A QUANTITATIVE STUDY
OF
GROWTH AND FRUITING
IN
INBRED AND CROSSBRED PROGENIES
FROM
TWO SOLO PAPAYA STRAINS

R. A. HAMILTON

A QUANTITATIVE STUDY
OF
GROWTH AND FRUITING
IN
INBRED AND CROSSBRED PROGENIES
FROM
TWO SOLO PAPAYA STRAINS

R. A. HAMILTON

CONTENTS

A QUANTITATIVE STUDY OF GROWTH AND FRUITING IN INBRED AND CROSSBRED PROGENIES FROM TWO SOLO PAPAYA STRAINS

R. A. HAMILTON

The papaya, *Carica papaya* L., is an important breakfast and dessert fruit in Hawaii. It ranks second to banana in acreage, production, and market value of fruits grown for fresh consumption. Commercial acreage varies from about 400 to 800 acres depending on prices, market conditions, availability of land, and weather. Most of the commercial production is found on the island of Oahu.

Although commonly referred to as a tree, the papaya is actually a large herbaceous dicotyledonous plant, usually consisting of a single, erect stem surmounted by a crown of large leaves. The stem is hollow and the tissue fleshy but quite firm. Plants are of three sexes—male, female, and hermaphrodite. Propagation is entirely from seed.

The culture is that of a short-lived perennial. Groves come into production in about 12 months from transplanting and are usually taken out and replaced after 2 or 3 years of production. This procedure is followed as a standard cultural practice for several different reasons. One reason is that as plants increase in height, picking becomes inconvenient and hazardous. Also, older plants tend to lose in production, fruit quality, and fruit size.

Production in the Hawaiian Islands is almost entirely from hermaphrodite plants of the Solo variety. Other types introduced into Hawaii have not achieved varietal status. Thus, Solo is one of the few authentic horticultural varieties of this crop in existence. The Solo hermaphrodite plant type produces distinctive pyriform fruits for which a consumer preference has been established. Hermaphrodite plants are apparently largely self-pollinating, having perfect flowers in which pollen is shed within the closed corolla.

Although Solo appears to be mainly the result of self-pollination, fairly distinct strains have developed. The breeding value of individual plants and strains has not been studied extensively. Breeding value can be determined by growing and studying the progenies of properly selected parental plants.

A progeny study was initiated in 1950 for the purpose of obtaining information on maintaining and improving the Solo type. It was proposed in this study to investigate the breeding behavior of individual plants and strains of the Solo variety with respect to plant vigor, bearing height, and earliness of flowering. The possible bearing of inbreeding and sex expression upon these characters was emphasized because of its practical importance. The study was confined to the Solo variety, with which growers in Hawaii are exclusively concerned. Previous data on crosses within and between strains have not been found. Facts about controlled inbreeding of papaya also seem to be limited. The present study was designed to compare the breeding behavior and general combining ability of individual plants for stem thickness, terminal growth, bearing height, and earliness. Plant vigor, of which terminal and diameter

growth rates are a measure, becomes of increasing importance to plant breeders as growers are obliged to use the same land for successive papaya plantings. Growers often tend to underestimate cultural problems associated with a continuous cropping system. Unsatisfactory growth and short-lived plants are often attributed to degeneration of seed stock or inbreeding effects. Height of bearing, as well as earliness of bearing, influence the profitable life of a papaya grove. Therefore, both early and low bearing are desirable objectives of a breeding program with this crop. It was also possible in this study to compare uniformity and vigor of progenies produced within two fairly distinct strains, and by crossing them. The results of selfing were compared with those from crossing, and the hermaphrodite and female plants were compared in various progenies.

LITERATURE

Literature relating to progeny testing in papaya is discussed under the following headings: (1) establishment and maintenance of varieties, (2) progeny testing, (3) quantitative inheritance, and (4) sex determination.

Establishment and Maintenance of Varieties

Hofmeyr(6) recognized the need for controlled pollination to assure a reasonable degree of uniformity in cross-pollinating dioecious papaya types. Commercial growers were cautioned that continuous close inbreeding of sibling plants to establish uniformity and quality was still in the experimental stage. It was stated that close inbreeding might lead to serious losses in plant vigor as in corn.

Wolfe and Lynch (24), in Florida, advocated mass selection followed by self-pollination or sib-pollination to maintain and improve papaya types in that state. The method of pollination would depend upon whether perfect-flowered or dioecious types were grown. The status of their findings was summarized as follows: "Until several fairly pure lines have been segregated, there is not much opportunity for breeding by recombination of characters, but a great deal can be done by growers who wish to practice mass selection."

Agnew (1, 2), working in Queensland, Australia, discussed the development of pure-breeding lines from both locally selected and introduced papaya types. Controlled sib-pollination methods were used in inbreeding desirable dioecious strains to obtain uniform lines with desirable fruit and plant characteristics. As a result of this work two inbred varieties, Improved Peterson and Bettina, were recently produced and released.

Kadam(10), in India, in a review of papaya breeding progress and prospects, stated that "a properly considered program of breeding papayas should start with inbreeding desirable individual plants to obtain uniformity of characters after which unrelated desirable inbreds should be crossed to determine whether or not it is possible to utilize F_1 hybrid seed for commercial seed."

Storey and Kamemoto (20), in discussing a series of good inbred Solo lines under test at the University of Hawaii, mentioned but did not elaborate on the statement that "there are indications that they (inbred lines) are losing vigor and they are to be tested further to determine inbreeding effects." However,

in 1950, Storey *et al.* (*21*) reported the distribution of large amounts of seed of Line 5 Solo, an inbred which had been grown from self-pollination seed for six generations. No further mention of loss of vigor from inbreeding was made in this report. Presumably, Storey considered the inbred Line 5 Solo strain to be of sufficient vigor and merit to warrant extensive testing as a commercial variety.

Traub *et al.* (*23*) presented an account of work in papaya breeding since 1932 in the United States. Dioecious types were worked with and varieties were developed and maintained by selective inbreeding, using controlled sib-pollination. These workers stated that evidence was found suggesting deleterious inbreeding effects on pollen germination and vigor of young seedlings. The possible necessity of periodic crossing of inbred lines to maintain pollen viability and plant vigor was pointed out. In this connection it was stated that "the cross of two inbred lines, Orlando ♀ (No. 706) x Fairchild ♂ (No. 745) gave more vigorous progeny than that from selfed parents." This statement was apparently based on observations of amounts of fruit set during a dry summer. No supporting data were given. The sexes of parental plants of each strain, crossed or self-pollinated to produce the seed for progenies referred to as "selfed parents," were not given. However, the F_1 generation was produced from a female by male cross.

Progeny Testing

Traub *et al.* (*23*) conducted a progeny test of 30 progenies produced from crosses within and between several individual plant selections and plants from inbred lines. Plant data recorded in this study included height and diameter of stem, spread of leaves, height of basal fruits, leaf type, and flower color. Data on fruit characteristics and taste qualities were also taken. An attempt was made to use this information in selecting promising inbred types for use as commercial varieties. Two were given varietal names, Fairchild and Kissimmee.

Hofmeyr (*7*) reported on progeny studies with dioecious papayas in South Africa. His report emphasized the importance of progeny testing and controlled pollination of selected sibling plants in the establishment and improvement of papaya lines for commercial planting. The danger of reduced plant vigor with continuous inbreeding was also considered important.

Quantitative Inheritance

Nakasone (*12*) conducted quantitative inheritance studies of growth and fruiting characteristics of papaya. Crosses of male and female plants from the Betty variety with hermaphrodite and female plants from the Line 5 Solo strain were made. The progeny tests included both parental types, the F_1, the F_2, and back-crosses of the F_1 to both P_1 and P_2. The F_1 means for height to first flower and number of nodes to first flower fell between the parental means, but nearer the mean of the low-fruiting Betty variety. No evidence of hybrid vigor was found in the F_1, and no loss of vigor was detected in comparing the F_1 with the F_2. Using lower flowering as a possible indication of heterosis, comparison of the F_1 and F_2 means suggests that F_2 plants flowered lower than the F_1 plants. The difference, 3.7 ± 0.97 inches, though not large, was significant

at the 1 percent probability point. In summarizing the results, Nakasone stated that analysis of the data suggested quantitative inheritance for the characters studied, and partial dominance for lower-flowering by the Betty variety. Geometric interaction of allelic genes was also suggested as a possible explanation. The mean of the P_1 was 25.4 ± 0.23 weeks to first flower and the mean of the P_2 was 32.8 ± 0.28 weeks. The wide difference of 7.4 ± 0.36 weeks between varieties is highly significant. The means of the F_1 and F_2 progenies were almost identical for earliness of flowering. The means and standard errors for "weeks to first flower" were 27.8 ± 0.15 for the F_1 compared with 27.5 ± 0.20 for the F_2. The difference of 0.3 ± 0.25 between F_1 and F_2 means seems unimportant. These data suggest partial dominance for earliness.

Storey (19), in Hawaii, reported a study dealing with the inheritance of height of bearing, an important consideration in papaya growing. A relatively high-fruiting inbred Solo strain was crossed with four different low-bearing foreign papaya accessions. The mean bearing height of F_1 progenies was found to be intermediate and closely approaching the arithmetic mean of the parental types. No evidence of segregation into distinct classes of bearing heights was found in the backcross of the F_1 to the higher fruiting parent. The conclusion was drawn that in any cross between varieties with different fruiting heights, the F_1 progeny may be expected to be intermediate between parental types, because of the apparent effect of multiple factors influencing this character.

Hofmeyr (8) reported on experiments on plant growth in papayas in 1938. It was concluded that either thickness of stem or height was a reliable index of plant vigor. This seemed particularly true when measurements were taken at or before plants began to set heavy crops of fruit.

Sex Determination

Because of three basic sex forms and numerous cyclic changes in fertility and sterility by both male and hermaphrodite plant types, a number of conflicting interpretations of the sex situation in papaya have been expressed. However, in 1938 Storey (17), in Hawaii, and Hofmeyr (8), in South Africa, came to similar conclusions with regard to the inheritance of sex in *Carica papaya*. The scheme for sex determination in papaya adapted from Storey and Jones (18), using the Mendelian symbols first proposed by Hofmeyr (8), is as follows:

Genes:
M_1 = dominant factor for maleness
M_2 = dominant factor for hermaphroditism
m = recessive factor for femaleness

Phenotypic effects:
M_1m = the male or staminate plant
M_2m = the hermaphrodite plant
mm = the female or pistillate plant

Inheritance:

Crosses and Selfs	Female Plants	Hermaphrodite Plants	Male Plants	Nonviable Combinations
1. mm x M_1m	1 mm	—	1 M_1m	—
2. mm x M_2m	1 mm	1 M_2m	—	—
3. M_1m selfed	1 mm	—	2 M_1m	1 M_1M_1
4. M_2m selfed	1 mm	2 M_2m	—	1 M_2M_2
5. M_2m x M_2m	1 mm	2 M_2m	—	1 M_2M_2
6. M_2m x M_1m	1 mm	1 M_2m	1 M_1m	1 M_2M_1

According to these workers, sex in papaya is inherited on a single factor basis. The factors determining sex constitute a triple allelic series. The segregation of female plants in all progenies, irrespective of parental sex, is explained on the assumption that both male and hermaphrodite plants are heterogametic for sex. The theoretical plant types, shown as nonviable in the table above, fail to appear because of a lethal condition in early stages of development of the M_1M_1, M_2M_2, and M_1M_2 zygotes. The M_1m and M_2m or heterogametic conditions are, however, viable.

In several countries, there is a belief among papaya growers that plants of one sex or the other grow faster in the young seedling stage. Numerous attempts have been made to separate plants of different sexes on the basis of seedling vigor or other seedling characteristics. Sakurai (15), working in Formosa, conducted a series of interesting field and laboratory tests on various methods and criteria by which papaya growers claimed to be able to distinguish the sex of papaya plants by the phenotype of young plants, and also from the external appearance of the seed, or its location within the fruit. He found none of the methods described to be of positive value in predicting the sex.

Elden (4), Hofmeyr (8), Pope (13), and Reyes (14) also investigated several methods proposed to separate pistillate seedlings from staminate seedlings on the basis of young seedling characteristics. None of these investigators found any of the methods investigated to be useful in determining sex of papaya plants prior to flowering. Kumar (11), in a preliminary study of growth rates of papaya seedlings prior to flowering, made the following statement: "Measurements of seedlings suggest that at 12 weeks old, male seedlings have a higher rate of stem elongation than do female or hermaphrodite seedlings. Further work is necessary, however, before definite conclusions can be drawn." No statement of differences in terminal growth rate between female and hermaphrodite plants was made by this worker. Presumably none were detected, and the statement that no definite conclusions can be drawn emphasized the preliminary nature of the study.

Sakurai (15), Hofmeyr (8), and Nakasone (12) conducted progeny tests in the field to determine if significant differences in quantitative growth characters could be detected between plants of different sexes in the same variety or progeny. These workers failed to detect significant differences between plants of different sexes in the pre-flowering stage. However, during the second year of growth, after the female plants had produced considerable numbers of fruit, Hofmeyr found significant differences in terminal growth rate in paired comparisons of male and female plants. This difference is attributed to the

comparative unfruitfulness of male plants resulting in more vegetative growth. The males, which sometimes produce a few perfect flowers, set relatively few fruits compared to the females and consequently increased in stature more rapidly. Sakurai and Hofmeyr both used height of stem at a given age as a growth index, while Nakasone measured and studied earliness of flowering, height of first flower, and number of nodes to first flower.

MATERIAL AND METHODS USED

Parental Plants

The parental strains were (1) Line 5, an inbred selection of Solo, and (2) Logan Solo, a grower's selection maintained from open pollination seed. Two hermaphrodites and one female from each of these strains were used as parental plants to produce seed for the progeny test.

Line 5 was used as one of the parental strains because it is an important commercial strain in Hawaii and because it is one of the most highly inbred papaya strains in existence. The self-progenies grown in this field test had been inbred eight consecutive generations by selfing perfect flowers on hermaphrodite plants.

Logan Solo, typical of many good growers' strains, by way of contrast in origin and propagation practice, was selected and grown from one plant generation to the next, exclusively from open pollination seedlings. The three Logan parental plants were open-pollination seedlings from a single plant selection made in a commercial papaya grove. The selection was made on the basis of flavor, quality, and desirable pyriform fruit shape.

There were noticeable differences between Line 5 and Logan plants growing together in 1950. The first Logan fruits to mature ripened approximately a week earlier than the first Line 5 fruits. Logan Solo also began to set carpelloid fruits earlier than Line 5. The tendency to produce carpelloid fruits was of longer duration in Logan than in Line 5. Although both Logan and Line 5 are readily recognized as types of the variety Solo, they differ enough so that they probably should be considered distinct strains.

TABLE 1. Self- and cross-pollinations made with six papaya plants to give seed for a progeny test.

PARENT PLANTS	LOGAN I ♂	LOGAN II ♂	LOGAN III ♀	LINE 5 IV ♂	LINE 5 V ♂	LINE 5 VI ♀
Logan I ♂	⊕	—	—	—	—	—
Logan II ♂	x	⊕	—	—	—	—
Logan III ♀	x	x	—	—	—	—
Line 5 IV ♂	x	x	x	*	†	—
Line 5 V ♂	x	x	x	x	⊕	—
Line 5 VI ♀	x	x	—	x	x	—

⊕ Self-pollination.

x Cross-pollination.

   * Missing. Open-pollination seed from plant IV was substituted in growing the seedling progenies for field testing.

   † Reciprocal cross of IV x V. This was the only reciprocal cross made and was used only as a filler progeny in the field test.

Seed

Individual flowers from each of the parental plants were self- and cross-pollinated in all possible combinations of parental plants, excluding reciprocals, as shown in table 1. Pollinations were repeated to assure at least one seed lot of each combination required. In crossing hermaphrodite plants, flowers were emasculated at least 3 days prior to anthesis in order to be certain that the anthers had not already dehisced. Emasculation was done with tweezers. Due caution was exercised not to injure the flower in the operation, because injured papaya flowers seldom set fruit. Hermaphrodite flowers were selfed by covering them with a small glassine bag before the flower opened.

Cross-pollinations were made immediately after emasculation, using a bud with dehiscing anthers as an applicator, after removal of the petals. Immediately after pollination, other flowers of the inflorescence were removed and the crossed flower covered with a small glassine bag. During the summer and fall of 1951 the mature seed was harvested.

The self-seed lot from plant IV of Line 5 was missing, the plant having been damaged in a windstorm. However, fruits from crosses remaining on this plant matured. Two open-pollination seed samples from pyriform fruits on plant IV were substituted for the missing self-seed. It seemed reasonably safe to consider this seed equivalent to self-seed because pollination studies carried on concurrently showed very little crossing.

In this pollination study, 18 pyriform open-pollination fruits were taken at random from hermaphrodite Solo plants exhibiting a recessive autosomal leaf character. These plants were isolated between plants showing the normal leaf character. Young seedlings resulting from self-pollination of the recessive tester plants would show the recessive leaf character, while those from crossing would appear as the normal dominant leaf type. However, out of 1,356 seedlings grown, only one seedling with the normal leaf type was found. This indicates that self-pollination was more than 99.9 percent in these samples. It is therefore suggested that the open-pollination seed samples from No. IV hermaphrodite plant were probably self-seed.

That seed from pyriform fruits borne on hermaphrodite plants of Solo (figure 1) results from self-pollination is suggested by the occurrence of bud pollination. The appearance of the predominant type of perfect flower, which produces pyriform fruits, is shown in the upper picture in figure 2. Pollen is shed directly on the stigmatic surface. This means that seed from this flower type is largely the result of self-pollination. Solo seed used for commercial groves is almost exclusively from this type of flower. Commercial seed is saved from fruits of good flavor and pyriform shape.

Some flowers of the type shown in the lower picture in figure 2, as well as others with nine to six stamens, intermediate in form between the upper and lower pictures in figure 2, are found on most Solo hermaphrodite plants during the winter season. These atypical flower forms develop into characteristic lobed

and deformed fruits which are unmarketable. There is an opportunity for cross-pollination in these atypical flower forms, because the anthers are inserted well below the stigma and the amount of pollen is reduced. These fruits are not used for seed and therefore cross-pollination does not seem to be an important factor in maintaining the Solo variety. Female plants are segregated in progenies from hermaphrodite parents, but are not profitable for commercial production because of consumer preference for pyriform fruits. Therefore, most growers remove female plants from their groves as soon as they can be detected from their pistillate flowers and ovoid fruits (figure 3).

Seedlings

Seedlings for the progeny test were grown from seed planted September 25, 1951. Approximately 150 seeds were planted for each progeny. On October 15, seedlings were transplanted into 3½-inch paper pots. No conscious selection of seedlings was made other than picking relatively uniform healthy plants for transplanting. The seedlings were uniform in size and appearance at transplanting time.

Soil

The experimental planting was located on a good soil type in an area considered suitable for commercial papaya production. The soil was a friable, clay loam with good surface and subsurface drainage. Sizeable commercial papaya groves were located in several nearby fields surrounding the progeny test planting.

Field Planting

The experimental plants for the progeny test were set out in the field on November 16. At this time the plants were about 6 centimeters in height with four to six true leaves. Transplanting was done in the afternoon. Plants were watered in by means of irrigation water run in the contour furrow marking each row. No plant losses resulted from transplanting and the plants did not wilt after being set out.

The field planting was set out as a 4 x 5 simple rectangular lattice design with four replications. This resulted in a field planting of 16 rows of 20 plants each. Spacing between rows was approximately 10 feet. The slope of the land in the direction of the rows was 2 to 3 degrees, and it was possible to lay out rows in a straight line for furrow irrigation. Figure 4, taken at right angles to the rows, and figure 5, taken diagonally across the field from the lower end, show relatively uniform spacing between rows and between plants in the row. Spacing between plants in the row was 8 feet. At this spacing there was little or no competition between young plants prior to flowering. The plants in papaya groves in Hawaii are often spaced as closely as 7 feet by 8 feet without apparent adverse effects on plant growth or fruit yield. In Trinidad, planting as close as 6 feet by 6 feet has been recommended by Thorold (*22*) for maximum yields.

FIG. 1. Hermaphrodite Solo papaya plant 8 months old. Note pyriform fruit shape.
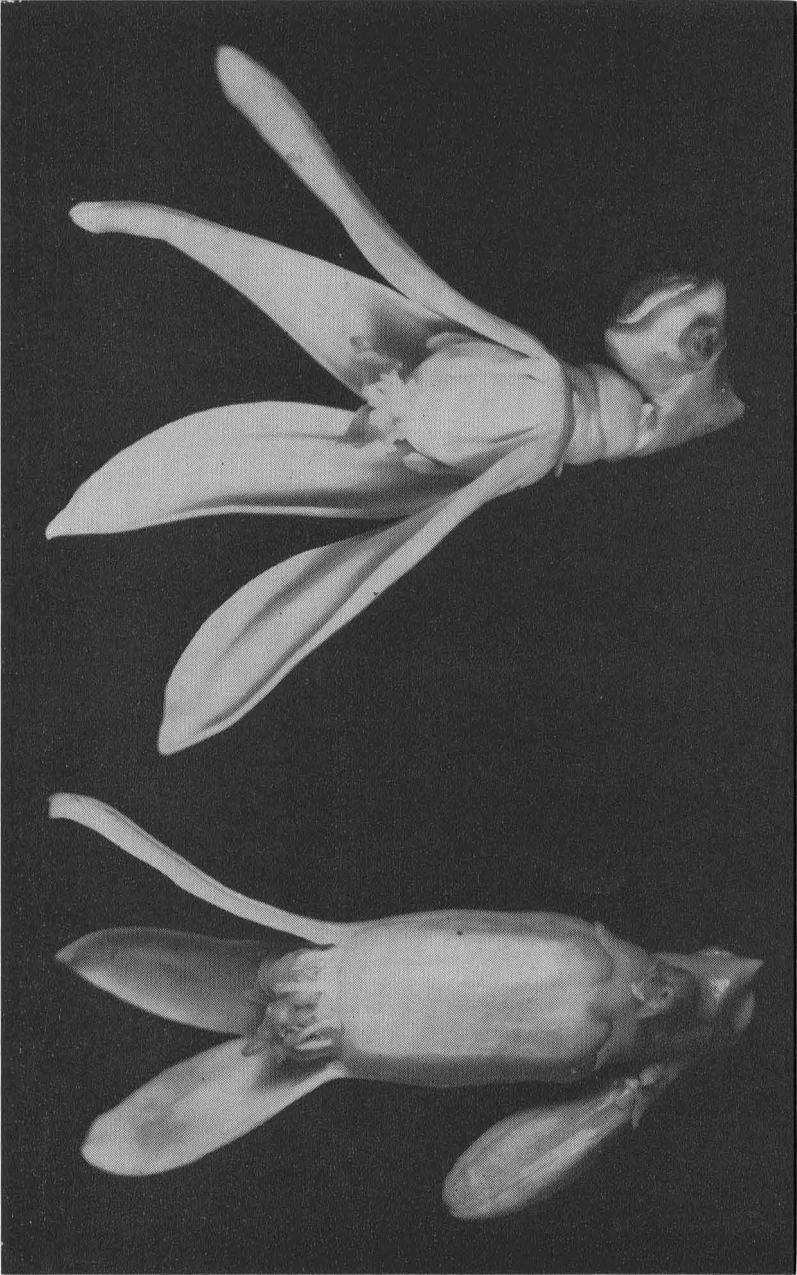
FIG. 2. *Left:* Perfect flower prior to anthesis, with petals cut away on one side to show bud pollination. *Right:* Atypical flower from same plant as left. Note stamens inserted below and well separated from stigma. More crossing probably occurs in this flower type, which produces cull fruits.
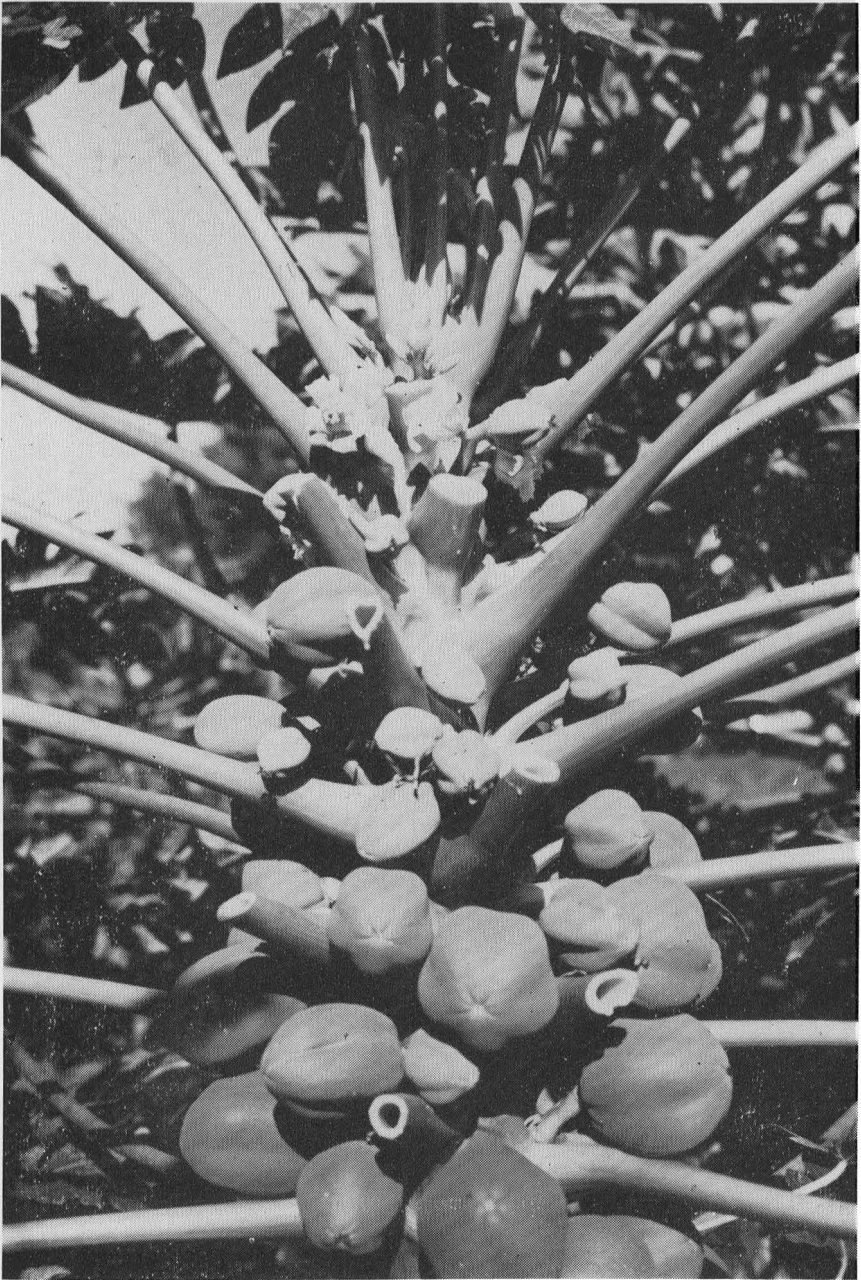
Fig. 3.   Eight-months-old female Solo plant, sibling of hermaphrodite in Fig. 1.   Note ovoid fruit shape developed from pistillate flowers.
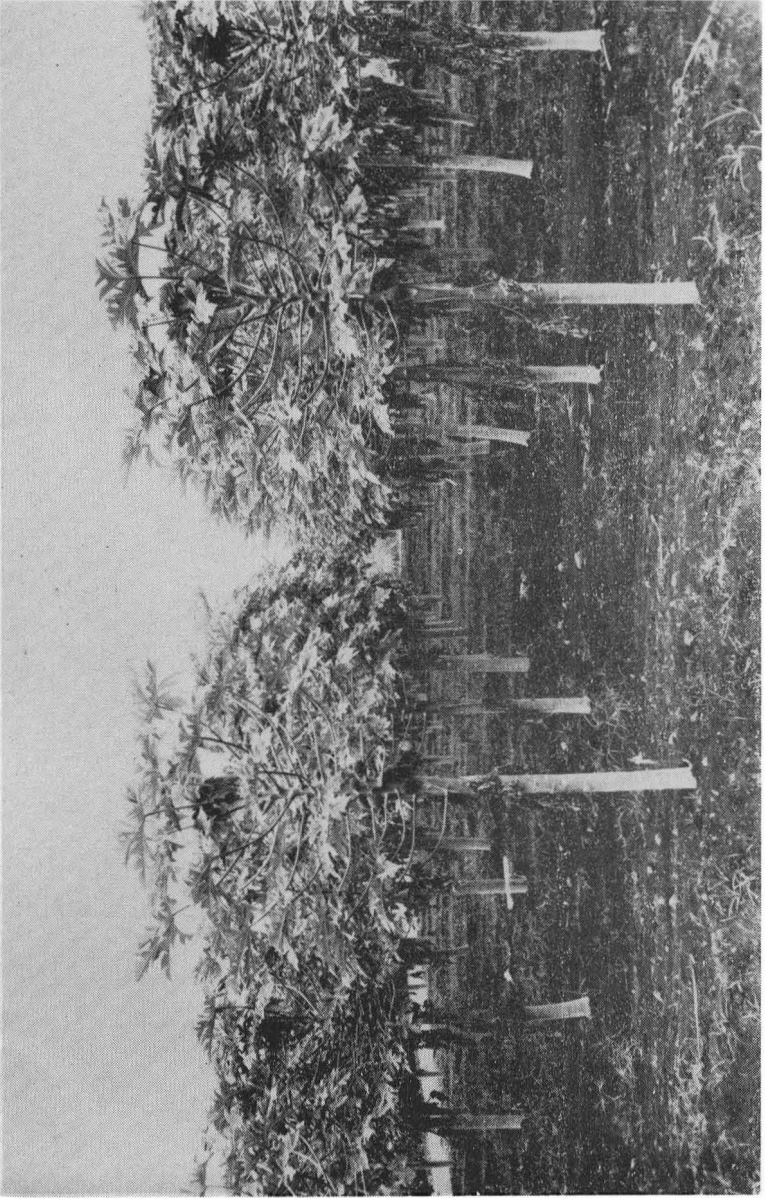
Fig. 4. View of progeny test papaya grove taken at right angles to rows.
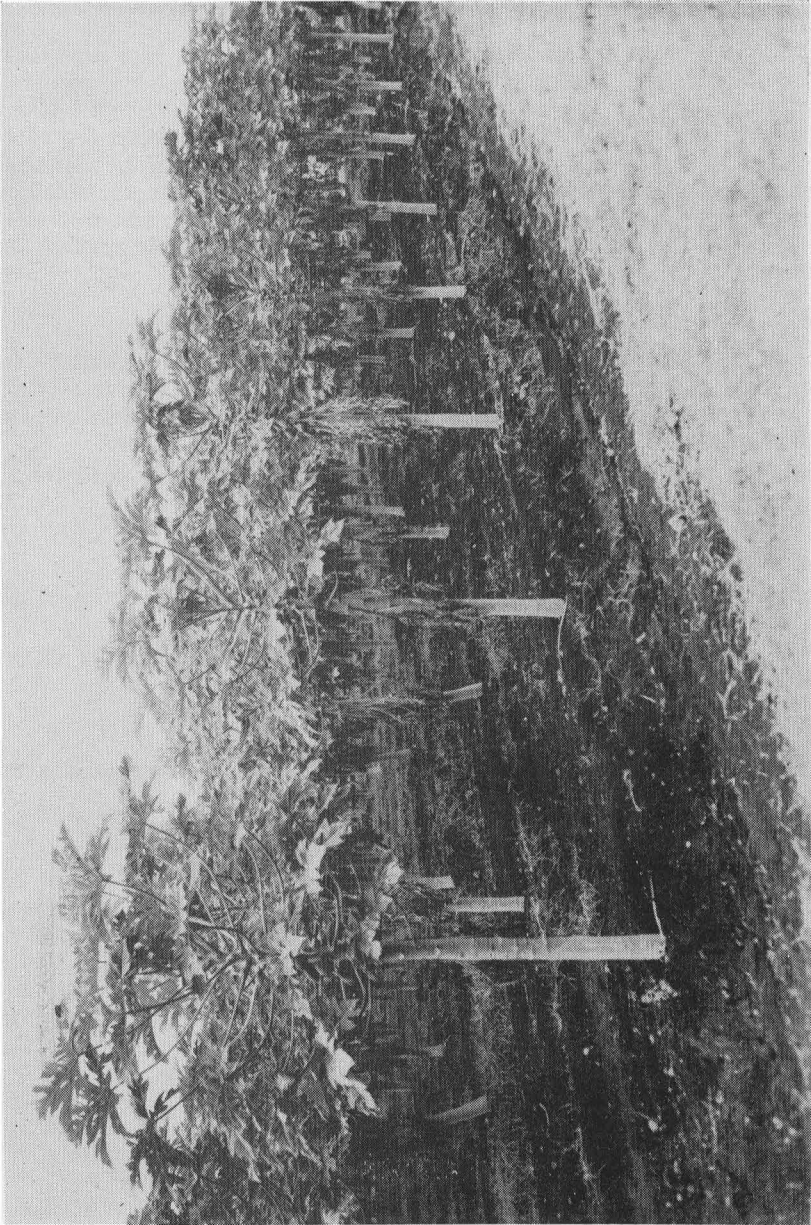
Fig. 5. Diagonal view of progeny test planting at eight months of age, showing irrigation furrows and uniform spacing of plants in contour rows.

No serious cultural difficulties were encountered in growing the plants except for intermittent wind damage during winter months. A wind storm on January 19, 1952, caused the outright loss of 12 plants. At several other times, tops were broken out of one or more plants, so that terminal growth data from these plants were not usable. This resulted in slightly different numbers of plants in the analysis of different characters studied. The data from damaged plants were usable for some characters, but not for all. A noticeable depressing effect on growth rates was observed in row 1 on the side of the field from which the prevailing westerly trade winds blow. A similar depressing effect was noted on growth rates in row 16 on the opposite side of the field. This was a fertility effect caused by removal of much of the topsoil from this row in grading the road along that side.

Culture

Cultural operations were similar to practices of commercial growers. The experimental plants were furrow irrigated, as necessary, usually once a week. Weeds were controlled by hand hoeing in the rows and shallow disk cultivation between rows. Three fertilizer applications were made as follows:

1. August, 1951, lime at the rate of 2½ tons per acre was spread evenly throughout the field and disked in.
2. November, 1951, ½ lb. 8-8-8 formula per plant was applied to the soil surface in a circle 1 foot from base of plant.
3. March, 1952, 1 lb. 8-8-8 formula per plant was plowed under in the irrigation furrow 1 foot from base of plants.
4. July, 1952, 1 lb. 4-8-12 formula per plant was plowed under in the irrigation furrow about 2 feet from base of plant.

Collection of Data

Data were taken on the following characters: (1) increase in stem diameter, (2) terminal growth rate, (3) bearing height, and (4) earliness.

Stem diameter measurements were taken at monthly intervals. Data used in the analysis of this character were the increases in stem diameter in millimeters during the 2-month period from April 25 to June 26. Most of the plants had begun to flower by the time the final diameter measurement was taken. Diameter measurements were made 10 centimeters above the cotyledonary node. Plants less than 7 centimeters in diameter were measured with a vernier caliper. Diameter of larger plants was computed to the nearest millimeter from the circumference measurement. This was done by dividing the circumference by the appropriate factor (3.1416). This method assumes the stems to be round, which they essentially are.

Terminal growth rate was recorded during a 1-month period from April 25 to May 26, as the difference between two successive monthly measurements of stem height, recorded to the nearest half-centimeter. At the date of the final terminal growth measurement, only a few plants had begun to flower.

The number of calendar days from November 16, 1951, the field transplanting date, to the day when the first flower opened was taken as the measurement of earliness.

Bearing height was measured in centimeters between the cotyledonary node and the leaf axil where flowering first occurred.

The measurements of stem height, stem circumference, and height of flowering were taken from a reference point 10 centimeters above the cotyledonary node, marked plainly with a small glass-headed pin.

Analysis of Data

The field test was arranged in a 4 x 5 simple rectangular lattice design, for analysis according to the incomplete block system devised by Harshbarger (5). The planting contained four replicates of four plants for each cross- or self-progeny grown. However, differences between sexes in the characters studied caused the elimination of female plant data in progeny evaluation. Wind damage to one border row and fertility variation in another caused the loss of growth data from these rows. Therefore, the lattice design was not usable in analyzing the data. However, the relative uniformity of soil conditions in the field, as shown by the evenness of plant growth, indicated suitability of an analysis based on variation within and between sexes, and within and between progenies. It is thought that the randomization was satisfactory to justify this type of analysis. With only hermaphrodite progenies being used, the number of plants available for measuring in specific progenies varied from 5 to 14. These specific progenies were in four different locations in the planting.

The procedure followed for the within and between type of analysis for stem diameter, terminal growth, and bearing height is given by Snedecor (16), section 10.8. The method is adapted to subsamples with different numbers of variates. The within variance was used in computing standard errors of differences between means.

To compare sexes, the error variance used in the analysis of variance was that within sexes. The F value was the ratio of between and within variances. This analysis was used to compare hermaphrodite with female plants in various progenies and groups of progenies. The total variance for all plants was computed. The variance due to sex was subtracted from the total. The remainder was divided by degrees of freedom for within sexes and provides an estimate of error variance. The error thus obtained is that of a single plant. Degrees of freedom giving this error are therefore equal to the total number of plants tested, minus two. Differences between sexes were found in all four characters. Because of these differences and because hermaphrodite is the sex primarily used for fruit production, it was desirable to emphasize the performance of hermaphrodite plants. Therefore, only hermaphrodite plants in the progenies were considered in testing the various combinations of parental plants. For the data on hermaphrodites only, the analysis of variance was computed as within and between progenies. The appropriate error for comparing progenies and progeny groups is that within progenies. Mean standard errors were obtained by dividing standard error of a single plant by the square root of the number of observations giving the respective means.

In discussing experimental results, comparisons reaching the 5 percent level in the "t" test are referred to as "significant," while those reaching the 1 percent level, or exceeding it, are considered and referred to as "highly significant." The use of these levels is made, fully appreciating the fact that significance

made at the 0.05 level may be expected to be in error about once in 20 instances and that at the 0.01 level may be expected to be wrong approximately 1 percent of the time.

RESULTS

Sex Segregation Ratios

In table 2, parental combinations are shown with numbers of hermaphrodite and female plants occurring in 18 progenies resulting from cross- and self-pollinations of six parent plants.   These are also the numbers of plants from which data were taken on height of bearing.   The number of plants from which data were taken on stem diameter and terminal growth was somewhat less, due to the elmination of border row data.   The numbers given in table 2 were approximately those used for earliness studies.   Damage to a few individual plants affected earliness data but had no apparent effect on bearing height.

The observed sex numbers (table 2) were tested by chi-square (x^2) for goodness of fit to the expected ratios.   Results of this test are given in table 3.   The five progenies from hermaphrodite parents selfed and the seven from hermaphrodite parents crossed are included in one test because the expected ratios are 2:1 in each case.   Included are two extra progenies which were used only in x^2 testing.   These progenies are duplications of two of those shown in table 2.

The plants from the eight female by hermaphrodite crosses gave a good agreement with an expected ratio of one female to one hermaphrodite.   The x^2 for goodness of fit to a 1:1 ratio for eight progenies also indicates a good fit.

Chi-square tests of the 12 individual progenies resulting from selfing or crossing hermaphrodite plants gave satisfactory fits, but the x^2 for the total numbers of female and hermaphrodite plants in these same progenies was 4.73 with 1 degree of freedom, which is significant.   Deviations as large as this would be expected only 2 to 5 percent of the time from random sampling.

TABLE 2.   Numbers of hermaphrodite and female plants segregating in progenies resulting from indicated pollinations of six parent plants.

PARENT PLANTS	LOGAN I ♂		LOGAN II ♂		LOGAN III ♀		LINE 5 IV ♂		LINE 5 V ♂		LINE 5 VI ♀	
	NO. ♂	NO. ♀	NO. ♂	NO. ♀	NO. ♂	NO. ♀	NO. ♂	NO. ♀	NO. ♂	NO. ♀	NO. ♂	NO. ♀
Logan I ♀												
Logan II ♀	11	5										
Logan III ♀	7	8	8	6								
Line 5 IV ♀	14	2	11	3	9	7						
Line 5 V ♀	12	4	8	7	7	9	11	4				
Line 5 VI ♀	8	7	7	8			11	4	6	10		
♂ ⊕	13	2	14	2	—	—	11	5	10	6		

TABLE 3. Chi-square test for goodness of fit to expected sex ratios in 12 hermaphrodite self- and cross-pollination progenies and 8 female by hermaphrodite progenies.

HERMAPHRODITE SELF- AND CROSS-POLLINATION PROGENIES	D F	x^2 FOR FIT TO EXPECTED SEX RATIOS	PROBABILITY
Sum of 12 progenies	12	13.20	.50-.30
Total (between sexes)	1	4.73	.05-.02*
Heterogeneity	11	8.47	.70-.50

Observed No. Plants = 138 ♂ :48 ♀
Expected No.   = 124 ♂ :62 ♀

FEMALE BY HERMAPHRODITE POLLINATION PROGENIES	D F	x^2 FOR FIT TO EXPECTED SEX RATIOS	PROBABILITY
Sum of 8 progenies	8	3.02	.95-.90
Total (between sexes)	1	.07	.80-.70
Heterogeneity	7	2.95	.90-.80

Observed No. Plants = 63 ♂ :59 ♀
Expected No.   = 61 ♂ :61 ♀

* Significant deviation at 5 percent.

Examination of the sex ratios of the 12 individual progenies from hermaphrodite self- and cross-pollination, reveals that this result is due to a small excess of hermaphrodite plants in 10 out of the 12 progenies. If a ratio of three hermaphrodites to one female plant is assumed, x^2 on the total female and hermaphrodite plants in these progenies is 0.07 with 1 degree of freedom, indicating a good fit, in fact much better than to a 2:1 ratio.

Possible explanations for observed deviations from the expected 2:1 ratio in progenies from hermaphrodite parents are: (1) non-random production of M_2 and m gametes by hermaphrodite parents, (2) unequal survival of these two types of gametes, (3) non-random fertilization, (4) unequal survival of M_2m and mm seedlings, and (5) unconscious selection at the time of potting or transplanting in the field.

The total plants in the 12 progenies is 186 and, on the basis of this limited test, conclusions with regard to sex ratios are probably not justifiable. The possibility of growing duplicate progenies from cross- and self-pollination seed lots, which gave the greatest excess of hermaphrodite plants, is suggested for further testing. These results cannot be explained by the tests made here. The evidence obtained by other workers indicates that hermaphrodite plants are heterozygous and the four hermaphrodite parent plants used were shown to be heterozygous for sex by the results of crosses with female parents.

Homogeneity of Variances

Variances of 18 pollination combinations and two filler progenies grown to complete the 4 x 5 lattice design were tested for homogeneity. Bartlett's test for homogeneity of variances (3) for samples of unequal size was used. The results and probability values are given in table 4.

TABLE 4. Results of Bartlett's test for homogeneity of variances of individual progenies with unequal sample size.

CHARACTER	D F	x^2	PROBABILITY
Stem diameter	20	19.53	.50-.30
Stem height	20	27.18	.20-.10
Bearing height	20	11.69	.95-.90
Earliness	20	29.36	.10-.05

The probability values of x^2 for stem diameter, stem height, and bearing height fail to suggest heterogeneity. For this reason, the variances were assumed to be homogeneous and the standard error of a single plant determination was used in computing the mean standard errors used. However, the probability value of x^2 for earliness is between 5 and 10 percent. This suggests that progeny variances for earliness data may not be homogeneous. It is also an indication that individual progeny variances may not constitute an unbiased sample from the same population source. When the earliness variances of all hybrid progenies from a common parent are tested for homogeneity using the F test described by Snedecor (16, section 10.13), several comparisons produce P values indicating less than 2 percent probability. This further confirms a tendency of variances for earliness to appear heterogeneous. Probably the earliness variances were not homogeneous. Therefore, variances used in computing mean standard errors for earliness were computed directly from the individual variates making up those means.

DIFFERENCES BETWEEN SEXES

In a preliminary analysis, significant differences were found between hermaphrodite and female plants in some progenies and group progenies, in each character studied. However, these differences which are shown in tables 5, 6, 7, and 8 were not consistent. The observed differences were in favor of hermaphrodite plants in some progenies and in favor of female plants in other progenies.

TABLE 5. Differences in rate of increase in stem diameter between hermaphrodite and female papaya plants in progenies from various combinations of six parent plants. Millimeters per 60 days. Hermaphrodite mean minus female mean.

PARENT PLANTS	LOGAN I ♂	LOGAN II ♂	LOGAN III ♀	LINE 5 IV ♂	LINE 5 V ♂	LINE 5 VI ♀
Logan I ♂						
Logan II ♂	1.6					
Logan III ♀	3.5	0.1				
Line 5 IV ♂	9.7*	0.1	5.0			
Line 5 V ♂	2.3	(-)6.3	3.3	(-)7.6*		
Line 5 VI ♀	1.4	7.1		7.6	2.4	
Hybrid Progeny[1] ♂ ⊕	2.1±1.62 (-)5.2	0.8±1.71 (-)11.2	2.8±1.74	1.0±1.74 1.4	(-)1.0±1.63 (-)3.7	3.2±1.71

* Significant difference at 5 percent.
[1] Difference between true means.

TABLE 6. Differences in monthly terminal growth rate between hermaphrodite and female papaya plants in progenies from various combinations of six parent plants. Centimeters per month. Hermaphrodite mean minus female mean.

PARENT PLANTS	LOGAN I ♂	LOGAN II ♂	LOGAN III ♀	LINE 5 IV ♂	LINE 5 V ♂	LINE 5 VI ♀
Logan I ♂						
Logan II ♂	0.0					
Logan III ♀	1.2	1.2				
Line 5 IV ♂	3.4	1.8	4.5*			
Line 5 V ♂	2.1	1.7	2.0	3.4		
Line 5 VI ♀	3.6	5.5*		4.5*	3.5	
Hybrid Progeny[1] ♂ ⊕	1.7±0.96 (-)3.6	1.7±1.03 (-)1.5	2.2*±1.05	3.1**±1.03 2.5	2.4*±0.98 1.6	4.0**±1.02

* Significant difference at 5 percent.
** Significant difference at 1 percent.
[1] Difference between true means.

TABLE 7. Differences in bearing height in centimeters between female and hermaphrodite papaya plants in progenies from various combinations of six parent plants. Female mean minus hermaphrodite mean.

PARENT PLANTS	LOGAN I ♂	LOGAN II ♂	LOGAN III ♀	LINE 5 IV ♂	LINE 5 V ♂	LINE 5 VI ♀
Logan I ♂						
Logan II ♂	21*					
Logan III ♀	6	17				
Line 5 IV ♂	(-)5	8	4			
Line 5 V ♂	11	(-)6	13	16		
Line 5 VI ♀	(-)2	20*		(-)14	14	
Hybrid Progeny[1]	5±4.0	10*±3.8	10*±4.1	2±4.2	10**±3.7	4±4.1
♂ ⊕	16	(-)7		(-)10	(-)3	

* Significant difference at 5 percent.
** Significant difference at 1 percent.
[1] Difference between true means.

TABLE 8. Differences in days to first flower between female and hermaphrodite papaya plants in progenies from various combinations of six parent plants. Female mean minus hermaphrodite mean.

PARENT PLANTS	LOGAN I ♂	LOGAN II ♂	LOGAN III ♀	LINE 5 IV ♂	LINE 5 V ♂	LINE 5 VI ♀
Logan I ♂						
Logan II ♂	(-) 3					
Logan III ♀	8	(-) 3				
Line 5 IV ♂	15	1	9			
Line 5 V ♂	14	8	3	(-)10		
Line 5 VI ♀	(-) 7	(-) 9		12	11*	
Hybrid Progeny[1]	2±3.4	(-)1±2.6	4±2.6	6±3.8	8**±2.6	0.0±3.5
♂ ⊕	5	10		1	12*	

* Significant difference at 5 percent.
** Significant difference at 1 percent.
[1] Difference between true means.

Stem Diameter

Observed differences in rate of increase in stem diameter between sexes in 14 cross-progenies and 4 self-progenies are given in table 5. Error variance is that within sexes, shown in table 9.

TABLE 9.   Analysis of variance of stem diameter.

SOURCE OF VARIATION	D F	S S	VARIANCE
Total	232	9,136	
Between sexes	1	3	3
Within sexes (error)	231	9,133	39.5

A possible tendency for certain parental plants to produce faster growing female progeny is suggested by negative values in table 5. Only one of the negative differences appears to be significant. Also only one positive value is significant. Other differences were not great enough to be considered significant with the numbers observed. Observed differences in diameter growth between hermaphrodite and female plants in progenies originating from female parents, shown in the row indicated by Hybrid Progeny, are larger in every instance than those from hermaphrodite parent plants. It is of interest to note that sex numbers from the female by hermaphrodite crosses are approximately equal. The only significant difference in diameter growth between female and hermaphrodite plants was found in all progeny of female by hermaphrodite crosses. The mean of hermaphrodite plants from this source was 49.9 mm. and the corresponding female plants averaged 47.0 mm. The difference of 2.9 $\pm$ 1.22 mm. is significant and suggests the possibility of more rapid diameter growth by hermaphrodite plants originating from this type of cross.

Terminal Growth

Differences in terminal growth rates of female and hermaphrodite plants in progenies resulting from cross- and self-pollination are shown in table 6. Differences in terminal growth between plant sexes in the group of progenies making up each general combining ability mean are also given in table 6. In table 10, the error variance computed within sexes is used in making an F test which is highly significant for differences in terminal growth between sexes. Authentic differences in the average terminal growth rates of female and hermaphrodite plants are therefore suggested.

TABLE 10.   Analysis of variance of terminal growth.

SOURCE OF VARIATION	D F	S S	VARIANCE
Total	237	3,639.3	
Between sexes	1	211.4	211.4**
Within sexes (error)	236	3,427.9	14.5

** Significant at the 1 percent level.

This difference, characterized by more rapid stem elongation in hermaphrodite plants, was found in progenies from selfing and crossing of Line 5 parents and in crosses of Logan and Line 5 parents, but not in those resulting from self- or cross-pollination of Logan parents.

Height of Bearing

Data on height of flowering, which is also the height at which the first fruit is borne, were taken from all plants in the progeny test planting. The possible effects of strain differences, self-pollination, and interstrain crossing were considered in the analysis of bearing height data. Table 7 presents observed differences in height of bearing between female and hermaphrodite plants in the 18 self- and cross-progenies tested (average bearing height of female plants minus that of hermaphrodites). It will be noted that 7 out of 18 differences are negative. In table 11, the error variance used in making an F test of differences between sexes is that within sexes. The analysis of variance for differences in bearing height of female and hermaphrodite plants suggests highly significant differences in bearing height between female and hermaphrodite plants.

TABLE 11.   Analysis of variance of bearing height.

SOURCE OF VARIATION	D F	S S	VARIANCE
Total	276	73,297	
Between sexes	1	1,844	1,844**
Within sexes (error)	275	71,453	259.8

** Significant at the 1 percent level.

Comparison of the means of female and hermaphrodite plants in all progenies shows that the bearing height of hermaphrodites in the field test was 5 ± 2.0 cm. lower than that of female plants. This significant difference confirms the F test, indicating differences between sexes in height of bearing. Therefore, it is probable that the average bearing height of hermaphrodites was less than that of female plants.

Earliness

The earliness data were probably not homogeneous and what appear in table 8 to be significant differences in earliness between plant sexes in the progenies from Line 5 No. V parent may not represent valid differences. Because the sample sizes were small and the variances heterogeneous, the observed differences shown in this table cannot be considered conclusive. However, both the sample size and the resulting reliability of the t test are increased considerably by computing the female and hermaphrodite plant means, using all plants of each sex in the 18 progenies. When this is done and the means compared, a significant difference of 4 ± 1.6 days is found. This difference is in favor of earlier flowering by the hermaphrodite plants.

EVALUATION OF HERMAPHRODITIC PROGENIES

As mentioned previously, hermaphrodite plants are used exclusively for commercial fruit production in Hawaii. It is therefore consistent with practice to use only hermaphrodite plants in evaluating these progenies.

Stem Diameter

Table 12 contains the means for the hermaphrodite plants in 14 individual cross-progenies and 6 hybrid progenies having one parent in common. It is apparent that various comparisons can be based on the data in this table. Some to be considered are as follows:

1. Between specific combining ability means which are computed from the progeny of a specific cross.
2. Between general combining ability means which are computed from the several cross-progenies having one parent in common.
3. Hermaphrodite self-progenies compared (a) with each other and (b) with their respective general combining ability means.
4. Between progenies from hermaphrodites selfed and crosses of female by hermaphrodite and hermaphrodite by hermaphrodite.
5. Between group-progeny means from pollinations within Logan and within Line 5, and that of all crosses between strains.
6. The group mean of 14 cross-progenies with the average of 4 self-pollination progenies.

TABLE 12. Stem diameter growth, in centimeters, made in 60 days by hermaphrodite plants in progenies resulting from various pollinations of six different parent plants.

PARENT PLANTS	LOGAN I ♂	LOGAN II ♂	LOGAN III ♀	LINE 5 IV ♂	LINE 5 V ♂	LINE 5 VI ♀
Logan I ♀						
Logan II ♀	47.6±1.85					
Logan III ♀	51.8±2.39	47.6±2.07				
Line 5 IV ♂	46.2±1.62	44.1±2.07	53.5±2.39			
Line 5 V ♂	45.6±2.07	46.2±2.62	49.5±2.39	47.9±1.85		
Line 5 VI ♀	47.6±2.21	44.9±2.21		51.8±1.77	52.8±2.39	
Hybrid Progeny[1]	47.4±0.88	46.2±0.95	50.4±1.14	48.4±0.85	48.3±0.99	49.5±1.05
♂ ⊕	43.8±1.69	44.8±1.85		46.8±1.77	48.1±2.07	

[1] These means represent true averages and are not the mean of means.

The means of the progenies obtained from selfing four hermaphrodite parent plants are shown in the bottom row of table 12. Stem diameter is given as the average increase over a 60-day period. The individual cross-progeny means provide information on specific combining ability, while the general combining ability means are the true averages of all hybrid plants having a given plant as a common parent. Obviously the general combining ability means are from larger samples than are the specific combining ability means.

The error variance for the F test between progenies, shown in table 13, is that within progenies. It is also used in t tests of the individual comparisons made. This analysis based on hermaphrodite plants provides an F test indicating significant differences between progeny means. When stem diameter is taken as a criterion of vigor, the cross pollination progeny of No. III female by No. IV hermaphrodite gave the most vigorous plants in the progeny test. However, 9 out of 13 other crosses gave progeny not significantly different from this cross. Therefore, selection among the 10 individual progenies with most rapid diameter growth rates may not be effective.

TABLE 13. Analysis of variance for diameter growth rates of hermaphrodite plants.

SOURCE OF VARIATION	D F	S S	VARIANCE
Total	151	5,760	
Between progenies	17	1,170	68.8*
Within progenies (error)	134	4,590	34.3

* Significant at 5 percent level.

The largest differences in general combining ability means were between the hybrid progeny from Logan II and the hybrid progenies of Logan III and Line 5 VI. Hybrid plants from Logan III exceed those from Logan II in diameter growth rate by 4.2 ± 1.49 mm. This is a highly significant difference, exceeding the 1 percent level. Hybrid plants of Logan II had a slower rate of increase in diameter than those from Line 5 VI. The difference of 3.3 ± 1.41 mm. is significant. The hybrid progeny of Logan III also increased in stem diameter significantly faster than those from Logan I. The difference of 3.0 ± 1.45 mm. reached the 5 percent probability level. Parental plant III is therefore probably superior to the other two tested in the Logan strain, for producing fast growing trunks in the progeny. Observed differences between general combining ability means of other parental plants were not significant. Close agreement between the three Line 5 parental plants in general combining ability for diameter increase suggests that Line 5 may be more uniform in this respect.

No significant differences were suggested in comparing the self-progeny means of the four hermaphrodite parents. When general combining ability means were compared with the self-progenies of the common parent plant, no significant differences were found.

Comparisons of the diameter increases in progenies from female by hermaphrodite crosses and hermaphrodite by hemaphrodite crosses are of interest. Fifty-seven plants in female by hermaphrodite progenies had a mean of 49.9 ± 0.78 mm. and the average growth rate of 54 plants in hermaphrodite by hermaphrodite progenies was 46.4 ± 0.80 mm. The difference of 3.5 ± 1.11 mm. is highly significant, reaching the 1 percent probability point. The progeny mean of female by hermaphrodite crosses also exceeds that of the hermaphrodite selfed progeny, by 4.2 ± 1.20 mm., which is also highly significant. This is suggestive of more rapid increase in stem thickness by plants from female by hermaphrodite crosses than by progenies of two hermaphrodites crossed. However, it was observed that crosses involving No. III female gave progenies

with rapid diameter growth and may be responsible for the difference. However, no difference was detected between the mean of group progenies of hermaphrodites selfed and that of progenies derived from crossing two hermaphrodites.

In comparing rates of increase in stem diameter of Line 5 and Logan strains, the average growth in stem diameter of all plants from self-pollination and crosses between Logan parent plants was compared with that from all progenies from crosses and selfing of Line 5 parent plants. This comparison gave a difference of 2.7±1.22 mm. in favor of faster growth by Line 5 plants. This difference is significant and Line 5 may be a more desirable source of breeding material for this character.

The mean of the F_1 plants from crosses between strains was 46.9±0.76 mm. which is close to 46.6±0.86 mm., the mean of Logan cross- and self-progenies. Differences are not suggested by these means. However, a difference of 2.4±1.15 mm., suggesting faster diameter growth by Line 5 plants, was found between the averages of F_1 hybrid plants and those resulting from selfs and crosses within Line 5. This was a significant difference. The mean of F_1 plants from interstrain crosses fell between the mean of plants from progenies from Line 5 parents and those from Logan parents, which does not suggest heterosis. Close agreement of the mean of all Logan progenies with that of F_1 progenies from interstrain crosses, and significant differences in comparison of these means with the average of all Line 5 progenies, may be suggestive of dominance in the growth rate of Logan progenies over that of Line 5 progenies. However, these results do not suggest hybrid vigor in the F_1 progeny of crosses between these strains.

The mean of 14 hybrid progenies was 48.2±0.56 mm. compared with 45.7±0.91 mm. in four self-pollination progenies. The differences is 2.5±1.07 mm., which is significant. This difference was probably due to the fact that about half of the hermaphrodite plants in 14 hybrid progenies came from female by hermaphrodite crosses which had significantly higher rates of increase in stem thickness than those from other crosses.

Data from the progeny test suggest that selection of superior breeding Logan plants for further testing may be possible. This possibility is suggested by the general combining ability mean of Logan female plant III. The three Line 5 plants showed no apparent differences in breeding behavior for stem thickness as tested by their hybrid progenies. Use of the female by hermaphrodite cross to produce desirable seed is also suggested as a possibility for further testing.

Terminal Growth

The appropriate error variance for an F test of differences between hermaphrodite progenies is that within progenies. This variance, shown in table 14, is also used in making up mean standard errors for individual progeny and group progeny comparisons. The F test for between progeny differences in the analysis of variance approaches but fails to reach the 5 percent point. Specific combining ability differences are therefore not demonstrated.

TABLE 14. Analysis of variance for terminal growth rates of hermaphrodite plants.

SOURCE OF VARIATION	D F	S S	VARIANCE
Total	156	2,412.3	
Between progenies	17	409.9	24.1
Within progenies (error)	139	2,002.4	14.4

Table 15 lists average terminal growth rates of hermaphrodite plants in the 18 self- and cross-progenies grown. Terminal growth data are given as cm. increase in stem height per month. The means of plants resulting from self-pollination are shown in the bottom row of this table.

TABLE 15. Terminal growth rates, in centimeters per month, of hermaphrodite papaya plants resulting from self- and cross-pollination of six parental plants.

PARENT PLANTS	LOGAN I ♂	LOGAN II ♂	LOGAN III ♀	LINE 5 IV ♂	LINE 5 V ♂	LINE 5 VI ♀
Logan I ♂						
Logan II ♂	39.6±1.14					
Logan III ♀	43.6±1.43	41.5±1.34				
Line 5 IV ♂	42.4±1.05	39.8±1.34	45.7±1.55			
Line 5 V ♂	41.2±1.34	44.0±1.70	42.3±1.55	42.0±1.14		
Line 5 VI ♀	42.6±1.43	42.1±1.43		43.6±1.14	43.8±1.55	
Hybrid Progeny[1] ♂ ⊕	41.7±0.56 39.2±1.05	41.1±0.61 42.5±1.14	43.2±0.73	42.6±0.54 41.5±1.14	42.4±0.63 43.6±1.34	43.1±0.68

[1] True averages.

When average terminal growth rates of individual cross-progenies were studied for indications of specific combining ability, no significant differences were found between the 11 highest means. This suggests that selection of specific parental combinations for rapid terminal growth based on these means may not be effective.

When the average terminal growth rate of hybrid progenies from No. III female parent was compared with the general combining ability means of the other five parent plants, a difference of 2.1 ± 0.95 cm., significant at the 5 percent point, was found between the mean of hybrid plants from No. III parental female and that of No. II hermaphrodite. The general combining ability mean of Logan III exceeds that of Logan I by 1.5 ± 0.92 cm., but this does not appear significant. Chance variations as large as this could occur approximately 10 percent of the time as a result of random sampling. These results suggest that Logan III parent probably has an advantage over Logan II parent in general combining ability for rapid terminal growth. Possibly plant III may also have some advantage in terminal growth rate over plant I. The observed difference between means is found in the same direction as a comparable difference in stem diameter between the progenies of these plants. The general combining ability mean of Line 5 VI was found to exceed that of

Logan II by 2.0 ± 0.91 cm., which is significant. Other observed differences in general combining ability were not found to be significant.

Individual self-pollination progenies in this study probably do not provide very dependable indications of breeding behavior because of small sample size. Comparison of the self-progeny means shows one significant difference of 4.4 ± 1.71 cm. between self-progenies of Logan I and Line 5 V. This more rapid growth rate by the self-progeny of Line 5 IV can probably be explained by an apparent difference between Logan and Line 5 strains. When the general combining ability means were compared with the self-progeny means of the common parent plant, only one difference was found. This was between the hybrid progeny mean and the self-progeny mean of Logan I. The difference is 2.5±1.19 cm. which is significant at odds of 19 to 1. It therefore appears possible that the hybrid progeny of one parent plant, Logan I, may have more rapid terminal growth than the self-progeny of this plant. However, with the self-progeny mean based on a relatively small sample of 13 plants in four widely separated areas, it is quite possible that the observed difference may be a location effect.

Important differences were found between group progenies resulting from self-pollination of hermaphrodites, female by hermaphrodite crossing, and hermaphrodite crossed with hermaphrodite. The hermaphrodite self-pollination progeny and that from hermaphrodite plants crossed had the same average terminal growth rate. However, the terminal growth rate of plants from female by hermaphrodite crosses exceeded the terminal growth of hermaphrodite self-progenies by 1.7±0.76 cm. per month, and that of progenies from hermaphrodite by hermaphrodite crosses by 1.7±0.71 cm. These are significant differences, exceeding the 5 percent level. It is therefore suggested that female by hermaphrodite crosses probably produced progeny with more rapid terminal growth than other types of pollination employed.

Progenies from Line 5 parents increased in stem height 1.7±0.77 cm. faster than progenies from Logan parents. This difference is significant, indicating that plants in progenies from Line 5 probably exceed plants in progenies from Logan strain in terminal growth rate. The mean of F_1 plants resulting from crosses between the two strains was between and not significantly different from the means of Line 5 and of Logan strain progeny. This suggests that hybrid vigor probably does not occur as a result of interstrain crossing between Logan and Line 5 parent plants. Also there is a lack of dominance.

When considered as a group, the mean of all 14 cross-progenies in table 8 was 42.3 ± 0.36 cm. and the group mean of four self-pollination progenies was 41.4 ± 0.58. These means differ by only 0.9 ± 0.68 cm. The observed difference is small and fails to suggest authentic differences in terminal growth between hybrid progenies and self-pollination progenies. A slightly faster growth rate shown by the cross-pollination progenies is probably due to the breeding behavior of female parental plants III and VI. These plants produced progeny having higher terminal growth rates than those produced by the other four parental plants. Progenies from self-pollination of hermaphrodite parents had the same average terminal growth rate as progenies resulting from crosses made between the parental hermaphrodite plants. As further negative evidence of heterosis it was noted there was no significant difference

between the most vigorous individual cross-progeny produced and the self-progenies of parental plants No. II from Logan strain and No. V from Line 5.

The results of the progeny study to determine the breeding behavior of six parental plants for terminal growth rate is in general agreement with results of the combining ability study of stem diameter. The Logan III female plant again produced hybrid progeny with more rapid growth rates than the other two Logan parental plants. The general combining ability mean of Logan III also appears higher than the hybrid progeny means of the three Line 5 parental plants. This occurs despite a significant difference of 1.7 ± 0.77 cm. between progenies within the Logan strain and progenies within Line 5, which is suggestive of more rapid terminal growth by Line 5 plants. It is possible that Logan III female may be the best parental plant for producing vigorous hybrid progeny, but significant advantages of this plant over Line 5 parental plants were not indicated by the general combining ability means. Line 5 female plant VI had a slightly higher general combining ability mean for rapid terminal growth than did the Line 5 hermaphrodite parental plants No. IV and No. V. As a result, the average terminal growth rate of female by hermaphrodite crosses appears higher than that of progenies from other pollination combinations. However, as in stem diameter studies, it cannot be conclusively stated that this is due to female by hermaphrodite crossing or to higher general combining ability for rapid terminal growth by female parental plants III and/or VI. The latter explanation is suggested as more logical.

HEIGHT OF BEARING

Average bearing heights of hermaphrodite plants in progenies grown from pollinations made with six parental plants are shown in table 16. The general combining ability means of the parental plants for bearing height are given, as well as average bearing heights of individual self- and cross-progenies. In table 17, the error variance used in testing for progeny differences is that within progenies. Mean standard errors computed from the within progeny variance are used in testing comparisons of individual progenies and progeny groups. Significant differences between progenies were not suggested by the F test.

TABLE 16.   Bearing height in centimeters of hermaphrodite progenies resulting from various combinations of six different parent plants.

PARENT PLANTS	LOGAN I ♂	LOGAN II ♂	LOGAN III ♀	LINE 5 IV ♂	LINE 5 V ♂	LINE 5 VI ♀
Logan I ♂						
Logan II ♂	157±4.8					
Logan III ♀	158±6.0	152±5.6				
Line 5 IV ♂	168±4.3	164±4.8	162±5.3			
Line 5 V ♂	155±4.6	166±5.6	157±6.0	161±4.8		
Line 5 VI ♀	156±5.6	147±6.0		171±4.8	161±6.5	
Hybrid Progeny[1]	159±2.2	158±2.4	157±2.9	165±2.1	159±2.4	161±2.8
♂ ⊕	157±4.4	158±4.3		168±4.8	162±5.0	

[1] True averages.

TABLE 17.   Analysis of variance for bearing height of hermaphrodite plants.

SOURCE OF VARIATION	D F	S S	VARIANCE
Total	177	46,583	
Between progenies	17	5,883	346.1
Within progenies (error)	160	40,700	254.1

There were no significant differences between 10 specific crosses producing the most desirable progeny from the standpoint of low bearing height. It is therefore suggested that it would be difficult to select outstanding parental combinations for low bearing height on the basis of the specific combining ability means.

The Line 5 IV parent plant produced hybrid progeny with an average bearing height significantly higher than that produced by Logan II or Logan III. The differences found were 7 ± 3.2 cm. and 8 ± 3.6 cm., respectively. These are significant differences. No other differences in bearing height were found between the general combining ability means of parent plants. It is therefore suggested that, with the exception of Line 5 IV, no critical distinction can be made between the other five parental plants with respect to their ability to produce low bearing progeny.

No differences were found in comparisons between the four self-progeny means, and none of the self-progeny means differed significantly from their respective general combining ability mean.

No differences of importance were found between group progenies resulting from hermaphrodite self-pollination, hermaphrodite cross-pollination, or female by hermaphrodite pollination. Apparently the type of pollination combination used in producing seed had little effect on the bearing height of the resulting progenies.

The most important difference in this character was found in comparing the mean of all Logan progenies with that of all Line 5 progenies. Five progenies from crosses and selfs of Line 5 parents produced 49 hermaphrodite plants with a mean of 165 ± 2.3 cm. The corresponding progenies from the Logan strain gave 53 hermaphrodite plants with an average bearing height of 157 ± 2.2 cm. The difference of 8 ± 3.2 cm. is significant, approaching the 1 percent level. It is therefore suggested that the Logan strain probably produced lower bearing hermaphrodite plants than Line 5. Low bearing height in the strains studied can probably be best maintained by cross- or self-pollination of Logan strain plants. In this connection, it is noted that the Logan III female, which produced the most vigorous hybrid progeny as measured by terminal growth and stem diameter, also gave hermaphrodite plants with low bearing height, which are desirable from the standpoint of ease and safety of picking. The mean of the hybrid progenies from crosses between Line 5 and Logan parental plants was intermediate between, but not significantly different from, the means of cross- and self-progeny within the Logan and within the Line 5 strains.

The mean of 14 crosses was approximately equal to the mean of four self-progenies. Hybrid vigor as expressed by low bearing height does not occur as a result of crossing between these strains, or between the six parental plants.

Limited selection possibilities for bearing height are suggested by the lack of outstanding differences in general combining ability shown by the hybrid progeny means of six parental plants. Hybrid progenies between strains tended to be intermediate in bearing height.

EARLINESS

Table 18 contains information on hermaphrodite progenies used in studying performance of progenies and breeding behavior of parental plants with respect to earliness. It is similar in form and content to tables used in studying combining ability for terminal growth, stem thickness, and bearing height. Since the data on earliness were probably heterogeneous, only group progenies are considered with respect to breeding behavior for earliness. Due to the larger sample size of group progenies, the means and variances of these groups should be more dependable than those of individual progeny means based on relatively few plants.

Because progeny variances for this character were probably not homogeneous, mean standard errors used in comparisons of earliness between various progenies and group progenies were computed from the variances of plants within progenies and within groups tested.

TABLE 18. Average days to first flower of hermaphrodite progenies resulting from various combinations of six different parent plants.

PARENT PLANTS	LOGAN I ♂	LOGAN II ♂	LOGAN III ♀	LINE 5 IV ♂	LINE 5 V ♂	LINE 5 VI ♀
Logan I ♂						
Logan II ♂	211±3.1					
Logan III ♀	203±3.9	212±2.5				
Line 5 IV ♂	213±2.3	208±5.5	211±4.7			
Line 5 V ♂	199±5.4	206±2.6	206±4.2	210±4.5		
Line 5 VI ♀	208±5.4	211±5.0		207±3.4	202±3.9	
Hybrid Progeny[1]	207±1.9	209±1.8	208±2.0	210±1.8	205±2.1	207±2.1
♂ ⊕	199±5.2	204±4.1		217±2.2	209±3.5	

[1] True averages.

The range between the highest and the lowest general combining ability means was 5 days, which does not appear significant. Plants within Line 5 progenies averaged 209 days to flowering, while those within the Logan strain had a mean of 205 days. These means are not significantly different. A mean of 208 days by F_1 plants from between-strains crosses does not suggest hybrid vigor in this character. Other group comparisons also fail to suggest real differences in earliness. The range between the strains, as well as between general combining ability means, is not sufficient to be of appreciable value in breeding for earliness in this crop. It is therefore probable that parental plants used fail to differ sufficiently in breeding behavior for earliness to be considered useful for improvement in this character.

SUMMARY AND CONCLUSIONS

A field test of 18 progenies was conducted in 1950 and 1951 to study effects of (1) plant sex, (2) strains, (3) hybrid vigor and inbreeding, (4) pollination combinations, and (5) combining ability of parent plants in quantitative characters.

Characters studied were (1) rate of increase in stem diameter prior to fruiting, (2) terminal growth rate prior to flowering, (3) bearing height in cm. to first flower, and (4) earliness as number of days to flowering. Data were taken on an individual plant basis.

Distinct strains of the Solo variety have developed naturally and through selection. This process has been facilitated by the characteristic of bud pollination found in the predominant perfect flower type which produces pyriform fruits preferred for market and seed purposes. The result of a concurrent pollination study, conducted with hermaphrodite Solo plants showing a recessive leaf character used as a marker, demonstrated more than 99.9 percent self-pollination in open-pollinated seed. This evidence suggests that Solo, as propagated from seed of pyriform fruits, is essentially self-pollinated.

Progenies in the field test were produced by making all possible self- and cross-pollinations, excluding reciprocals, with two hermaphrodites and one female from each of two Solo variety strains. Parental plants were from a seven generation inbred strain and an open-pollinated commercial strain. Data were taken on (1) rate of increase in stem diameter prior to fruiting, (2) terminal growth rate prior to flowering, (3) bearing height in cm. to first flower, and (4) number of days to flowering.

Although the individual progenies from self- or cross-pollination of hermaphrodite parents gave satisfactory fits to the expected sex ratio, a significant deviation from this expected 2:1 ratio of hermaphrodite to female plants was observed in the total progeny from hermaphrodite parents. Both Storey and Jones (18) and Hofmeyr (8) presented evidence in support of the 2:1 ratio. No reason for the excess of hermaphrodite plants found in the progenies resulting from self- or cross-pollination of hermaphrodite parents in the present study was apparent. It is possible that some unknown factor or factors may have been operative in reducing the number of m gametes or the viability of the mm zygotes. Evidence of the nature of such action was not apparent in the progeny test.

Segregation for female and hermaphrodite sex in all progenies studied made it possible to compare the performance of the two sexes in four characters. Important differences in both terminal and diameter growth rates found between female and hermaphrodite plants in certain specific progenies suggest the possibility of further studies with the object of determining the sex of plants prior to flowering. Because these differences in growth rate tend to be relatively small, it is suggested that only certain specific parental combinations may be of value in attempts to determine plant sex prior to flowering.

Because of differences found between female and hermaphrodite plants in the four characters studied, only hermaphrodite plant data were used in progeny testing. In earliness, the observed difference between strains and between hybrid progeny means of individual parent plants was less than 1 week, which

is of negligible importance. Further analysis of this character was not considered necessary.

Comparisons possible in studying hybrid vigor and inbreeding are (1) selfed progenies of parental plants with their F_1 progeny, (2) mean of self-progenies compared with the mean of cross-progenies, and (3) mean of all interstrain crosses with the average of all intra-strain crosses and selfs made among parental plants of each strain. These comparisons failed to demonstrate differences suggestive of hybrid vigor. The F_1 mean either fell between parental means or was approximately equal to one parental mean. The means of four hermaphrodite self-progenies did not differ significantly from the means of their respective hybrid progenies. Neither loss of vigor from inbreeding nor hybrid vigor in F_1 plants was suggested by results of this progeny test.

As measured by terminal growth and stem thickness, the inbred strain produced more vigorous plants than the commercial strain. However, the commercial strain produced lower bearing progeny which is more desirable from the standpoint of ease and safety in picking.

Most comparisons between the hybrid progeny means of individual parent plants fail to suggest differences. The observed uniformity of breeding behavior might be expected from the known inbreeding in the inbred strain and the high degree of inbreeding in the commercial strain implied by mode of pollination.

Progeny from female by hermaphrodite crosses showed more rapid terminal and diameter growth than plants in progenies from crossing and selfing hermaphrodite parents. The differences appeared to result from good combining ability by the commercial strain female parent.

General combining ability means of parental plants from the inbred strain were apparently similar for stem diameter, terminal growth, and bearing height, suggesting uniformity in breeding behavior. The commercial strain female parent had an advantage over the hermaphrodite plants of that strain for producing vigorous growing progeny. The general combining ability mean of this female parent was fully equal to that of parent plants from the inbred line in both terminal and diameter growth. This female parent also produced low bearing progeny. The possibility is suggested that desirable parent plants may be selected from commercial strains by means of a progeny test. Such parent plants may be of value in maintaining Solo strains with good plant vigor and other desirable characteristics.

These observations and the evidence presented seem to be in substantial agreement with observations by Hofmeyr (9) with respect to inbreeding dioecious varieties. In a review of papaya breeding progress in South Africa in 1941 this worker concluded that: "Although some of our dioecious varieties have been inbred five generations by sib-pollinations, the reduction in vigor is hardly noticeable." It does not appear that papayas studied in South Africa were subject to appreciable reductions in vigor through inbreeding. The self-progenies of the Line 5 strain were known to be highly inbred because eight successive plant generations were grown from self-pollination seed. The Logan self-progenies may also be highly inbred because Solo seed used is taken from hermaphrodite plants, which are characteristically bud pollinated. It is therefore logical to expect that inbreeding Solo strains by selfing may not result in a

serious reduction in plant vigor, as in corn and certain other cross-pollinating crops.

LITERATURE CITED

(1)   AGNEW, G. W. J.
      1941. NOTES ON THE PAPAW AND ITS IMPROVEMENT.   Queensland Agr.
      Jour. 56 (5) : 358–373.

(2)   AGNEW, G. W. J.
      1951. THE PAPAW.   Queensland Agr. Jour. 73 (4) : 197–211.

(3)   BARTLETT, M. S.
      1937. SOME EXAMPLES OF STATISTICAL RESEACH IN AGRICULTURE AND
      APPLIED BIOLOGY.   Roy. Statis. Soc. Jour. Suppl. 4: 137–183.

(4)   ELDEN, H. VAN.
      1935. GENETIC AND BREEDING ASPECTS OF THE PAPAYA.   Cong. Internatl.
      d'Hort. Compt. Rend. (XIéme). Sect. IV, Théme 7, 2 pp.

(5)   HARSHBARGER, B.
      1947. RECTANGULAR LATTICES.   Va. Agr. Expt. Sta. Mem. I, 26 pp.

(6)   HOFMEYR, J. D. J.
      1933. PAPAW SELECTION.   Farming in So. Africa 8: 159–160.

(7)   HOFMEYR, J. D. J.
      1936. INHERITANCE IN THE PAPAYA-PROGENY STUDIES OF SELECTED
      PARENTS.   Farming in So. Africa 11: 107–109.

(8)   HOFMEYR, J. D. J.
      1938. GENETICAL STUDIES OF CARICA PAPAYA L. I.   So. Africa Dept. Agr.
      and Forestry Sci. Bul. 187, 64 pp.

(9)   HOFMEYR, J. D. J.
      1941. GENETICS OF CARICA PAPAYA L.   Chronica Botanica 6: 245–247.

(10) KADAM, B. S.
      1942. THE NEWER KNOWLEDGE OF SEX INHERITANCE IN THE PAPAYA.
      Indian Jour. Genet. and Plant Breeding 2 (1) : 66–68.

(11) KUMAR, V.
      1951. STUDIES IN CARICA PAPAYA L. PRELIMINARY OBSERVATIONS ON THE
      RELATION OF SEX TO THE PRE-FLOWERING GROWTH OF PAPAYA SEEDLINGS
      AND INTERNAL CHARACTERS OF SEEDS. Indian Jour. Hort. 8 (1) : 26–34.

(12) NAKASONE, H. Y.
      1952. STUDIES ON THE INHERITANCE OF FRUITING HEIGHT OF CARICA PA-
      PAYA L.   Thesis, University of Hawaii Library.

(13) POPE, W. T.
      1930. PAPAYA CULTURE IN HAWAII.   Hawaii Agr. Expt. Sta. Bul. 61, 40
      pp.

(14) REYES, T. P.
      1925. A STUDY OF SEX CHANGE IN PAPAYA AND CORRELATION BETWEEN SEX
      AND CERTAIN MORPHOLOGICAL CHARACTERS OF SEEDLINGS.   Philippine
      Agr. 14: 391–412.

(15) SAKURAI, Y.
      1929. THE FIELD EXPERIMENTS ON THE SEX DETERMINATION OF SEEDS AND
      YOUNG SEEDLINGS OF PAPAYA FRUIT.   Jap. Soc. Trop. Hort. 1 (2) :
      131–154.   Japanese text, English summary.

(16)   SNEDECOR, G. W.
       1946.   STATISTICAL METHODS.   Iowa State College Press, Ames. 485 pp.

(17)   STOREY, W. B.
       1938.   SEGREGATION OF SEX TYPES IN SOLO PAPAYA AND THEIR APPLICATION
       TO THE SELECTION OF SEED.   Amer. Soc. Hort. Sci. Proc. 35: 83–85.

(18)   STOREY, W. B., AND W. W. JONES.
       1941.   PAPAYA PRODUCTION IN THE HAWAIIAN ISLANDS.   Hawaii Agr. Expt.
       Sta. Bul. 87: 5–31.

(19)   STOREY, W. B.
       1943.   PAPAYA—INHERITANCE STUDIES.   Hawaii Agr. Expt. Sta. Biennial
       Rpt. 1941–42: 86–87.

(20)   STOREY, W. B., and H. KAMEMOTO.
       1947.   PAPAYA.   Hawaii Agr. Expt. Sta. Biennial Rpt. 1944–46: 82.

(21)   STOREY, W. B., R. A. HAMILTON, AND H. Y. NAKASONE.
       1951.   PAPAYA.   Hawaii Agr. Expt. Sta. Biennial Rpt. 1948–50: 99–100.

(22)   THOROLD, C. A.
       1949.   MANURIAL EXPERIMENTS WITH PAPAW   (C. PAPAYA L.).   Trop. Agr.
       (Trinidad).

(23)   TRAUB, H. P., T. R. ROBINSON, AND H. E. STEVENS.
       1942.   PAPAYA PRODUCTION IN THE UNITED STATES.   U. S. Dept. Agr.
       Cir. 633, 36 pp.

(24)   WOLFE, H. W., and S. J. LYNCH.
       1942.   PAPAYA CULTURE IN FLORIDA.   Fla. Agr. Ext. Bul. 113.   Rev.
       1950, 32 pp.