening around midday of the following day. In group B cultivars the flowers had their first opening in the afternoon

and their second in the morning of the following day.

5. The female stage of the A-type cultivars and the male stage of the B-type cultivars coincided in all cases. For the male stage of the A-type cultivars and the female stage of the B-type cultivars the opening of the flowers was not always coincidental. Hence, when interplanting reciprocating cultivars care must be taken to ensure that their male and female stages coincide sufficiently to allow reciprocal pollination.
6. In the A-type cultivars there was overlapping of the periods in which the two sets of flowers remained open; the degree of overlapping differed among cultivars. Of the B-type cultivars only the cultivar 'Hashimoto' exhibited some overlapping.
7. The flowers of the cultivar 'Hashimoto' started opening as early as 1-2 a.m.; also the flowers of some other cultivars started opening during darkness. This suggested that the role of daylight in flower opening is doubtful.
8. The principal insect visitors of avocado flowers were *Polistes canadensis* (wasp) and *Metabolybia singulata* of the family *Vespidae.* Honey bees *(Apis mellifera)* rarely visited the flowers. Insects appeared to be necessary for pollination and subsequent crop production.
9. Hand pollination appeared to be effective; 10.2 to 44.4 per cent and 13.9 to 46.5 per cent initial fruit set was obtained from cross- and self-pollination, respectively. In the cultivars ‘Simmonds’ and 'CRC 4-16' in which fruit attained maturity the percentage set of mature fruits was 2.04 and 5.81, respectively. When all the flowers which were cross- and self-pollinated by hand were considered then the percentage of mature fruits was 1.5.
10. Hand cross-pollination of the stage II flowers resulted in fruit set. This suggested that egg cells remained in a proper condition for fertilization during the second period of opening of the flowers.
11. In the absence of pollination there was initial fruit set in seven of the 12 tested cultivars. The fruit set varied between cultivars (1.5- 39.4 per cent). Initiated fruits were on the trees for only a short period. This suggested that autonomous parthenocarpy occurs in avocados.
12. On five trees of different cultivars, the percentage of mature parthenocarpic fruits varied from 2.3 to 100. The cultivar 'Esparta' produced only seedless fruits. In some of the "cukes" there were rudimentary seeds, which suggested that embryo development started and abortion occurred at a later stage.
13. In the cultivar 'Fujikawa' most of the flowers shed pollen during the end of their first period of opening and therefore, self-pollination was possible even without insect activities. However, fruits which most probably resulted from self-pollination were seedless and substantially smaller in comparison with the fruits from open pollinated flowers; the small seedless fruits were of no commercial value. Hence, this cultivar would appear to require cross-pollination.
14. In general it would seem that mixing A- and B-type cultivars in an orchard increases the probability of pollination.

Acknowledgments

I wish to express my gratitude to Professor Egbert A. Tai who suggested this field of study, gave invaluable advice throughout the experimental work and reviewed part of the manuscript. I am also greatly indebted to Dr. M. S. Sandhu for his guidance in the research project.

Sincere thanks are due to Mr. L. Hosein, Dr. E. J. Duncan and Dr. B. G. F. Springer for valuable suggestions.

Finally, I wish to thank the Government of Trinidad and Tobago for awarding the postgraduate scholarship which made these investigations possible.

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