TECHNICAL BULLETIN NO. 39 MARCH 1959

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ACKNOWLEDGMENTS

The authors wish to thank the following personnel of the Hawaii Agricultural Experiment Station for assistance in this study: T. Nishida for the donation of carpenter bee hives and for insect identification; C. Higa for the loan of a honey bee hive; and F. A. I. Bowers for the use of some passion fruit plants. They also wish to thank W. Mitchell of the Bureau of Entomology, U. S. Department of Agriculture, Honolulu, Hawaii, for the loan of the wire cage. The help rendered by former botany graduate students, E. T. Ozaki and A. J. Gilmartin, is also acknowledged with appreciation.

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INTRODUCTION

The development on the use of the yellow passion fruit (*Passiflora edulis* forma *flavicarpa* Degener) for beverage, ice cream, sherbet, pastries, and other confectionaries has resulted in increased plantings of this crop in Hawaii. With this expansion, various cultural problems have been brought to the attention of the Hawaii Agricultural Experiment Station by farmers growing this crop and by the processors of passion fruit juice. In the studies reported here factors which may limit fruit set, fruit production, and juice yield have been given special attention.

THE PLANT

The botanical relations and the history of the commercial types of passion fruit have been described (*4*). It is a member of the genus *Passiflora* and is characterized by hypogynous, choripetalous flowers with five stamens, a tripartite style, and corona (*11*). The stamens and pistil are on an androgynophore. The plant is a woody, perennial vine which is a vigorous climber. The flowers are borne singly in the leaf axils of new growth. Studies in nodal anatomy revealed an anamolous development of the flower bud. There is a common flower-tendril primordium from which is first differentiated, the tendril, and subsequently, from the base of the axillary structure, the flower. In cases where the flower development is much delayed, the distance between the leaf axil and the point where the peduncle emerges from the tendril may be as much as an inch or more (fig.1).

Whereas, in other countries, the *Passiflora edulis* Sims is the commercial type, in Hawaii the related yellow-fruited form *P. edulis* forma *flavicarpa* Degener is the type cultivated commercially. The yellow passion fruit differs from the purple type in having a yellow rather than a purple pericarp, brown rather than black seeds, and partially nocturnal rather than strictly diurnal flowering (*26*).

The yellow passion fruit was introduced into Hawaii in 1923 from Australia where it presumably originated as a sport of the purple passion fruit. The yellow type is best adapted to elevations from sea level to 2,500 feet, whereas the purple type favors higher elevations. In spite of the more pleasant flavor of the purple type, it has not become commercially acceptable in Hawaii because of its smaller fruit and lower yield (*4*).

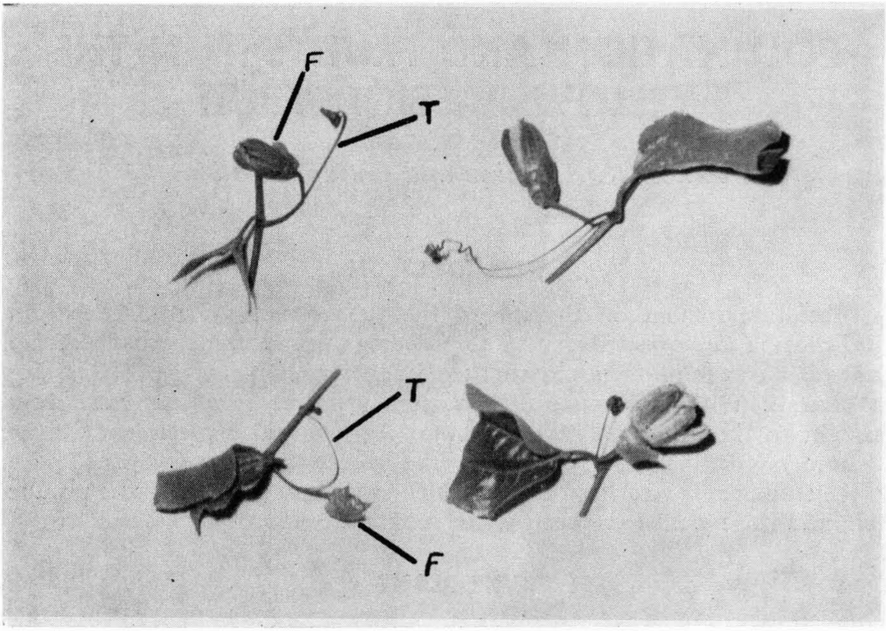

FIGURE 1. The emergence of the flower from the tendril caused by common flower-tendril primordium. T = tendril. F = flower.

METHODS

The studies reported herein were started in 1954 and concluded in 1958. They entailed observations on approximately 6,000 flowers on 130 individual seedling plants and some clonal plants. The field experiments were conducted at the Waimanalo Experimental Farm and at the Mid-Pacific Experimental Farm. Experiments were also performed in the laboratory.

In controlled pollinations in the field, the flowers were covered just prior to opening with 2-pound brown paper bags to prevent contamination by undesirable pollen. The bags were opened and the pollination performed within 2 hours after flower opening. The flowers were then covered again. Paper clips were employed to fasten the bags to the peduncles (fig. 2). This system was also practical when it was desirable to protect the developing fruit from fruit flies. It was demonstrated that the temperature within the bag may be as much as 8° F. higher than the ambient air temperature. However, no detrimental effect on fruit set or fruit growth could be attributed to this temperature differential.

Artificial pollinations were effected either by bringing the exposed microsporangial surface covered with microspores in direct contact with the stigmatic surface, thus transferring the pollen to the stigma or by transferring

FIGURE 2. Brown paper bags employed to prevent contamination in controlled pollinations.

the pollen with a small glass applicator. Self-pollination was effected with pollen from the same flower or from another flower on the same plant. Emasculation was not practiced following the discovery of the self-incompatible nature of the plant.

Fruit set or lack of it can be determined 2 days subsequent to pollination by observing the growth of the ovary. However, in most cases, fruit set percentage was determined approximately 1 week after pollination. The number of flowers opening each day on a single plant is usually small. Thus, it was necessary at times to repeat identical experiments at different times. However, since the results were similar, the data in such cases were combined for presentation.

All laboratory experiments were conducted at room temperature. All special procedures are described under appropriate headings.

Aside from cultural practices such as fertilizer application, irrigation, weed control, and disease control, factors seemingly related to fruit set and juice yield were extensively studied.

The term "incompatibility" as employed in this paper refers to failure of viable pollen to fertilize the ovule *(6)*.

RESULTS

Flower Receptivity and Pollen Viability

The flower of the yellow passion fruit normally opens about noon and closes about 10 o'clock in the evening. (The flower of the purple type opens at dawn and closes by noon.) Flowers pollinated as early as 10 o'clock in the morning and as late as 10 o'clock in the evening have set fruit. Under natural conditions, however, the most effective time for pollination is after the styles have completely recurved subsequent to flower opening. At this time, not only is the stigmatic surface in a position most apt to be brushed by pollinating insects (fig. 3), but the increased stickiness of the stigmatic surface by this time further insures that the pollen remains in place.

The stigma was found to be receptive only on the day of flower opening. Pollen may be kept viable for at least 1 day under refrigeration (45° F.) provided it is not allowed to come in contact with free moisture. Some fresh flowers when pollinated with such stored pollen set fruit. However, in nature the viability of pollen probably does not extend beyond 24 hours.

FIGURE 3. Pollen-laden carpenter bee effecting pollination by brushing against the anther and stigma in its quest for nectar. Arrow points to carpenter bee.

Open Pollination

Fruit set by open or natural pollination in the field was observed to be generally inferior to that which could be induced by hand pollination. Factors contributing to this condition will be discussed later. Data recorded in table 1 for three plants not only indicate the low fruit set but also its extreme variability among plants for open-pollinated flowers.

TABLE 1. Fruit set by open pollination

PLANT	NUMBER OF FLOWERS	NUMBER OF FRUITS SET	PERCENT FRUIT SET
C-37	209	34	16.3
C-77	35	1	2.8
M-20	41	20	48.8

Self-pollination

A total of 130 individual seedling plants was employed in the determination of self-compatibility. A total of 2,603 hand self-pollinated flowers was involved in this study. Of these, only 25 or .96 percent set fruit. The data for some representative plants presented in table 2 indicate that the yellow passion fruit is for all practical purposes self-incompatible. Individual flowers self-pollinated by carpenter bees and honey bees caged in 10-pound brown paper bags or mosquito screen cages (4″ × 5″ × 7″) with the flower failed to set fruit.

TABLE 2. Fruit set by hand self-pollination

PLANT	NUMBER OF FLOWERS POLLINATED	NUMBER OF FRUITS SET	PERCENT FRUIT SET
C-37	162	3	1.8
C-39	64	0	0.0
C-77	83	0	0.0
C-80	88	0	0.0
W-1	40	0	0.0
W-9	20	0	0.0
W-10	21	0	0.0
W-24	29	2	6.9
W-43	21	0	0.0
W-70	21	0	0.0
W-82	25	3	12.0
M-3	29	0	0.0
M-4	27	0	0.0
M-5	22	0	0.0
M-6	25	0	0.0
M-7	21	0	0.0
M-11	24	0	0.0
M-12	34	0	0.0
M-13	24	0	0.0
M-14	28	0	0.0
M-15	20	0	0.0
M-16	38	0	0.0
M-17	32	0	0.0
M-18	25	0	0.0
M-19	20	0	0.0
M-20	25	0	0.0
M-21	21	0	0.0
M-22	27	2	7.4
M-23	30	0	0.0
M-24	21	0	0.0
M-25	27	1	3.7
F-1	21	0	0.0
F-3	25	1	4.0

Cross-pollination

Studies on cross-pollination were conducted on 2,573 flowers involved in 65 crosses and reciprocal crosses. Cross-compatibility and cross-incompatibility are clearly revealed in the pollination data of four plants recorded in table 3.

TABLE 3. Fruit set by hand cross-pollination

RECIPROCAL CROSSES	NUMBER OF FLOWERS POLLINATED	NUMBER OF FRUITS SET	PERCENT FRUIT SET
C-37 and C-39	258	237	91.9
C-37 and C-77	83	2	2.4
C-37 and C-80	106	2	1.9
C-39 and C-77	250	242	96.8
C-39 and C-80	167	162	97.0
C-77 and C-80	80	3	3.8

Whereas plants C-37, C-77, and C-80 are essentially mutually incompatible with each other, plant C-39 is mutually highly compatible with all the other three (table 3). These four seedling plants were originally selected by the Horticulture Department, assisted by the Food Processing Laboratory, for their outstanding fruit and juice yields and juice quality.

The data in table 3 were obtained from reciprocal crosses which produced similar results with respect to fruit set. There are, however, cases in which reciprocal crosses do not produce similar results. This is evidenced by the data in table 4.

The limited data obtained seem to indicate the possibility of male sterility as the factor causing the difference in response between reciprocal crosses. When plant W-89 was used as the male parent, no fruit set on either plant W-84 or plant W-88; however, as a female parent, it was functional in that it set fruit with pollen from either plant (table 4).

TABLE 4. Fruit set in reciprocal crosses

CROSS ♀ ♂	NUMBER OF FLOWERS POLLINATED	NUMBER OF FRUITS SET	PERCENT FRUIT SET
W-83 × W-88	40	23	57.5
W-88 × W-83	32	0	0.0
W-94 × W-99	31	0	0.0
W-99 × W-94	46	38	82.6
W-84 × W-89	20	0	0.0
W-89 × W-84	20	12	60.0
W-88 × W-89	22	0	0.0
W-89 × W-88	41	34	82.9

Other cross-pollination data in table 5 further indicate the variability in the degree of cross-compatibility.

TABLE 5. Miscellaneous cross-pollinations in relation to fruit set

CROSS	NUMBER OF FLOWERS POLLINATED	NUMBER OF FRUITS SET	PERCENT FRUIT SET
♀ ♂			
F-1 × C-37	47	34	72.3
F-2 × C-37	92	50	54.3
F-3 × C-37	226	150	66.4
H-1 × C-37	44	35	79.5
W-29 × C-37	10	10	100.0
C-80 × F-2	11	11	100.0
C-80 × F-3	19	16	84.2
W-19 × W-12	11	9	81.8
W-13 × W-14	10	6	60.0
W-79 × W-80	10	6	60.0
W-77 × W-80	10	10	100.0

Pollen Transfer Agents

Wind. The pollen of passion fruit has been assumed not to be wind-borne because of its heavy sticky nature. To determine the effect of wind on pollen transfer, two plants at Waimanalo Experimental Farm were individually caged with mosquito screens (6′ × 6′ × 12′) which prevented the entrance of pollinating insects. Although these plants flowered profusely, no fruit set over a period of several months. Adjacent uncaged plants set fruit readily.

In the same field, two other experiments were conducted to ascertain the movement of air-borne pollen by collecting the pollen in traps (glass plates 5″ × 7″ covered with thin layers of gelatin colored lightly with crystal violet on one side, covered with a roof to prevent washing away of adhering surface by rain, and mounted 4 feet above the ground on a stake). Gelatin was found to make a better adhering surface than vaseline or lanolin. The crystal violet was taken up avidly by the pollen and thus was made easily identifiable. A microscope was employed to count the pollen grains embedded in the traps. In the first experiment, six pollen traps were placed on the leeward side of the field. They were placed with the glass plates perpendicular to the pervailing wind direction in a single straight row at varying distances from the edge of the field. According to the results in table 6, the number of pollen grains collected in the traps was so small that no precise conclusions could be drawn as to the effect of the weather on pollen movement although there is a tendency for the pollen to be carried farther away with increase in the wind velocity.

TABLE 6. Number of wind-borne pollen grains trapped at varying distances from the field

DATE	WEATHER	DISTANCE FROM EDGE OF FIELD (FEET)					
		20	50	80	110	140	170
June 26, 1956	rain and wind	8	6	3	3	0	0
June 28	calm	32	9	----	----	----	----
June 29	windy	8	8	2	4	3	4
July 1	very calm	0	0	0	0	0	0
July 2	calm	2	3	0	1	1	1
July 3	windy	6	5	0	2	4	2
July 4	windy	10	5	0	2	1	0
July 5	light breeze	6	3	1	0	0	2
July 6	light breeze	9	19	4	2	0	0
July 7	light breeze	8	2	1	2	0	1

In the second experiment, the pollen traps were placed within the field, midway between rows or 7½ feet from the middle of either row, either facing the row or facing the wind. The results are presented in table 7.

TABLE 7. Number of wind-borne pollen grains trapped within the field

DATE	POSITION OF POLLEN TRAP					
	Row 1 facing row	Row 2 facing row	Row 2 facing wind	Row 5 facing row	Row 5 facing wind	Row 9 facing row
July 7, 1956	1	19	27	7	4	4
July 8	21	69	80	68	119	79
July 10	54	30	103	3	11	28
July 11	21	10	30	31	57	25
July 12	30	20	42	38	27	71

In general, the traps facing the wind collected more pollen than those facing the row (table 7). However, as shall be shown later, even if all of the 119 pollen grains collected in the trap facing the wind in row 5 on July 8 were to land on a stigma, the surface area of which is only approximately 1/250th of that of the adhering surface of the trap, this would still be an insufficient amount of pollen to bring about normal fruit set (table 18). Thus, the conclusion that passion fruit pollen is dispersed only to a limited extent by wind and that if wind pollination occurs at all, fruit set is not to be expected from it seems logical.

Insects. The carpenter bee (*Xylocopa varipuncta* Patton) is generally considered to be the main pollinating agent of the yellow passion fruit (*15*). In its quest for nectar in the nectary situated at the base of the gynophore, this large insect invariably brushes the anthers and stigmas, thus effectuating pollination (fig. 3). The relative efficiency of the carpenter bee as a pollinating agent as compared to that of smaller insects such as the honey bee (*Apis mellifera* L.) and wasps (*Polistes* spp.) was determined at the Mid-Pacific Experimental Farm. Parts of a plant were enclosed in a wire cage (½-inch mesh on a 5′ × 5′ × 6½′ frame) which excluded carpenter bees but permitted smaller insects to enter (fig. 4). To increase the

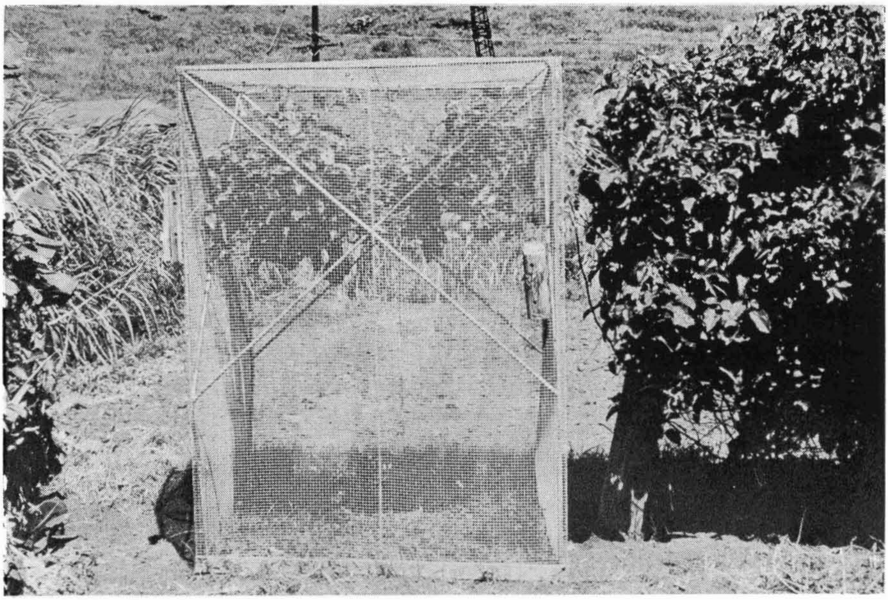

FIGURE 4. Parts of a plant enclosed in wire cage which prevented the entry of carpenter bees but allowed free movement of smaller insects in and out of the cage. Vines were trimmed to show the details of the cage.

insect activity in the vicinity of the experimental plant, a honey bee hive and four carpenter bee hives (1-foot sisal logs) were placed near the cage.

During the 1-year duration of the experiment, only honey bees and wasps were observed within the cage. The number of flowers and fruits set within the cage and in a 3-foot portion of the plant immediately adjacent to the cage is recorded in table 8.

TABLE 8. Fruit set as affected by caging to prevent pollination by carpenter bees

POSITION	NUMBER OF FLOWERS	NUMBER OF FRUITS SET	PERCENT FRUIT SET
Cage	260	39	15.0
Open	364	144	39.6

According to the results in table 8, even honey bees and wasps are to a degree effective pollinators. On the assumption that the fruits set in the open were the result of pollination by both the carpenter bees and honey bees and wasps, the smaller insects accounted for approximately 38 percent of the total natural fruit set. Limited data revealed that fruits set in the cage and in the open were about the same in size and juice yield, indicating that for those flowers that set fruit, pollination was equally effective.

Some insects which frequent the passion fruit flower have been observed to be pollen destroyers. Some honey bees are pollen gatherers, while others are nectar gatherers. The hover flies (*Eristalis arvorum* Fab.) feed on pollen. The long-horned grasshoppers (*Conocephalus saltator* Sauss.) cut away anthers and possibly feed on the pollen, too. However, the damage incurred by these insects is probably insignificant, especially in view of the fact that they are potential pollinators.

Style Recurvature in Relation to Fruit Set

Normally, shortly after the flower opens, the erect styles recurve, and shortly before flower closing they return to an upright position. Style recurvature is completed in approximately 1 hour. In styles which do not recurve completely, the degree of recurving varies from complete lack of it to nearly complete recurving (fig. 5). Flowers with upright styles present a physical problem in pollination. In these the great distance between the stigma and coronal surface prevents even the carpenter bees from coming in contact with the stigmatic surface, thus lessening the chance of pollination.

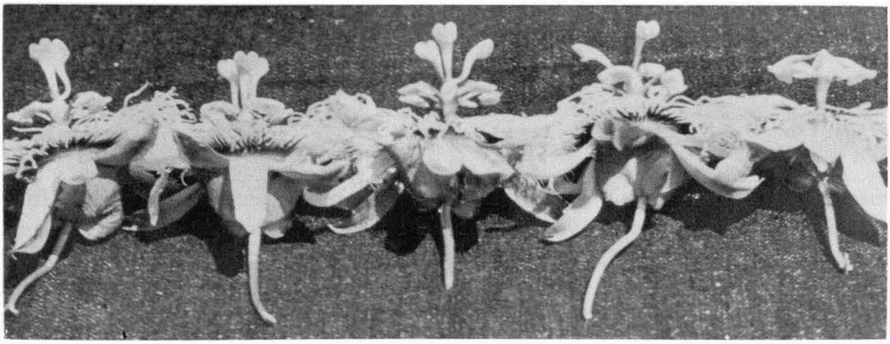

FIGURE 5. Degree of recurving of the styles in passion fruit flowers. Extreme right flower normal; others abnormal.

Furthermore, upright-styled flowers present a physiological problem. These flowers do not set fruit even when hand pollinated with pollen from compatible plants. However, pollen from upright-styled flowers is viable and functional in that it is capable of setting fruit on a compatible plant. A typical relationship between two plants is shown in table 9.

TABLE 9. Fruit set in flowers with upright styles

POLLINATION	NUMBER OF FLOWERS POLLINATED	NUMBER OF FRUITS SET	PERCENT FRUIT SET
M-20 pollen on M-18 upright-styled flower	57	0	0
M-18 pollen of upright-styled flower on M-20 flower	36	36	100
M-20 pollen on M-18 normal flower	73*	73	100

*Includes reciprocal cross.

Plant M-18 is a plant with a relatively high percentage of flowers with upright styles and plant M-20 is completely devoid of these abnormal flowers (table 10). These plants are mutually compatible with each other. Whereas normal flowers of plant M-18 set fruit when pollinated with pollen from plant M-20, upright-styled flowers failed to set fruit (table 9). However, the pollen from upright-styled flowers was effective in setting fruit on plant M-20.

Although flowers with upright styles possess slightly smaller ovaries than normal flowers and are in general somewhat yellower than normal ones, no anatomical difference between the two types could be observed.

The frequency of the occurrence of flowers with upright styles was determined on plants at the Mid-Pacific Experimental Farm. A typical observation is shown in table 10 in which data for 3 successive days are presented.

The percentage of upright-styled flowers in different plants ranges between wide limits—from 0 to over 50 (table 10). This variation in the production of these abnormal flowers is presumably genetical.

TABLE 10. Frequency of occurrence of flowers with upright styles

PLANT	TOTAL NUMBER OF FLOWERS ON 3 SUCCESSIVE DAYS	NUMBER OF FLOWERS WITH UPRIGHT STYLES	PERCENT OF FLOWERS WITH UPRIGHT STYLES
C-37	107	38	35.5
C-39	103	17	16.5
C-77	116	4	3.4
C-80	124	0	0.0
M-3	33	0	0.0
M-4	14	0	0.0
M-5	77	0	0.0
M-6	127	13	10.2
M-7	46	2	4.3
M-11	130	0	0.0
M-12	75	3	4.0
M-13	52	8	15.4
M-14	61	0	0.0
M-15	122	1	0.8
M-16	103	19	18.4
M-17	161	20	12.4
M-18	211	108	51.2
M-19	146	1	0.7
M-20	181	0	0.0
M-21	118	2	1.7
M-22	18	6	33.3
M-23	17	9	52.9
M-24	86	0	0.0
M-25	187	4	2.1

Flower Production

The total flower production for a complete season was not determined. However, data obtained for a major part of a season indicated a variability in the individual plants for the entire season. The flower production of plants in the Mid-Pacific Experimental Farm as presented in table 11 shows the wide variation in the monthly production of flowers as well as in the total for the period of observation.

TABLE 11. Flower production in the Mid-Pacific Experimental Farm

PLANT	JULY, 1957	AUGUST	SEPTEMBER	OCTOBER	NOVEMBER	TOTAL
C-39	6	5	13	23	5	52
C-77	6	42	11	4	11	71
C-80	32	35	50	9	7	133
M-3	7	9	24	6	4	50
M-4	1	6	19	9	0	35
M-5	2	5	10	0	2	19
M-6	1	41	24	20	4	90
M-7	0	45	8	5	11	69
M-11	15	5	10	10	0	40
M-12	19	18	47	10	1	95
M-13	19	23	37	19	7	105
M-14	1	19	25	20	11	76
M-15	1	21	14	6	4	46
M-16	0	18	7	6	2	33
M-17	2	36	45	13	2	98
M-18	0	74	60	0	0	134
M-19	4	53	42	5	0	104
M-20	38	86	97	82	31	334
M-21	2	35	21	6	2	66
M-22	7	57	30	2	0	96
M-23	6	46	43	2	0	97
M-24	3	12	15	13	1	44
M-25	15	74	55	11	0	155

TABLE 12. Flower production in the Waimanalo Experimental Farm

PLANT	NOVEMBER 4, 1957	NOVEMBER 15	NOVEMBER 25	DECEMBER 6	DECEMBER 11	TOTAL
W-83	62	43	10	1	0	116
W-84	83	11	5	0	0	99
W-85	64	24	8	1	0	97
W-86	62	22	8	1	0	93
W-87	77	5	1	0	0	83
W-88	86	40	3	0	0	129
W-89	72	16	4	0	0	92
W-90	98	49	4	0	0	151
W-91	41	3	0	0	0	44
W-92	56	50	1	0	0	107
W-93	40	12	3	0	0	55
W-94	104	43	6	0	0	153
W-95	22	10	2	0	0	34
W-96	40	39	10	0	0	89
W-97	72	37	16	1	0	126
W-98	63	35	12	0	0	110
W-99	74	17	6	0	0	97
W-100	53	53	16	0	0	122
W-101	60	14	2	0	0	76
W-102	136	63	3	0	0	202

Data collected for a few days toward the close of the flowering season from plants in the Waimanalo Experimental Farm also show variation in flower production (table 12).

Limited data seem to indicate that time of peak flower production may also vary from plant to plant (table 11).

Time of Flower Opening

Flower opening begins in the early afternoon. The opening time, however, may vary with different plants as evidenced by the data on the opening time of the first flower for each plant (table 13).

Carpenter bees and honey bees tend to concentrate their activities on the first-opened flowers. Thus, the advantage of flowers on different plants opening at about the same time of day is apparent in that cross-pollination is enhanced. Cross-pollination is further enhanced if the periods of flowering during the year in different plants coincide.

TABLE 13. Time of opening of first flower of different plants (October 4, 1956, at Mid-Pacific Experimental Farm)

PLANT	FLOWER OPENING TIME (P.M.)
M-25	12:30
M-20	12:40
M-13	12:45
M-3, M-4, M-5, M-6, M-7, M-11, M-15, M-16, M-17, M-18, M-19, C-77, C-80	1:00
M-21	1:05
M-24	1:07
C-39	1:10
M-14, M-23	1:22
M-12, C-37	1:30
M-22	1:36

Stigma Wetting

Poor fruit sets have been reported from areas of heavy rainfall in Hawaii. This prompted a study on the effect of wetting the flowers on fruit set. In one experiment conducted at the Waimanalo Experimental Farm, flowers on a stand of clonal plants were artificially wetted with an atomizer at varying intervals after pollinating with pollen from a mutually compatible plant. Care was exercised to thoroughly wet the stigmas. The results in table 14 indicate that 100 percent fruit set can be expected only when the stigmas are kept dry for at least two hours after pollination. This time interval was later determined to correspond to the time necessary for pollen germination.

TABLE 14. Effect of stigma wetting on fruit set

TIME OF STIGMA WETTING AFTER POLLINATING*	NUMBER OF FLOWERS POLLINATED	NUMBER OF FRUITS SET	PERCENT FRUIT SET
Immediately	50	0	0.0
½ hour	30	0	0.0
1 hour	33	2	6.1
1½ hours	31	8	25.8
2 hours	48	48	100.0
2½ hours	50	50	100.0
No wetting	50	50	100.0

*Plant C-39 pollen on plant C-80 stigma.

Pollen grains permitted to germinate on the stigma are not destroyed by subsequent wetting which does not interfere with ovule fertilization or fruit set (table 14). Ungerminated pollen grains, however, burst immediately upon contact with free moisture and are thereby destroyed.

In another experiment, flowers were subjected to cycles consisting sequentially of pollination, wetting of stigmas, and drying (table 15).

TABLE 15. Effect of successive pollinating, drying, and wetting sequences on fruit set

TREATMENTS	NUMBER OF FLOWERS USED	NUMBER OF FRUITS SET	PERCENT FRUIT SET
Pollinated*	35	35	100.0
Pollinated, wetted†	50	0	0.0
Pollinated, wetted, dried, repollinated	30	30	100.0
Pollinated, wetted, dried, repollinated, wetted	30	0	0.0
Pollinated, wetted, dried, repollinated, wetted, dried, repollinated	30	2	6.7

*Plant C-39 pollen on plant C-77 stigma.
†Immediately after pollinating.

As in the previous experiment, stigmas wetted immediately after pollinating failed to set fruit (table 15). Furthermore, fruit set resulted when the stigmas were wetted once and then dried prior to second pollination. However, very little fruit set occurred following a second wetting and drying cycle. In view of the discovery of the requirements for germination of pollen grains (discussed in another section), it is postulated that some water-soluble substance necessary for germination present on the stigmatic surface is washed away by the repetitive wettings.

In a third experiment, frequent showers were simulated. One-half of a row of plants started from a single clone (plant C-37) was sprayed with water from a hand sprayer and the other half was left unsprayed. Natural pollination was allowed, and after the flowers opened, three successive sprays were made at hourly intervals. In the sprayed area, none of the 100 flowers set fruit, whereas 32 of the 92 flowers in the unsprayed area set fruit (34.8 percent). Moreover, in the sprayed area, bee activity was greatly reduced as compared with that in the unsprayed area. Therefore, in addition to the adverse effect of the wetting on the pollen grains, the lack of fruit set in the sprayed area was probably also due to insufficient pollination attributable to reduced insect activity.

Hand vs. Natural Pollination

Fruit set from natural pollinations is usually poor (table 1) as compared with that from hand pollinations involving compatible plants (tables 3, 4, 5). Experiments were conducted which showed that fruits from hand-pollinated flowers are also larger (fig. 6) and yield more juice than those from open-pollinated ones. The results of a typical experiment conducted at the Mid-Pacific Experimental Farm are recorded in table 16.

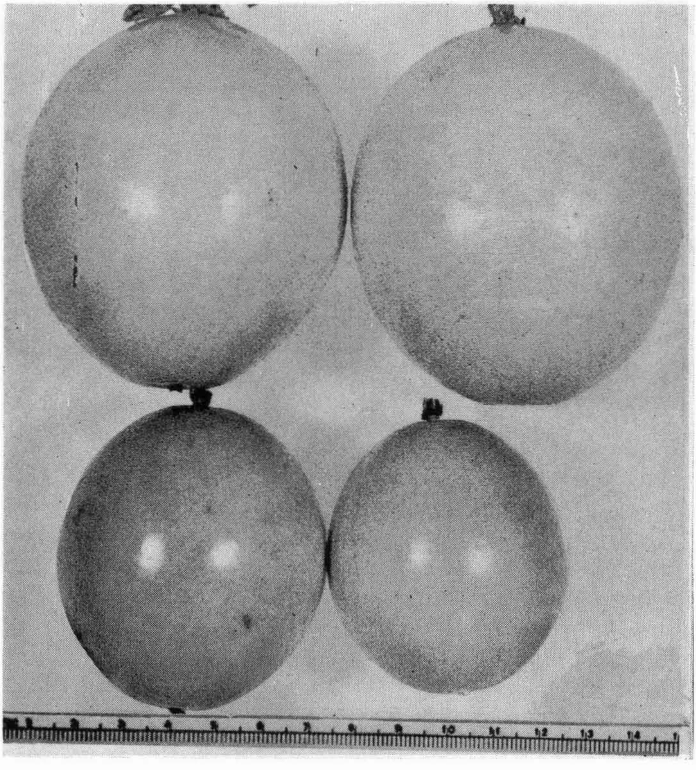

FIGURE 6. Upper row, fruits from plant C-37 hand pollinated with plant C-39 pollen. Lower row, fruits from same plant C-37 but naturally pollinated. (Scale in centimeters.)

TABLE 16. Effect of hand and natural pollination on fruit set, fruit size, fruit weight, juice yield, and number of seeds

POLLINATION METHOD	NUMBER OF FLOWERS POLLINATED	NUMBER OF FRUITS SET	PERCENT FRUIT SET	MEAN FRESH WEIGHT (gm.)	MEAN WIDTH (cm.)	MEAN LENGTH (cm.)	MEAN VOLUMETRIC DISPLACEMENT (ml.)	MEAN NUMBER OF SEEDS†	MEAN JUICE YIELD	
									Gm.	Percent of fresh weight
Hand*	20	20	100	112.2	6.78	7.28	178	277	49.8	44.4
Natural	20	14	70	62.2	6.07	6.29	129	110	19.9	32.0

*Plant M-20 flower pollinated with plant C-39 pollen. All differences between treatment means are significant at $P = .01$.

†As represented by the number of fully developed funiculi.

In these as well as in other experiments in which data from mature fruits were desirable, fruits were enclosed in paper bags until safe from fruit fly damage (to be discussed in another section). A string was tied to the peduncle after the fruit was exposed. By tying the other end of the string to the vine, the fruit was prevented from being lost by dropping on the ground at maturity.

All differences in the mean values between fruit set by hand pollination and that set by natural pollination are statistically highly significant (table 16). The volumetric displacement value was determined by immersing the fruit in a given volume of water. Since it is easier to count the funiculi on the parietal placenta than the seeds in a mass of degenerating arils after the pulp is removed from the fruit and since each fully developed funiculus represents a matured ovule (seed), the funiculi were counted rather than the seeds. The juice yield was determined by extracting with a microblender followed by hand squeezing through cotton cloth and weighing the extracted juice.

Number of Stigmas

The passion fruit flower has three stigmas (tripartite style). The question arose as to the relative importance of the number of stigmas in terms of fruit set and fruit and juice yields. Removal of one or two stigmas prior to pollination demonstrated conclusively that the number of stigmas present is immaterial in determining fruit set and fruit and juice yields, provided the cross is compatible and sufficient amount of pollen is employed. This is well illustrated in the data from one of the experiments conducted at the Mid-Pacific Experimental Farm (table 17)).

Pollination, fertilization, and ovule development proceed similarly regardless of the relationship between the individual stigmas and the three respective carpels of the ovary. Regardless of the number of stigmas pollinated, the seeds were found to be equally distributed throughout the common tripartite carpellary cavity of the fruit. However, when insufficient pollen is applied to allow fertilization of all fertilizable ovules, only those nearest the stylar base are fertilized (fig. 7). Thus, the ovules nearest the stigma are fertilized first and as more pollen tubes enter the carpels, ovules further removed become fertilized.

Influence of Degree of Pollination on Fruit Development

Apparently parthenocarpic fruit development does not occur in the yellow passion fruit. Various potentially parthenocarpy-inducing chemicals including naphthaleneacetic acid, 2,4-dichlorophenoxyacetic acid, and indoleacetic acid were ineffective in causing fruit set. Pollen extract was also employed without success.

TABLE 17. Number of stigmas as affecting fruit set, fruit size, fruit weight, juice yield, and number of seeds

NUMBER OF STIGMAS	NUMBER OF FLOWERS POLLINATED*	NUMBER OF FRUITS SET	PERCENT FRUIT SET	MEAN FRESH WEIGHT (gm.)	MEAN WIDTH (cm.)	MEAN LENGTH (cm.)	MEAN VOLUMETRIC DISPLACEMENT (ml.)	MEAN NUMBER OF SEEDS	MEAN JUICE YIELD	
									Gm.	Percent of fresh weight
1	20	20	100	129.6	6.48	7.49	173	285	57.0	44.0
2	20	20	100	132.2	6.52	7.60	177	278	59.5	45.0
3	20	20	100	131.7	6.52	7.65	177	271	56.2	42.7

* Plant C-80 flower pollinated with plant C-39 pollen. All differences between treatment means are not significant.

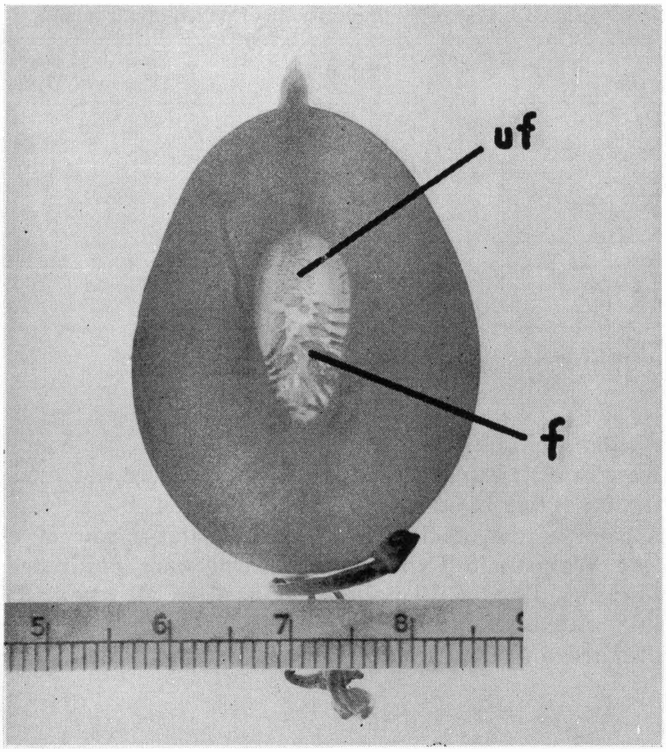

FIGURE 7. Longisection through young insufficiently pollinated fruit. uf = unfertilized ovules. f = fertilized ovules. (Scale in centimeters.)

Since in cross-pollinations involving compatible crosses in which presumably maximum amount of pollen was placed on the stigma, higher fruit set, larger fruit, and greater juice yield resulted than in natural pollinations, it was believed that the degree of pollination may have some effect on the development of the fruit. This was investigated by applying varying amounts of pollen for pollinations. Known numbers of pollen grains were delivered to stigmas by means of drawn-out glass rod tips. The pollen-holding capacity of each glass rod applicator was determined. A drop of water was placed on the cross-hatched surface of a transparent plastic strip. The pollen grains were transferred to the drop and counted with the aid of a microscope. The pollen applicators and their pollen-holding capacities are listed in table 18.

Exploratory studies indicated that the minimum number of pollen grains required for fruit set is approximately 190. The lack of fruit set with 119 pollen grains collected in the pollen trap discussed under the

TABLE 18. Pollen-holding capacity of pollen applicators

APPLICATOR	NUMBER OF POLLEN GRAINS (mean of 20 determinations)
1*	43
4*	142
6	189
7	228
8	271
9	358
10	592
10 2X†	1,184
10 3X‡	1,776

* No fruit set.
† Applicator 10 used twice.
‡ Applicator 10 used thrice.

section on wind pollination is thus evident. Pollen applicators 1 and 4 which delivered much less than 190 pollen grains were not used in further experimentation (table 18).

Flowers from a row of clonal C-37 plants and a row of clonal C-77 plants at the Waimanalo Experimental Farm were pollinated with the pollen applicators. Plant C-39 pollen was used in all cases as this pollen is compatible with both plants C-37 and C-77 (table 3). The number of flowers pollinated and the number of fruits set therefrom are recorded in table 19.

TABLE 19. Number of flowers pollinated with pollen applicators and resultant number of fruits set

	PLANT C-37		PLANT C-77	
APPLICATOR	Number of flowers pollinated	Number of fruits matured	Number of flowers pollinated	Number of fruits matured
6	91	38	44	20
7	45	20	33	20
8	44	20	24	18
9	30	21	22	18
10	27	22	26	26
10 2X	21	18	20	20
10 3X	23	22	30	30

Upon fruit maturity, the number of seeds, fruit set percentage, fruit volumetric displacement, fruit length, fruit width, fruit weight, juice weight, and juice percentage were determined in relation to amount of pollen delivered in the initial pollination (fig. 8).

The curves in figure 8 indicate that probably the maximum effect of pollination was not attained even with the largest number (1,776) of pollen grains. This is especially so in the case of number of seeds, fruit weight,

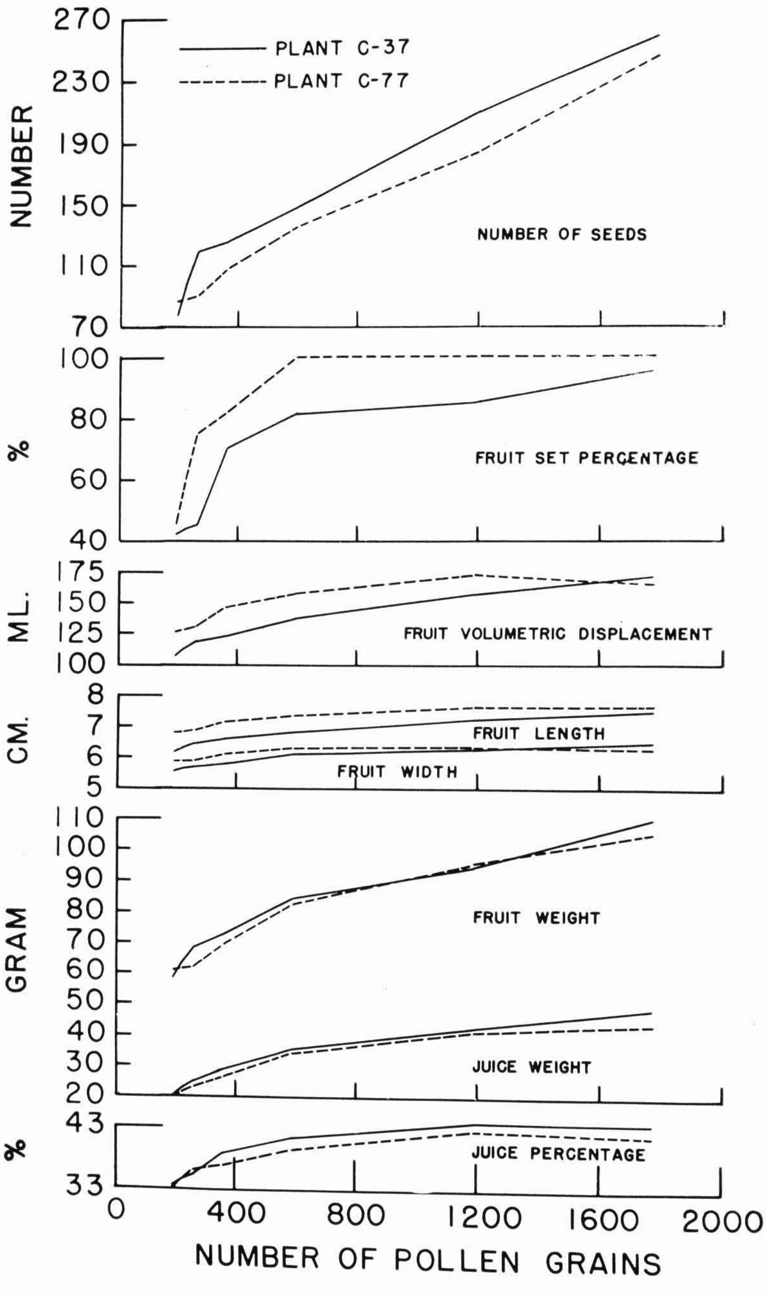

FIGURE 8. Effect of degree of pollination on fruit set, size and weight of fruit, number of seeds, and juice yield of plants C-37 and C-77.

and juice yield. The curves of these factors failed to reach the "plateau" stage. Unfortunately, it was not possible to apply more pollen with the applicators available. The mean potential number of seeds (developed and undeveloped funiculi) in a plant C-37 fruit was determined to be 344, and that in a plant C-77 fruit was 349. Assuming that the fruits of plant M-20 and plant C-80 have approximately the same potential number of seeds, the use of open anthers on the stigmatic surface to accomplish pollination in other experiments undoubtedly placed more pollen grains on the stigma than by the use of the special pollen applicators. This is evidenced by the greater number of mature seeds formed by the anther applications (tables 16, 17) than by the use of the glass applicators (fig. 8).

As evident in figure 8 and table 20, the relative efficiency of the pollen grains in effecting seed development decreases with the increase in the number of pollen grains delivered to the stigmas. This is probably due to the increased competition among the pollen grains for germination sites in a limited pistil area and to increased competition among the pollen tubes for fertilization of the ovules.

TABLE 20. Relationship of number of pollen grains employed and number of seeds resulting from the pollination

NUMBER OF POLLEN GRAINS	MEAN NUMBER OF SEEDS		MEAN NUMBER OF POLLEN GRAINS PER SEED	
	Plant C-37	Plant C-77	Plant C-37	Plant C-77
189	77.4	85.6	2.4	2.2
228	98.0	88.0	2.3	2.6
271	118.8	89.6	2.3	3.0
358	125.4	106.7	2.8	3.4
592	148.4	134.9	4.0	4.4
1,184	208.8	182.0	5.7	6.5
1,776	257.0	243.9	6.9	7.3

The mean size (width, length, and volumetric displacement) of the fruit from plant C-77 is in general greater than that of plant C-37 (figs. 8, 9). However, the greater number of seeds and accompanying higher yield of juice in the C-37 fruit than in the C-77 fruit compensate for difference in fruit size so that fruits from the two plants weigh approximately the same. This relationship is further reflected in the higher juice percentage in C-37 fruit than in C-77 fruit.

The difference in the response of the two plants in terms of fruit set percentage due to the degree of pollination is rather striking (fig. 8). Plant C-37 required approximately three times more pollen than plant C-77 to obtain almost 100 percent fruit set.

It is obvious that, in general, the effect of the degree of pollination on fruit set, size and weight of fruit, number of seeds, and juice yield is similar for both plants (fig. 8).

In order to examine more precisely the relationships resulting from differential degrees of pollination, the data in this experiment were subjected to statistical analyses involving regressions and correlations (*24*). Assuming linear relationships to exist between the number of pollen grains and the various resulting factors investigated (fig. 8), linear regression coefficients were calculated for the fruits of the two plants. The results are tabulated in tables 21 and 22.

TABLE 21. Linear regressions of number of pollen grains on certain factors—plant C-37 fruit

FACTOR	REGRESSION COEFFICIENT	"t" VALUE
Number of seeds	+.1041	13.012**
Fruit set percentage	+.0301	4.025*
Fruit volumetric displacement	+.0404	10.100**
Fruit length	+.0008	8.889**
Fruit width	+.0005	7.143**
Fruit weight	+.0304	9.500**
Juice weight	+.0170	8.095**
Juice percentage	+.0061	3.812*

* Significant at P = .05.
** Significant at P = .01.

TABLE 22. Linear regressions of number of pollen grains on certain factors—plant C-77 fruit

FACTOR	REGRESSION COEFFICIENT	"t" VALUE
Number of seeds	+.0992	30.061**
Fruit set percentage	+.0203†	.310‡
Fruit volumetric displacement	+.0264	3.342*
Fruit length	+.0006	6.000**
Fruit width	+.0003	3.000*
Fruit weight	+.0293	9.767**
Juice weight	+.0153	7.286**
Juice percentage	+.0050	3.571*

* Significant at P = .05.
** Significant at P = .01.
† Up to first 100 percent fruit set, .1208 with "t" value of 4.137*.
‡ Not significant.

The regression coefficients for the fruit of plant C-37 are in general of high order, the "t" values of the various factors being mostly highly significant (table 21). The coefficients of the fruit of plant C-77 are also good, but not as high as those of plant C-37 (table 22). The cause of the statistically nonsignificant value for fruit set percentage in plant C-77 is readily visible in figure 8. If the regression were calculated only up to the point where 100 percent fruit set was first obtained, a significant coefficient resulted (table 22). A curvilinear relationship would seem more appropriate than a linear one in this case.

Having determined graphically (fig. 8) and statistically (tables 21, 22) the positive relationship between the degree of pollination and the various fruit factors investigated, attempts were made to observe more critically with further statistical treatment the visible relationships among the fruit factors (fig. 9). The correlation coefficients for these factors are presented in tables 23 and 24.

That all the factors are positively intercorrelated is supported by the correlation coefficients for the two plants (tables 23, 24). In the fruit of plant C-37, all factors are highly correlated with each other, the correlating coefficients in all cases being significant at the P = .01 level. In the fruit of plant C-77, of the 28 coefficients treated, 23 are of the order of high significance (1 percent level), and 5 are significant at the 5 percent level.

TABLE 23. Correlations between certain factors—plant C-37 fruit

CORRELATING FACTORS	CORRELATION COEFFICIENT
Number of seeds and fruit set percentage	+.896**
Number of seeds and fruit volumetric displacement	+.994**
Number of seeds and fruit length	+.994**
Number of seeds and fruit width	+.984**
Number of seeds and fruit weight	+.991**
Number of seeds and juice weight	+.987**
Number of seeds and juice percentage	+.916**
Fruit set percentage and fruit volumetric displacement	+.928**
Fruit set percentage and fruit length	+.931**
Fruit set percentage and fruit width	+.952**
Fruit set percentage and fruit weight	+.936**
Fruit set percentage and juice weight	+.950**
Fruit set percentage and juice percentage	+.987**
Fruit volumetric displacement and fruit length	+.997**
Fruit volumetric displacement and fruit width	+.996**
Fruit volumetric displacement and fruit weight	+.996**
Fruit volumetric displacement and juice weight	+.997**
Fruit volumetric displacement and juice percentage	+.945**
Fruit length and fruit width	+.999**
Fruit length and fruit weight	+.993**
Fruit length and juice weight	+.996**
Fruit length and juice percentage	+.950**
Fruit width and fruit weight	+.996**
Fruit width and juice weight	+.999**
Fruit width and juice percentage	+.964**
Fruit weight and juice weight	+.997**
Fruit weight and juice percentage	+.942**
Juice weight and juice percentage	+.961**

** Significant at P = .01.

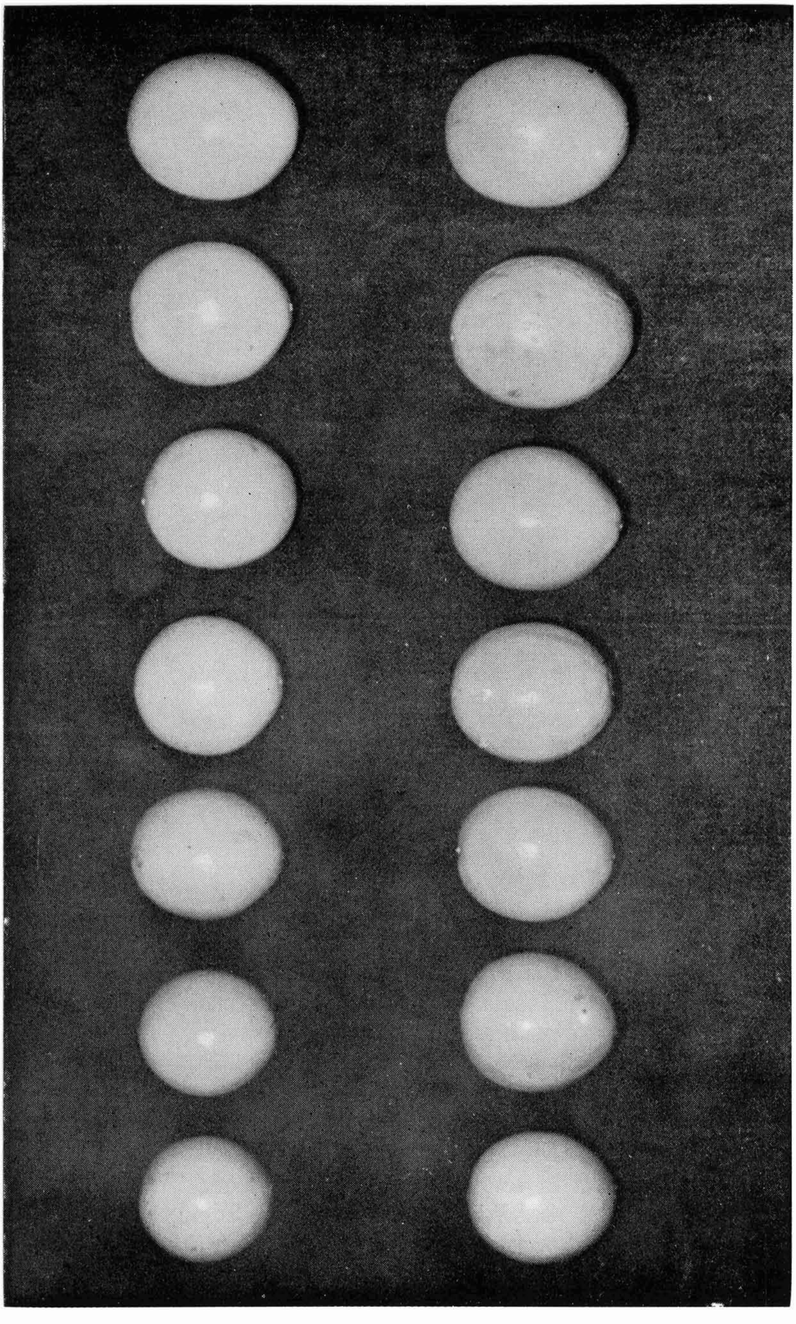

FIGURE 9. Effect of degree of pollination on fruit size. Number of pollen grains applied from left to right, respectively: 189, 228, 271, 358, 592, 1184, 1776. Top row: plant C-37. Bottom row: plant C-77.

TABLE 24. Correlations between certain factors—plant C-77 fruit

CORRELATING FACTORS	CORRELATION COEFFICIENT
Number of seeds and fruit set percentage	+.756*
Number of seeds and fruit volumetric displacement	+.850*
Number of seeds and fruit length	+.919**
Number of seeds and fruit width	+.821*
Number of seeds and fruit weight	+.984**
Number of seeds and juice weight	+.962**
Number of seeds and juice percentage	+.859*
Fruit set percentage and fruit volumetric displacement	+.920**
Fruit set percentage and fruit length	+.904**
Fruit set percentage and fruit width	+.938**
Fruit set percentage and fruit weight	+.835*
Fruit set percentage and juice weight	+.874**
Fruit set percentage and juice percentage	+.951**
Fruit volumetric displacement and fruit length	+.990**
Fruit volumetric displacement and fruit width	+.996**
Fruit volumetric displacement and fruit weight	+.925**
Fruit volumetric displacement and juice weight	+.957**
Fruit volumetric displacement and juice percentage	+.983**
Fruit length and fruit width	+.982**
Fruit length and fruit weight	+.974**
Fruit length and juice weight	+.991**
Fruit length and juice percentage	+.981**
Fruit width and fruit weight	+.911**
Fruit width and juice weight	+.940**
Fruit width and juice percentage	+.972**
Fruit weight and juice weight	+.993**
Fruit weight and juice percentage	+.926**
Juice weight and juice percentage	+.962**

* Significant at $P = .05$.
** Significant at $P = .01$.

"Hollow" Fruits

To the grower or the processor, the use and conception of a "hollow" fruit is to designate a fruit that is relatively light to the hand in reference to its external dimensions. Thus, it may vary in external dimensions from a relatively small underdeveloped fruit to a nearly fully developed one. The number of fully matured seeds in such fruits is also variable but always relatively low in number (fig. 10).

Employing such a criterion of hollow fruits, composite collections of fruits from seedling plants in orchard rows indicated that the percentage of these abnormal fruits is very low. A more exacting investigation was conducted on individual seedling plants during a part of the fruiting season at the Waimanalo Experimental Farm. The results tabulated in table 25 show that the prevalence of hollow fruits is low and that it ranges within rather narrow limits (approximately 0 to 6 percent).

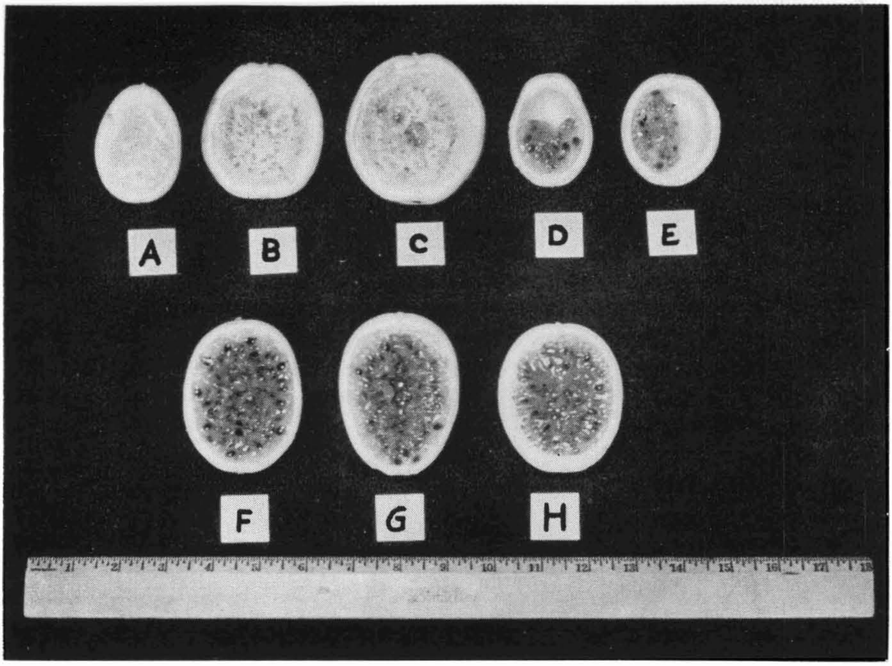

FIGURE 10. Varying size and number of seeds in "hollow" fruits. Fruits A to E are hollow. Fruits F to H are normal. (Scale in inches.)

Gilmartin (*11*) arbitrarily considered fruits with 30 percent or less of their ovules fully matured into seeds as hollow. On this basis, she obtained results similar to those obtained in the present study. The data accumulated in the present study (table 25) do not support the thesis that hollow fruit formation is genetical in origin (*11*).

Fruit Fly Damage

The Oriental fruit fly (*Dacus dorsalis* Handel), the melon fly (*Dacus cucurbitae* Coquillett), and possibly, the Mediterranean fruit fly (*Ceratitis capitata* Wied.), if unchecked, do severe damage to passion fruit (*4*). Of these, the Oriental fruit fly is probably the most damaging. Damaged fruits are marked by unsightly scars which extend deep into the pericarp, resulting in the formation of craters embedded in hard corky tissues (fig. 11). The data in table 26 indicate that if these fruits survive the attack and mature, they are probably not damaged to the extent that their size and juice yield are reduced to any appreciable degree. The differences in the means of the factors studied between stung and normal fruits were shown to be nonsignificant statistically (table 26).

TABLE 25. Occurrence of hollow fruits on plants at Waimanalo Experimental Farm

PLANT	SEPTEMBER, 1957		OCTOBER		NOVEMBER		DECEMBER		JANUARY, 1958		FEBRUARY		GRAND TOTAL		PERCENT HOLLOW FRUITS
	Hollow	Total	Hollow	Total	Hollow	Total	Hollow	Total	Hollow	Total	Hollow	Total	Hollow	Total	
W-83......	2	59	1	74	0	154	2	197	0	107	0	2	5	593	.8
W-84......	7	51	1	18	0	49	1	108	0	47	0	1	9	274	3.3
W-85......	0	35	0	24	2	111	2	152	0	42	0	1	4	365	1.1
W-86......	10	48	5	99	2	160	3	136	0	37	0	5	20	485	4.1
W-87......	2	39	0	120	3	302	1	197	0	134	0	1	6	793	.8
W-88......	4	80	2	70	1	228	4	112	1	108	0	0	12	598	2.0
W-89......	1	38	2	61	1	159	3	146	1	40	0	1	8	445	1.8
W-90......	4	46	3	39	1	132	6	129	1	43	0	7	15	396	3.8
W-91......	4	69	2	125	11	371	8	208	1	90	0	5	26	868	3.0
W-92......	1	31	0	83	1	305	0	174	0	40	0	13	2	646	.3
W-93......	1	100	2	78	6	362	6	295	1	176	0	3	16	1,014	1.6
W-94......	2	14	1	14	1	124	3	96	2	81	0	11	9	340	2.6
W-95......	7	36	6	78	6	145	4	158	1	63	0	0	24	480	5.0
W-96......	0	7	1	25	5	172	6	119	0	59	0	3	12	385	3.1
W-97......	1	27	2	78	1	180	8	101	0	43	0	5	12	434	2.8
W-98......	2	35	3	60	2	158	6	223	0	138	0	11	13	625	2.1
W-99......	10	62	6	67	10	143	7	218	1	78	0	1	34	569	6.0
W-100....	4	30	3	48	5	122	4	126	1	56	0	3	17	385	4.4
W-101....	2	41	3	56	2	135	4	143	0	74	0	1	11	450	2.4
W-102....	0	18	1	76	3	152	3	138	2	72	0	2	9	458	2.0

TABLE 26. Effect of fruit fly damage on fruit size and juice yield

SAMPLE*	NUMBER OF FRUITS	MEAN FRESH WEIGHT (gm.)	MEAN WIDTH (cm.)	MEAN LENGTH (cm.)	MEAN VOLUMETRIC DISPLACEMENT (ml.)	MEAN NUMBER OF SEEDS	MEAN JUICE YIELD	
							Gm.	Percent of fresh weight
Fruit fly-damaged	126	85.1	5.67	6.45	115	214	32.4	38.1
Normal	60	87.3	5.71	6.59	119	222	35.4	40.5

* Composite samples from 24 seedling plants at Mid-Pacific Experimental Farm. All differences between treatment means are not significant.

Preliminary studies indicated that fly damage occurring when the fruit is extremely young results in the fruit shriveling and dropping prematurely (fig. 11). An effort was made to determine the stage of development at which the fruit is no longer vulnerable to fruit fly attack. The period from pollination to maturity varies (61–80 days) with different plants (table 27). However, once the fruit has reached a certain maturity, fly ovipositing will not alter its subsequent development from the normal except for the unsightly ovipositing scars.

TABLE 27. Time required from pollination to fruit maturity

PLANT	NUMBER OF FRUITS	MEAN NUMBER OF DAYS TO HARVEST
C-37	141	79.9
C-77	67	69.7
C-80	5	79.2
W-83	3	68.0
W-86	6	64.8
W-87	10	62.0
W-88	12	70.8
W-89	5	65.0
W-93	23	66.9
W-96	6	60.8
W-98	15	67.8
W-99	6	66.2
W-100	12	73.2
M-20	37	76.0
M-22	44	62.5

Immediately after pollination with compatible pollen, the pollinated flowers were enclosed in brown paper bags for varying periods of time, subsequently uncovered, and exposed to fruit flies. The results of an experiment conducted at the Mid-Pacific Experimental Farm, where no fruit fly control measures were practiced, are recorded in table 28.

According to table 28, all fruits up to 9 days subsequent to pollination can be expected to be stung by the fruit fly and to drop prematurely. Ten to 11 days after pollination 50 percent of the fruits may be stung and all stung fruits are expected to drop before maturity. When protected for a

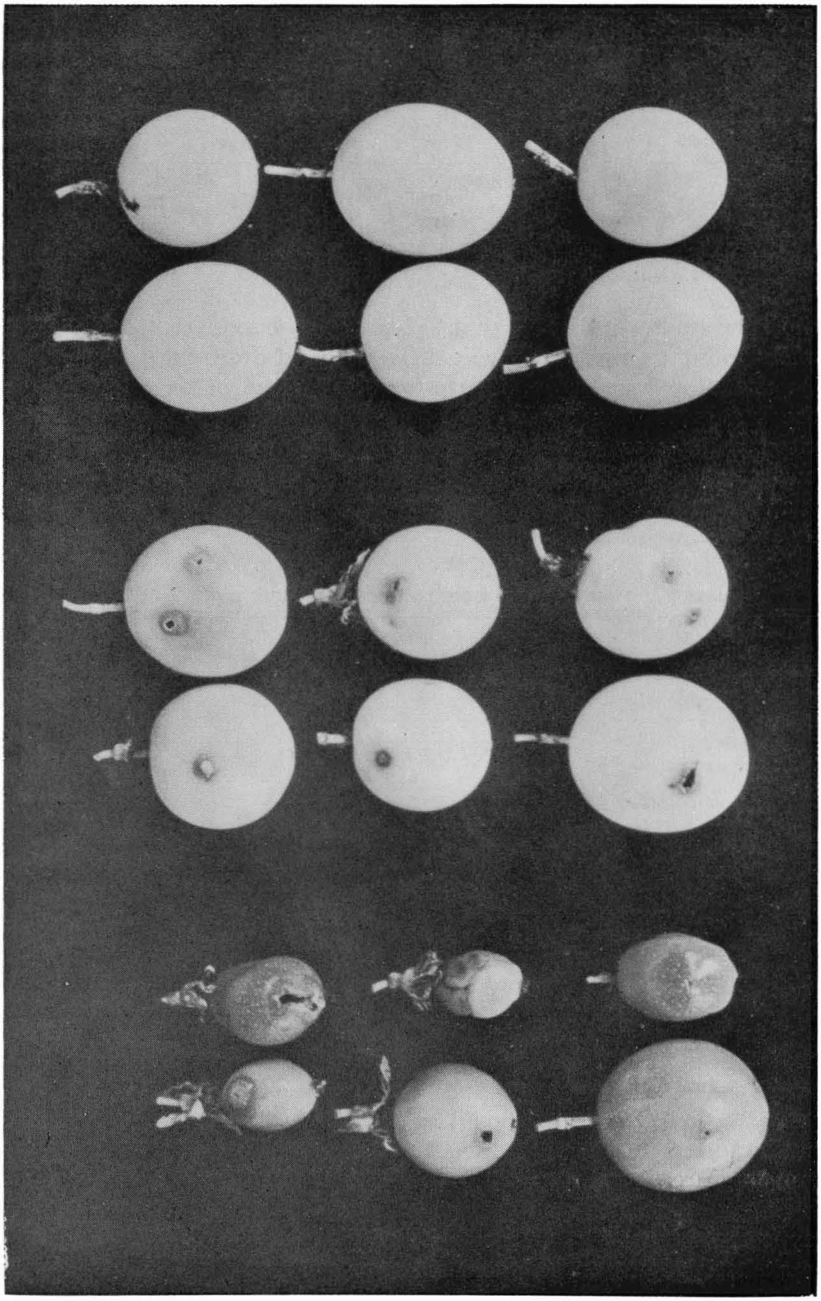

FIGURE 11. Fruit fly-damaged fruits. Left column: fruits that dropped prematurely. Middle column: fruits that survived the attack and matured normally. Right column: undamaged fruits.

TABLE 28. Relation of age of fruit and fly ovipositing to fruit maturity—plant M-20 pollinated with M-22 pollen

DAYS COVERED	TOTAL NUMBER OF FRUITS	NUMBER OF FRUITS STUNG	NUMBER OF STUNG FRUITS DROPPED	NUMBER OF STUNG FRUITS MATURED
3	6	6	6	0
4	8	8	8	0
5	6	6	6	0
7	6	6	6	0
9	6	6	6	0
10	8	4	4	0
11	8	4	4	0
12	18	8	4	4
13	8	0	0	0
14	6	0	0	0
15	12	0	0	0
16	8	0	0	0
17	8	0	0	0
18	8	0	0	0
19	8	0	0	0
23	6	0	0	0

period of 12 days from the fruit fly and then exposed, again approximately half of the fruits were stung, and half of these damaged fruits survived. Fruits covered for 13 days and longer before exposing were not vulnerable to the sting of the fruit fly.

The anatomical basis for resistance to oviposition is dependent on the development of a mechanically resistant exocarp. The mechanical resistance results from the sclerification of the external and subsurface cells of the outermost layers of the pericarp. The development of these sclerified cells is variable, possibly dependent on the particular current physiology and genetic composition of the parent plant.

In another experiment on another plant the results were not as clear cut as those of the above experiment. In one instance, a stung fruit which was never protected from the fruit fly tolerated the attack and reached maturity. Even a 19-day-old fruit was stung and survived. These discrepancies are believed to be caused by several factors. In the first place, the effect of the covering, especially for extended periods, on the vulnerability of the rind to fruit fly puncture after the fruit is exposed is a matter of conjecture. In the second place, exactly when the attack occurred after the fruit was exposed could not be observed. Furthermore, the severity of the attack (number of oviposition punctures) may determine tolerance or lack of it. Then, too, the magnitude of the fruit fly population may determine the severity of the attack and the number of fruits stung. In general, however, it seems reasonable to conclude from the foregoing that if the young fruits are not attacked by the fruit fly for 10 to 11 days, the chances of surviving the attack thereafter are almost assured (table 28). Thus, the importance of fruit fly control in the field is self-evident from these studies.

Growth of Ovary

The vulnerability of the fruit to fruit fly sting is related to the hardness of the rind which in turn is related to the stage of development of the fruit. Hence, the growth behavior of the ovary after pollination was studied. Starting at the time of pollination and daily thereafter, the width and the length of the ovary were measured with vernier calipers. When not being measured, the fruits were kept enclosed in brown paper bags to prevent exposure to fruit fly. Initial experiments indicated that the ovary makes a significant growth the first day after the flower opens even when unpollinated, selfed, or pollinated with pollen from an incompatible plant. For further growth, however, pollination with pollen from a compatible plant is required.

Growth studies made on four compatible crosses produced data which when plotted resulted in very striking identical curves. The growth curves of one of these crosses are reproduced in figure 12.

The growth for both the width and length of the fruit is very rapid up to the 11th day. From then on the growth rate drops rapidly to the 18th day when the maximum size is attained (fig. 12). The period of most rapid growth coincides with the period of highest susceptibility to fruit fly attack and subsequent fruit drop (table 28). The period of reduced rate of growth and the commencement of pericarp sclerification coincides with increased resistance to the attack. Thus, the harder the pericarp, the greater the resistance to fly attack.

Fruit Set on Flowering Behavior

In the passion fruit, flowers are produced only on new growth, and the flowering season in the yellow type is long with the first flowers opening around April and the last ones in December at the Waimanalo and Mid-Pacific Experimental Farms. Depending on elevation, some variation in the flowering time is expected with different localities.

For approximately 3 months after the termination of the flowering season, the plant makes extensive vegetative growth. During the first 2 months of this period, no visible flower buds are found in the leaf axils or on the tendrils. Around March, first buds are visible. In approximately 40 days after they become visible to the naked eye, they open as the first fully matured flowers of the new flowering season.

In the meantime the shoot is vigorously producing new growth and new flower buds. The growth rate of the shoot tip of a plant was determined during a flowering and fruiting season. The length of the shoot from an initially marked point to the tip was measured at intervals during a 28-day period. The mean lengths of 10 shoot tips and the regression equation and line depicting the rate of elongation are shown in figure 13.

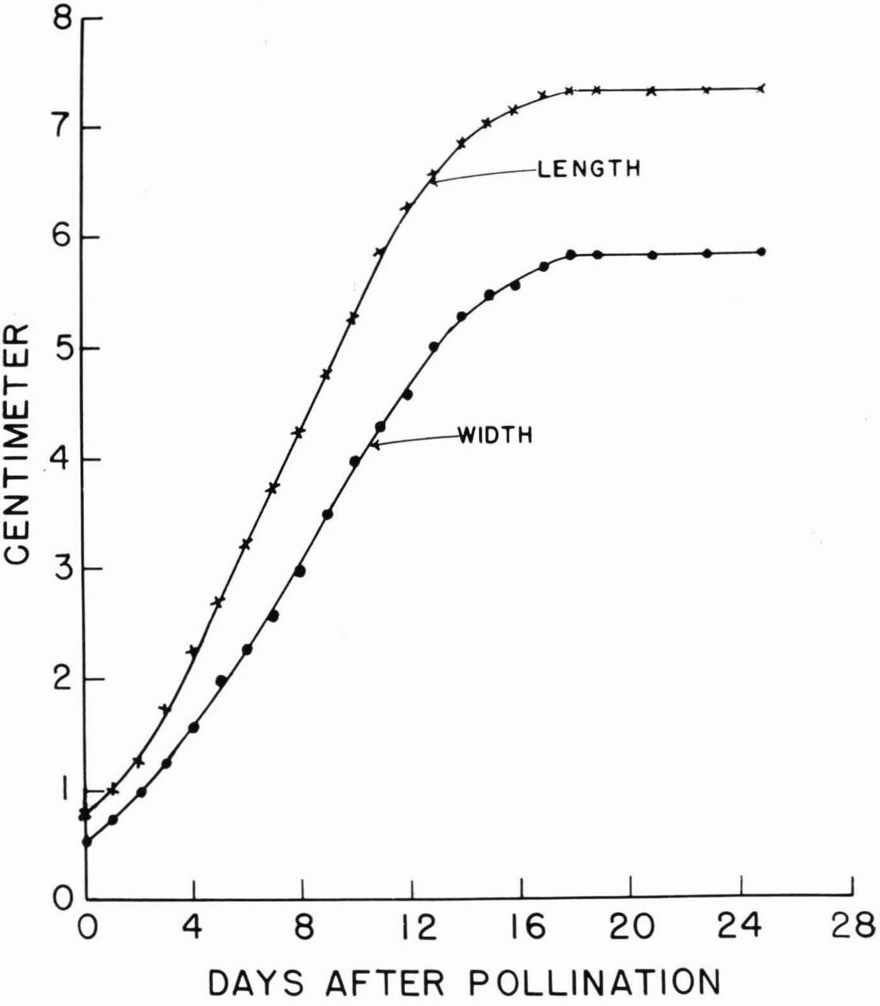

FIGURE 12. Growth of ovary (mean of eight ovaries)—plant C-37 pollinated with plant F-1 pollen.

Throughout the flowering season, a flower bud appears in each leaf axil; however, not all buds develop into full flowers. Under natural field conditions, therefore, even if all normal flowers set fruit, the stem is alternated by sections of fruit set and no fruit set.

A study was made to determine whether the flowering behavior is influenced by fruit set. Two clonal plants of plant C-80 were used for the study at the Mid-Pacific Experimental Farm. All flowers of one plant

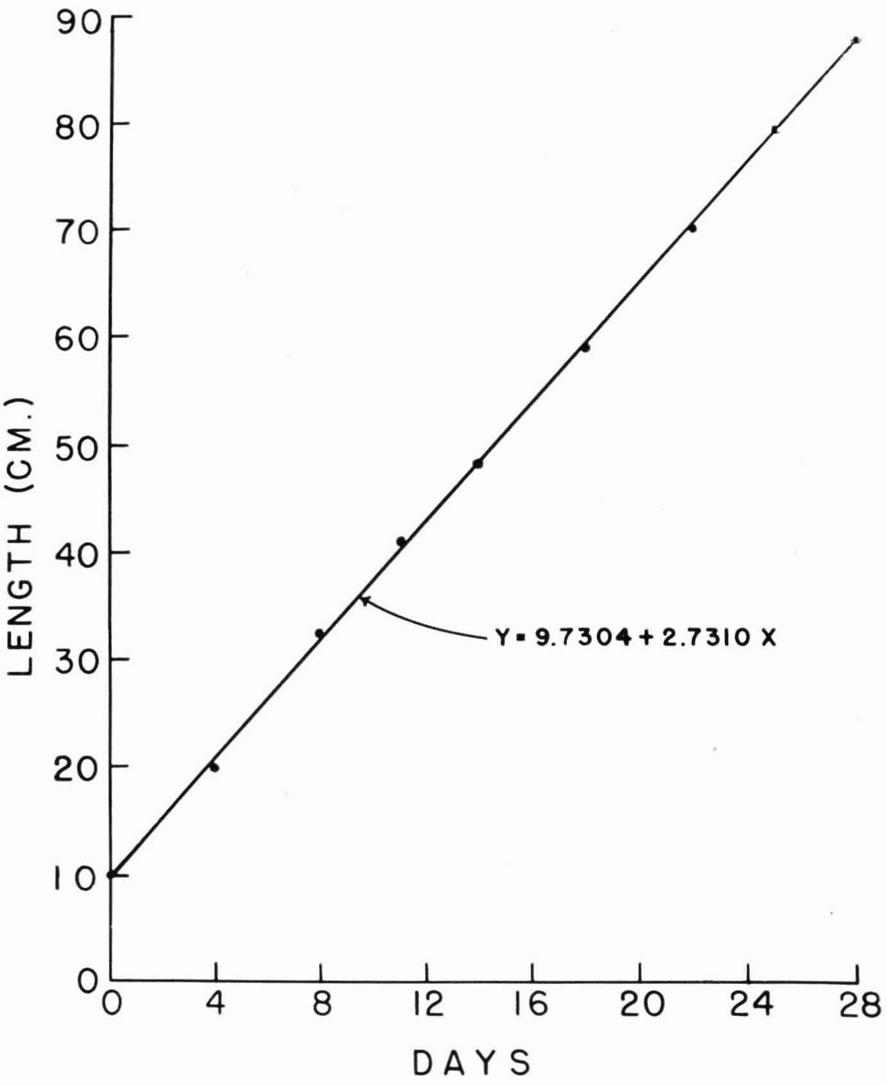

FIGURE 13. Elongation of shoot tip during flowering and fruiting season (mean length of 10 shoots of plant C-37).

were removed as they opened; i.e., this plant was not allowed to set fruit during the experiment. The other plant was allowed to flower and fruit naturally. At the beginning of the flowering season, 15 normal shoots of each plant were selected. The node with the first visible flower bud of each shoot was labelled number 1 node. Thereafter each node was labelled chronologically. The status of each flower bud—normal or aborted (dropping at various stages of development prior to opening)—was recorded for each node throughout the flowering season.

In table 29 the mean number of flowers for each alternate fruit set and no set period is tabulated for each plant.

TABLE 29. Effect of fruit set on flowering behavior

SUCCESSIVE FLOWER PRODUCTION	MEAN NUMBER OF FLOWERS PER SHOOT	
	Plant with flowers intact	Plant with flowers removed
Aborted	6.7	5.3
Normal	2.6	2.0
Aborted	6.0	2.3
Normal	1.8	1.8
Aborted	12.4	6.7
Normal	2.0	1.8
Aborted	5.3	7.6
Normal	2.2	1.4
Aborted	5.8	5.2
Normal	1.3	1.5
Aborted	5.7	7.5
Normal	1.6	1.0
Aborted	9.0	
Normal	3.0	
Aborted	10.3	
Normal	3.0	
Aborted	10.5	
Normal	1.0	
Aborted	6.0	

In general, the cyclic flowering behavior of the two plants is similar (table 29). The production of normal and aborted flowers is also about the same up to the time the experiment was terminated for the plant with the flowers removed. For both plants the ratio of aborted flowers to normal flowers during the experiment was approximately 4:1.

Pollen Germination

It was previously pointed out that upon contact with free moisture, the pollen grains burst almost instantly. In normal germination, the pollen tube is an extension of a portion of the intine. During germination the pollen tube pushes aside a section of the reticulately sculptured extine. Occasionally two pollen tubes appear from a single pollen grain. This phenomenon probably has not been previously reported in dicotyledons. When a pollen grain bursts, a viscous material of apparently high reflective index which remains visible for a few seconds, exudes (fig. 14). This exudation is extruded in 2 to 5 seconds. This is followed by the explosive expulsion of the remaining contents of the pollen grain as a fan-shaped exudate.

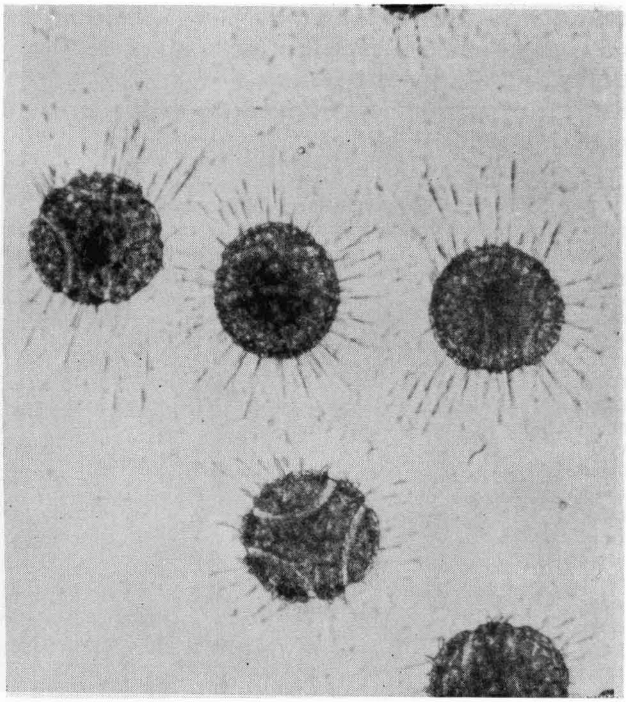

FIGURE 14. Pollen grains just prior to bursting showing exuded viscous material.

Preliminary studies *in vitro* were conducted to determine the nature of the bursting and the requirements for germination of the pollen grains. On the assumption that the bursting was caused by excessive movement of water into the pollen grain brought about by high osmotic pressure of its cellular contents and cell walls of insufficient strength to resist rupture, attempts were made to prevent the bursting by the use of solutions of various chemicals for germination media. It was discovered that relatively high concentrations of substances are required to prevent the bursting. Bursting did not occur in 1 M sucrose, .5 M $CaCl_2$, .5 M KCl, or 1 M mannitol. In addition, ripe passion fruit juice (total soluble solids about 17 percent) and natural flower nectar (total soluble solids about 50 percent) were effective in preventing the bursting of the pollen grains. These, however, were ineffective in promoting germination.

Using 1 M sucrose to maintain the required osmotic concentration in the germination medium, other substances were incorporated in attempts to induce germination. Stigma extract (18 or 36 stigmas ground with enough water to make final extract volume of 1–3 ml.) and indoleacetic acid (10–640 mgm./l.) were ineffective when used as adjuncts to sucrose solutions placed as drops on a glass slide in the bottom of a covered petri dish at room temperature. However, germination resulted when a strip of filter paper was saturated with the germination solution (excess drained off) and the pollen grains sown on it rather than on the drops. Pollen grains sown on a thin layer of agar in which the germination solution had been incorporated resulted in successful germination. Thus, it seems that excessive moisture may possibly hinder the oxygen requirement for germination.

Macerated stigmas were found to be just as effective as stigma extract in promoting germination. Effective concentrations of indoleacetic acid are in the neighborhood of 100 mgm./l.

That the germination-promoting substance is diffusible was further demonstrated by placing decapitated stigmas on 1 percent agar containing 1 M sucrose for 2½ hours, then sowing pollen grains on the medium. The pattern of diffusion was indicated by the progressive decrease in germination outwardly from the stigma contact zone.

Moisture control is very critical in the germination of passion fruit pollen grain. When pollen extracts or indoleacetic acid solutions are employed in conjunction with agar and sucrose solutions, the sugar concentration must be adjusted accordingly to allow for the dilution effect of the other substances so that an osmotic equivalent of at least 1 M may be maintained, otherwise the bursting of pollen grain occurs. Furthermore, excessive amounts of water used in the germination chamber as a deterrent to desiccation of pollen grains may cause the agar to absorb water excessively and thus dilute the medium to such a degree as to cause the pollen grains to burst.

It seems that the pollen grain of passion fruit requires two factors for germination: (a) an osmotic pressure of the germination medium almost equal to that of the pollen grain contents (nearly isotonic solution) to prevent bursting. The papillose nature of the stigma possibly accomplishes this by presenting a small contact surface in relation to the volume of the pollen grain. (b) some germination-promoting substance like indoleacetic acid. While indoleacetic acid and stigma exudate apparently caused germination of the pollen grain in the present investigations, these substances merely promoted the growth of the pollen tubes after germination in other plants (*1*). The material of the curious exudate that occurs prior to pollen grain bursting in hypotonic solutions may also be a factor in germination.

DISCUSSION

Under normal conditions, lack of natural fruit set in horticultural fruit plants may be due to any of the following factors:

1. Flower structure that prevents insect pollination. In Delicious apple, e.g., because of the upright filaments, spreading petals, and short pistils of the flower, honey bees collecting nectar and pollen are not forced to come in contact with the anther or stigma (*19*).

2. Dichogamy (pollen and stigma maturing at different times, thus preventing pollination). In some varieties of pecan *(2, 23)*, walnut *(30, 31)*, and pistachio *(20)*, the pollen is shed first, and the stigma matures only after the pollen is nonfunctional (protandry). In other varieties of pecan *(2, 23)* and walnut *(30, 31)* and in cherimoya *(21)*, the stigma becomes receptive long before the pollen is shed, and when the latter is mature, the former is nonfunctional (protogyny).

3. Inviable pollen as evidenced in the J. H. Hale peach *(9)* and Collinson avocado *(7)*.

4. Incompatibility. Self-incompatibility exists in some varieties of apple *(25, 27)*, peach *(10)*, pear *(18, 28)*, prune *(13)*, plum *(12, 14)*, feijoa *(22)*, blueberry *(5)*, sweet cherry *(8, 17)*, and macadamia nut *(29)*. Cross-incompatibility exists in species crosses between *Prunus domestica* and *P. triflora* in the plum *(14)* and in crosses between varieties of sweet cherry *(8, 17)*.

Of the above factors the last seems to be the one primarily involved in the lack of fruit set in the yellow passion fruit under ordinary conditions. Initial studies *(3, 4, 11)* as well as additional data from more exhaustive studies presented herein indicate that the yellow passion fruit is self-incompatible and to a certain extent cross-incompatible.

In compatible crosses, lack of fruit set may be caused by other factors which are genetic and environmental. Due to the inherent characteristics of the pollen, it is not conducive to wind transport which thus plays no significant role in cross-pollination. Flowers with upright styles which do not set fruit is another genetic manifestation varying in degree from plant to plant. Variations in the total flower production and time of flower opening in the different plants also influence fruit set.

The most important natural environmental factor preventing fruit set in compatible crosses is weather, especially rain which causes pollen grains to burst. The obvious detrimental effect of disease and insecticidal sprays applied when the flowers are in bloom is thus seen. Pollinating insects may also be destroyed by insecticidal sprays. Rain as well as cloudiness also reduces insect activity, thus hindering pollination. The number of pollinating insects is another factor determining extent of fruit set. Fruit flies, if unchecked, can be a serious factor in reducing fruit set, especially during the developmental period of the ovary.

On the basis of the relative populations of the pollinating insects prevailing during the experiments, about two-thirds of fruit set were due to the activities of the carpenter bee which is physically more adapted to causing pollination than the honey bee, wasps, and other smaller insects which were responsible for about one-third of fruit set. In spite of the apparent effectiveness of these insects as pollinators under conditions presumably favorable for pollination (sufficient amount of available pollen from compatible plants, a sufficient number of pollinating insects, favorable weather, etc.), it was demonstrated that hand-pollinated flowers produced significantly higher fruit set and larger fruit with higher yield of juice than naturally-pollinated flowers. Data obtained from studies in which the effect of degree of pollination was determined indicated the limited pollinating ability of the carpenter bee. On the basis of the relative efficiency of pollen grains for seed development as determined by the degree of pollination (table 20) and on the basis of number of seeds formed by hand and natural pollinations (table 16), approximately seven times more pollen was applied on the stigma by hand than by the insects. Therefore, the wisdom of investigating the possibility of acquiring more efficient pollinators than carpenter bees does not seem farfetched.

That fruit set, size of the fruit, number of seeds, and juice yield vary positively with the number of pollen grains employed was demonstrated. Furthermore, these factors resulting from pollination were closely correlated with each other. It seems likely, therefore, that inadequate pollination is the primary cause of the so-called "hollow" fruit which contains relatively few seeds. The development of the seeds results from ovule fertilization and is necessary for the formation of juice which forms in the aril (pulp sac). Thus, the importance of pollination is evident.

The positive relationship between the number of seeds and size of the fruit in passion fruit is reminiscent of a similar relationship between the number of achenes and the weight of the receptacles in the strawberry *(16)*.

The presence or absence of fruits on the plant apparently does not influence the normal alternate flower maturation sequence. When it is considered that only one-fourth of the buds produced eventually open as normal blooms, it becomes imperative that heavy pollination, ideal weather conditions, and fruit fly control be assured for high crop and juice yields.

Since pollen failed to cause fruit set when placed on stigma cyclically wetted and dried and since stigma extract and indoleacetic acid stimulated germination of pollen in artificial culture, it seems likely that the substance essential for germination *in vivo* is indoleacetic acid or some other growth regulator which is easily diffusible and probably equally readily washed away from the stigmatic surface by water. The possibility of the absence of this substance in upright-styled flowers needs to be investigated.

PRACTICAL ASPECTS

The studies reported herein have resulted in some practical considerations for the growing of yellow passion fruit. In addition to proper cultural practices in trellising, pruning, fertilizer application, irrigation, and weed and disease control, the grower should take into consideration the following factors:

1. The use of clonal plants, since fruit and juice yields, juice quality, flower production, time of flowering, and other factors are variable with different seedling plants.

2. The selection of clonal material characterized by high fruit yield; high yields of juice of high commercial quality as determined by aroma, flavor, acidity, vitamin content, total soluble solids content, etc.; and high production of flowers with none or a low percentage of upright-styled blooms.

3. The planting in the same field of selected clonal plants compatible with each other in respect to pollination and fertilization and the distributing of these plants in the field to insure the maximum possibility for cross-pollination.

4. The selection of clonal plants that cyclically come into bloom about the same time during the season and whose flowers open approximately at the same time of the day to insure maximum cross-pollination.

5. The increase in number of pollinating insects, especially carpenter bees, in the field to insure not only cross-pollination but also maximum pollination for each bloom. This can be accomplished by installing additional nesting posts in the field.

6. The maintenance of effective fruit fly control throughout the fruiting season to decrease loss of fruit by fruit fly stings.

7. The judicious application of insecticidal and fungicidal sprays so as not to decrease insect activity or populations and not to burst exposed pollen. This can be accomplished by applying these sprays only when the flowers are closed or at times when the plants are not flowering.

SUMMARY

1. Problems concerned with fruit set in the yellow passion fruit are presented and attempts to solve them are described.

2. Self-incompatibility and cross-incompatibility in certain clones are the inherent basic characteristics attributing to lack of fruit set.

3. Lack of or poor fruit set in mutually compatible crosses may be caused by insufficient pollination, wetting of pollen, presence of a large percentage of upright-styled flowers, fruit fly damage, varying flower production and blossom opening time, and combinations of these.

4. The passion fruit is insect-pollinated, the carpenter bee being the most active. Wind pollination is practically nil and results in no fruit set.

5. However effective carpenter bees may be as pollinators, fruits from hand-pollinated flowers are larger and yield more juice than those from naturally-pollinated flowers.

6. The number of pollen grains placed on the stigma influences the fruit set percentage, size of the fruit, number of matured seeds, and juice yield, the positive linear regressions in general being highly significant.

7. The varying resultant factors due to differential degree of pollination are also related to each other, the positive correlations in general being of highly significant order.

8. Pollen grains require a substratum of sufficiently high osmotic concentration to prevent bursting, and indoleacetic acid or some natural growth regulator for germination.

9. Upright-styled flowers are female sterile but male functional.

10. The fruit is vulnerable to fruit fly damage only during the actively growing stage.

11. Flower production and flower opening time vary with different plants.

12. With scrutinous consideration given to the results of the research, practical aspects for the growing of yellow passion fruit are formulated.

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