

**RELATIONSHIPS OF MINIMUM TEMPERATURE AND GROWTH RATE
WITH SEX EXPRESSION
OF PAPAYA PLANTS (CARICA PAPAYA L.)**

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RELATIONSHIPS OF MINIMUM TEMPERATURE AND GROWTH RATE WITH SEX EXPRESSION OF PAPAYA PLANTS (*CARICA PAPAYA* L.)

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A phenomenon of physiological interest and of agricultural importance in Hawaii is the seasonal production of various floral types by hermaphroditic papaya plants. For instance, many hermaphroditic plants bear distorted (carpellodic) flowers in April and May. (For description of floral types, see later.) The "solo" type of flowers usually predominates in July, August, and September, and in March and April. Furthermore, in some cases, even "sterile" flowers are produced in place of the other flowers by the same plants in November and December. It seems, therefore, that the change in floral types is closely associated with one or more seasonal factors; the most likely of these are day-length and temperature.

Of the two seasonal factors, day-length and temperature, the temperature factor can be experimentally separated by growing papaya plants at several levels of elevation in the Hawaiian Islands. This paper reports results obtained when papaya plants were grown at different elevations.

MATERIALS AND METHODS

The three localities selected for this study were the Hawaii Agricultural Experiment Station farms at Honolulu, Oahu; Kainaliu, Hawaii; and Makawao, Maui.¹ The elevations of the three respective places are approximately 100 feet, 1,500 feet, and 2,100 feet. Rainfall averages² compiled for Honolulu, Kainaliu, and Makawao are 38 inches (20-year average), 72 inches (26-year average), and 77 inches (30-year average), respectively. Plants at the Honolulu farm were irrigated more or less regularly throughout their growing season, while those at the Kainaliu and Makawao farms were dependent upon rainfall.

Papaya seeds of the *Solo* variety were obtained from fruits, which were borne on plants growing at the Hawaii Agricultural Experiment Station farm at Waimanalo, Oahu. (These plants came from seeds supplied by Mr. Choichi Horinouchi of Waimanalo.) Each selfed flower was selected from plants which were bearing relatively few carpellodic fruits.

Although it was intended to mix seeds from two fruits and randomly

¹The three localities hereafter will be designated as Honolulu, Kainaliu, and Makawao.

²Data supplied by Dr. Paul Ekern of the Agronomy Department, Pineapple Research Institute, and Mr. Toshi Hayashi of the Geophysics Department, Hawaiian Sugar Planters' Association Experiment Station.

use them for each locality, this was not possible due to poor germinating conditions at Makawao. Plants at Honolulu and Kainaliu came from seeds of the original two fruits, while those at Makawao came from seeds of another fruit.

Seeds were sowed in flats on August 20, 1953 at each locality. Those at Honolulu and Kainaliu germinated, and the young plants were planted at their respective places on October 12, 1953 and November 24, 1953. After two unsuccessful attempts at germinating seeds at Makawao, seeds were sowed on May 4, 1954 at the Territorial Board of Agriculture and Forestry's nursery at Kahului, Maui, where germinating temperature is more favorable. The young plants were planted in the field at Makawao, Maui on July 22, 1954.

Growth measurements of the plants at each locality were made at the end of the study by measuring the circumference of the trunk at 6 inches from the ground. The height of the plants was also measured from this point. In addition, plants at the Honolulu farm were measured at monthly intervals at the time the floral types were recorded.

Plants in the three localities were subjected to differential treatments of fertilizers but since responses in growth of the plants or in change of floral types were not detectable, the mean percentage of each flower type is used for comparisons among localities.

The types of flowers were recorded for a period of approximately a year for each plant that was studied. The numbers of plants used were 32, 18, and 29 at the Honolulu, Kainaliu, and Makawao farms, respectively.

The percentage of each type of flower was converted to the angle whose sine is the square root of the percentage, before statistical analyses were applied (4). In applying multiple regression to the data, the percentages of type 2 or types 2 and 3 were considered the dependent variable (Y) and the other factors as the independent variables (X_1 , X_2 , etc.). The correlation method, as described in Snedecor (4), was used to obtain the standard partial regression coefficients.

The day-length data were derived from the *Tables of Sunrise, Sunset, and Twilight* published by the United States Naval Observatory (3).

DESCRIPTION OF FLORAL TYPES

The papaya plant consists of a main stem from which leaves with their long petioles arise with a phyllotaxy of 8/21. Flowers and fruits are borne in the axil of each petiole; the floral buds mature acropetally. The inflorescence is of the cymose type. Each axillary inflorescence gives rise to several buds, but usually only the terminal bud develops into a mature fruit.

According to Storey (5), the flowers and fruits produced by hermaphroditic plants may be classified into four types (figs. 1, 2). The following is essentially a summary from his publication:



FIGURE 1. Floral types produced by hermaphroditic papaya trees. *Upper left*, type 4+; *upper right*, type 4; *lower left*, type 2; and *lower right*, type 3. See text for description.

Type 4+. This type of flower has 10 functional stamens but lacks a functional pistil, although a vestigial pistil lacking a stigma is invariably present. This type of flower is the most staminate of the hermaphroditic types of flowers described here.

Type 4. This type of flower possesses an elongate pistil and the resulting fruit is long-cylindrical. The petals are fused together for $\frac{1}{4}$ to $\frac{3}{4}$ of their length and form a fairly rigid corolla tube. At the throat of the corolla tube are 10 stamens arranged in a double series, one series being opposite the petals and sessile, the other being alternate on short stalks.

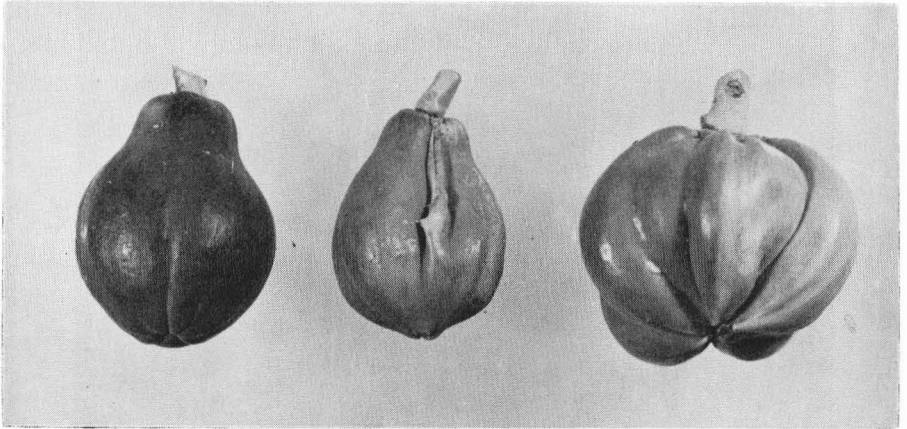


FIGURE 2. Hermaphroditic fruit types corresponding to the floral types which are presented in figure 1. From left to right, types 4, 3, and 2.

A type 4 fruit derived from this type of flower is the "solo" papaya which is sold on the market.

Type 3. This type of flower is intermediate between types 2 and 4. It has from six to nine functional stamens. The reduction in the number of stamens from 10 as in the type 4 flower is the result of the fusion of from one to four stamens with the carpel.

Type 2. This type of flower has five functional stamens. The other whorl of five stamens opposite the corolla in the type 4 flower has, in this type, apparently become carpellogenic and fused to the normal carpels. This type of flower is least staminate and most pistillate of the hermaphroditic flowers.

FLORAL RECORDS

Only the terminal flower of each inflorescence, which represents floral type of the same morphological age, was recorded as to the type. The types of flowers and fruits were recorded acropetally at each monthly observation date for each plant. The most matured unopened flower bud was then labeled. This became the first flower or fruit on the next observation date.

It is assumed in this study that the ontogenetic effect of the external environment leading to a change in the morphology of the flower takes place at the time when the floral bud is at a stage just prior to formation of stamens and pistil. In a similar study on sex expression of papaya plants, relatively high correlation and partial regression coefficients of carpellogeny with temperature were indicated at this bud stage (1). In order to relate carpellogeny with temperature and day-length, it is necessary to estimate the date when the flower bud is at the stage just prior to stamens and pistil formation. Since this stage can be determined accurately only by micro-

scopic observation after dissection, procedures have been used for estimating the date corresponding to the desired stage of bud development. These procedures are based on the assumption that the mean number of days required for a bud to develop at each stage is the same at all stages at any given time. By use of this assumption the date corresponding to the desired bud stage is estimated from the mean number of days required for a bud to develop into a flower by determining relative maturity of the buds. The mean number of days required for a bud to develop can be determined readily in the field without dissection of the buds.

The mean number of days required for a bud to develop was determined at each observation date by either one of two methods. In the first method, a young leaf, which is one inch long, is tagged, and the number of days that it takes for the corresponding flower bud in its leaf axil to mature into a flower is recorded. The total number of buds per plant is estimated from counts made on two representative plants.

The following example illustrates this method:

If x = number of days that it takes for the smallest visible bud to develop into a flower,

25 = total number of buds on the plant,

17 = number of buds counting from a young bud, whose corresponding leaf is tagged, to the first open flower,

and 40 = number of days it takes for the bud, whose corresponding leaf is tagged, to develop into a flower,

then x is solved from the following algebraic expression:

$$\frac{x}{25} = \frac{40}{17},$$

$$x = 58.8 \text{ days.}$$

Therefore, the mean number of days required for a bud to develop into a flower is 58.8 days/25 buds or 2.35.

The following example illustrates the second method:

If x = number of days that it takes for the smallest visible bud to develop into a flower,

25 = total number of buds on the plant,

14 = mean number of flowers and fruits that were recorded from each plant at an observation date,

and 30 = number of days between the observation date and the previous observation date,

then x is solved from the following algebraic expression:

$$\frac{x}{25} = \frac{30}{14},$$

$$x = 53.6 \text{ days.}$$

Therefore, the mean number of days required for a bud to develop into a flower is 53.6 days/25 buds or 2.14.

Microscopic observations of buds were made from 10 plants that were grown at the Hawaii Agricultural Experiment Station farm at Poamoho, Oahu. The number of buds on each plant ranged from 21 to 25. Bud observations were made at intervals throughout the year. Each bud, which was numbered acropetally from the largest to the smallest, was examined for the presence of stamens or pistil. The first bud without stamens or pistil was then identified by number.

The ratio of the bud number without stamens or pistil to the total number of buds on each plant was calculated. This ratio was relatively constant at different seasons of the year. The mean ratio was multiplied by the total number of buds at each locality at each observation date to obtain the number of the bud at the desired stage. This bud number was then multiplied by the number of days required for a bud to develop into a flower to obtain the estimated date corresponding to the desired bud stage. For each date estimated in this fashion, mean day-lengths, and maximum and minimum temperatures were determined for a period of approximately 30 days beginning with the estimated date. These means were then used in the correlation and multiple regression analyses with percentage of type 2, or type 2 and type 3 flowers.

The mean differences in percentages of carpellic flowers for selected dates were tested by the group comparison method as described in Snedecor (4).

RESULTS AND DISCUSSION

Relationship of Flower Types to Seasonal Factors

Before percent type 2 flowers were compared between localities (tables 1, 2, 3), the following comparisons were made for corresponding dates of each year within localities, which had approximately the same day-length and temperature:

Honolulu—Mean percent type 2 flower of 39 percent on May 12, 1954 is significantly greater than 7 percent on May 25, 1954 at 1 percent level of probability.

Makawao—Mean percent type 2 flower of 100 percent on July 29, 1955 is significantly greater than 23 percent on July 31, 1956 at 1 percent level of probability.

Thus, it is evident that age (or growth rate; see later) has some influence on carpellicity.

In general the percentage of type 2 flowers produced at Kainaliu was much higher than at Honolulu. The proportion of type 2 flowers was also relatively high at Makawao during the early months of observation. However, during the period between January to July of 1956 relatively low percentages of type 2 flowers were recorded at this locality during some months. These low percentages of type 2 flowers at Makawao were reflected in higher percentages of type 3 flowers. The latter situation is quite different from

TABLE 1. Percentage of each flower type produced at Honolulu at each date (32 plants)

% FLOWER TYPES	DATES DURING 1954-55													
	5/12/54	6/16	7/20	8/25	9/29	10/20	11/23	12/20	1/26/55	3/2	3/30	4/27	5/25	6/22
% 2	39	10	1	3	1	2	7
% 3	20	19	20	5	7	10	23	5
% 4	41	71	79	93	96	50	21	18	64	89	92	88	68	95
% 4+	7	4	50	79	82	36	3	2

TABLE 2. Percentage of each flower type produced at Kainaliu at each date (18 plants)

% FLOWER TYPES	DATES DURING 1955									
	3/24/55	4/18	5/23	6/20	7/18	8/16	9/13	10/13	11/14	12/13
% 2	95	98	100	97	97	96	80	85	92	94
% 3	4	2	3	3	2	15	15	7	5
% 4	1	2	5	1	1

TABLE 3. Percentage of each flower type produced at Makawao at each date (29 plants)

% FLOWER TYPES	DATES DURING 1955-56												
	7/29/55	9/1	10/3	10/31	11/30	1/3/56	1/31	3/1	4/3	5/1	6/1	7/2	7/31
% 2	100	98	57	90	77	63	31	42	60	8	13	22	23
% 3	----	2	36	5	23	34	47	33	33	89	87	78	77
% 4	----	----	7	5	----	3	22	25	7	3	----	----	----

TABLE 4. Carpeloid flowers and fruits (% 2 and 3) borne by plants at the three localities expressed as percentages

LOCALITY	DATES DURING 1954-56													
	5/12/54	6/16	7/20	8/25	9/29	10/20	11/23	12/20	1/26/55	3/2	3/30	4/27	5/25	6/22
Honolulu	59	29	21	----	----	----	----	----	----	8	8	12	30	5
Kainaliu	99	100	100	100	100	98	95	100	99	99	99	99	99	99
Makawao	100	100	93	95	100	97	78	75	93	97	100	100	100	100

that shown for Honolulu where low percentages of type 2 flowers are reflected in high percentages of type 4 flowers.

When the total carpellocid flowers and fruits (% 2 and 3) borne by the plants at the three localities are compared (table 4), it can be readily seen that most of the flowers and fruits produced by plants at the Kainaliu and Makawao farms are of the carpellocid type. On the other hand, flowers and fruits produced by plants at Honolulu (table 1) are composed largely of type 4 flowers and fruits ("solo" type) except during the months of October, November, and December when type 4+ flowers (sterile type) are most prevalent.

TABLE 5. Day-length and temperature data for each locality with the corresponding mean percentages of floral types. (Mean annual temperature data were taken for 1955.)

LOCALITY	DAY-LENGTH* (hours) RANGE	MEAN MINIMUM TEMPERATURE (Fahrenheit)	MEAN MAXIMUM TEMPERATURE (Fahrenheit)	MEAN PERCENTAGES OF FLORAL TYPES			
				2	3	4	4+
Honolulu	10.88-13.45	69.7	80.8	4	8	70	18
Kainaliu	11.03-13.46	59.9	76.1	93	6	1	
Makawao	10.98-13.55	58.3	72.0	53	42	5	

*Day-lengths of Latitude North 21° were used for Honolulu (Latitude North 21° 20') and Makawao (Latitude North 20° 50'). For Kainaliu (Latitude North 19° 35'), day-lengths of Latitude North 20° were used. Corrections in day-lengths due to elevations were made as described in TABLES OF SUNRISE, SUNSET, AND TWILIGHT (3).

The range in day-length (table 5) is similar at each locality. The greatest difference in minimum day-length between localities is only 0.15 hours (9 minutes) for the comparison of Honolulu and Kainaliu.

The mean annual maximum temperature at Honolulu was 4.7 degrees higher than at Kainaliu, and the latter locality had a value of 4.1 degrees higher than at Makawao. The mean annual minimum temperature at Honolulu was 9.8 degrees higher than at Kainaliu, and the latter locality had a value only 1.6 degrees higher than at Makawao. It is evident, therefore, that the great difference in carpellocy found between Honolulu on the one hand and Kainaliu or Makawao on the other hand is due to temperature, since day-length is essentially the same at the three localities.

In order to check on which temperature index (maximum or minimum) is more closely related to carpellocy, correlation and multiple regression analyses were applied to the data.

In table 6 the correlation coefficients determined between the factors studied relative to percent carpellocid flowers are presented for each of the three localities. Minimum temperature is significantly correlated negatively at the 1 percent level of probability with percent carpellocid flowers at both

TABLE 6. Correlation coefficients between the factors indicated and percent carpellic flowers at the three localities³

FACTOR	HONOLULU	KAINALIU	MAKAWAO
Number of observations (n)	249	162	348
Minimum temperature	-.259**	-.233**	+.478**
Maximum temperature	+.093	-.037	+.274**
Day-length	+.279**	-.185	+.438**

**Significant at 1 percent level of probability.

TABLE 7. Standard partial regression coefficients (b') of percent carpellic flowers on indicated factors with their "t" values and the multiple correlation coefficients (R) at the three localities⁴

FACTOR	HONOLULU		KAINALIU		MAKAWAO	
	b'	"t"	b'	"t"	b'	"t"
Multiple correlation coefficient (R)		.583		.27		.523
Minimum temperature	-.817	9.49**	-.120	1.016	+.068	.681
Maximum temperature	+.545	5.17**	-.192	1.851	+.250**	3.699**
Day-length	+.279	3.82**	-.215	1.483	+.394**	4.521**

**Significant at 1 percent level of probability.

Honolulu and Kainaliu. However, it is significantly correlated positively at Makawao. Day-length, on the other hand, is significantly correlated positively at the 1 percent level of probability with percent carpellic flowers for both the Honolulu and Makawao plants.

The standard partial regression coefficients of percent carpellic flowers on the various factors (table 7) indicate for the Honolulu plants that the minimum temperature is significant negatively at the 1 percent level of probability. None of the standard partial regression coefficients for the Kainaliu plants is significant. The standard partial regression coefficients of percent type 2 flowers are significant positively at the 1 percent level of probability for both the maximum temperature and day-length in the case of the plants grown at Makawao farm.

When the data for the three localities are combined and correlation analyses and multiple regression applied (table 8), minimum and maximum temperatures are both negatively correlated with percent carpellic flowers

³Percent type 2 flowers were used as the dependent variable for the Kainaliu and Makawao statistical analyses, while percent types 2 and 3 flowers were used for the Honolulu analysis.

⁴See footnote 3.

TABLE 8. Correlation coefficients (r), standard partial regression coefficients (b') with their "t" values, and the multiple correlation coefficient (R) of factors indicated and percent carpellocid flowers when the data for the three localities are combined⁵ $n = 759$

FACTOR	CORRELATION COEFFICIENT (r) **	STANDARD PARTIAL REGRESSION COEFFICIENT **		MULTIPLE CORRELATION COEFFICIENT (R) **
		b'	"t"	
Minimum temperature	-.365	-1.277	22.71	.703
Maximum temperature	-.145	+ .983	17.56	
Day-length	+.357	+ .477	18.06	

**All coefficients including the "t" values are significant at $p = .01$.

at the 1 percent level of probability, while day-length is positively correlated at the 1 percent level. When the standard partial regression coefficients are determined, it is found that minimum temperature is significant negatively at the 1 percent level of probability while maximum temperature and day-length are significant positively at the 1 percent level of probability. It is evident, therefore, that the great difference in carpellocy found between Honolulu on the one hand and Kainaliu or Makawao on the other must be due to the difference in minimum temperatures.

The variations in carpellocy within localities are of much smaller magnitude than between localities. However, these variations can to a large extent be accounted for. For instance, at Honolulu, the plants produced more carpellocid flowers when the minimum temperature was lower, and sterile flowers (type 4+) predominated when it was high.

Under Kainaliu conditions, carpellocy was very high for all seasons. The minimum temperature prevailing apparently was low enough to induce it during all seasons. The partial regression coefficient of carpellocid flowers on minimum temperature was not significant probably because of the low minimum temperature prevailing at all seasons of the year.

Relationship of Carpellocy to Growth Rate

TABLE 9. Size of the plants at termination of the studies

LOCALITY	DURATION OF STUDY	NUMBER OF PLANTS	TREE HEIGHT (FEET)	CIRCUMFERENCE (INCHES)
Kainaliu	3/24/55-2/7/56	18	12.6	27.5
Honolulu	5/12/54-5/25/55	31	10.6	22.6
Makawao	7/29/55-8/21/56	29	8.8	23.4

⁵See footnote 3.

Difference in height between:

Kainaliu and Honolulu plants significant at 1 percent level of probability.

Kainaliu and Makawao plants significant at 1 percent level of probability.

Honolulu and Makawao plants significant at 1 percent level of probability.

Difference in circumference between:

Kainaliu and Honolulu plants significant at 1 percent level of probability.

Kainaliu and Makawao plants significant at 1 percent level of probability.

Honolulu and Makawao plants not significant.

Where the minimum temperature was even lower than at Kainaliu as at Makawao, carpellody was also high throughout the year but not as high as at Kainaliu. Here, however, the plants were growing under poor conditions. In a previous study at Poamoho, Oahu (2), it was found that plants growing at a faster rate due to frequent irrigation produced significantly more carpellic fruits than plants irrigated less frequently and growing at a slower rate.

In the present study, plants grown at Honolulu also varied in carpellody according to growth rate. It has already been shown that when carpellody is compared in Honolulu and Makawao at corresponding dates of each year within each locality, significantly less carpellody was indicated the following year. This is probably due to the slower rate of growth manifested by plants during the second year of flowering.

When the growth data obtained from the Honolulu plants were subjected to correlation and multiple regression analyses, a significant correlation coefficient of $+0.62$ ($n = 249$) was obtained between carpellody and rate of stem elongation. Furthermore, the standard partial regression coefficient of carpellody on stem elongation of $+0.49$ was significant at the 1 percent level of probability ("t" value of 8.26). In determining this coefficient, maximum temperature, minimum temperature, and day-length were the other independent variables in the multiple regression analysis. It was also determined that carpellody was significantly correlated ($p = .01$) with the rate of increase in stem circumference ($r = .57$ with n of 96). It is evident, therefore, that the growth rate is one of the factors related to carpellody of papaya plants.

When the size of the plants at Kainaliu and Makawao is compared (table 9), it is readily seen that plants at Kainaliu were significantly taller and had greater circumference than those at Makawao. Therefore, the greater percentages of type 2 flowers produced by plants at Kainaliu as com-

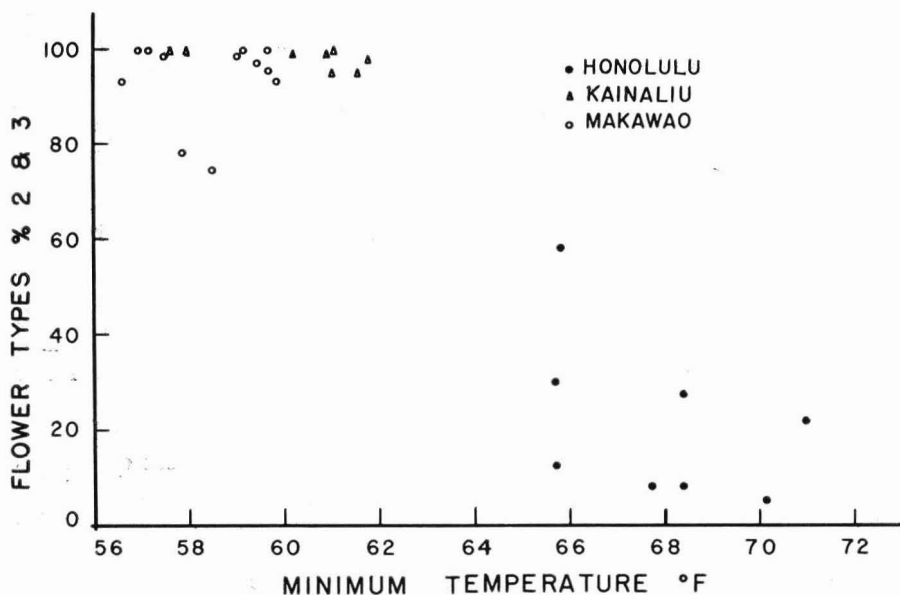


FIGURE 3. Effect of minimum temperature on the production of carpellic flowers at the three localities.

pared to those of Makawao may be related to the fact that plants at Kainaliu were growing at a faster rate than those at Makawao. However, growth rate cannot be the primary factor accounting for differences in carpellicity between localities, since Honolulu plants had the least carpellicity but intermediate growth rate.

The percentages of carpellic flowers at the three localities are plotted in relation to the minimum temperature (fig. 3). Each symbol on the figure represents the mean percentage of carpellic flowers produced by 32, 18, or 29 plants at Honolulu, Kainaliu, or Makawao farms, respectively. The figure indicates that below a mean minimum temperature of approximately 69° F., papaya plants of the strain studied produce carpellic flowers in increasing proportions until at about 60° F.; nearly all the flowers that are produced are of the carpellic types.

SUMMARY

Papaya plants of the *Solo* variety, derived from seeds whose plants were bearing uniformly few carpellic flowers and fruits, were planted at three levels of elevations at the Hawaii Agricultural Experiment Station farms at Honolulu, Oahu (100-foot elevation), at Kainaliu, Hawaii (1,500-foot elevation), and at Makawao, Maui (2,100-foot elevation). Floral records

were obtained continuously for approximately one year from 32, 18, and 29 plants at Honolulu, Kainaliu, and Makawao farms, respectively. Floral types were recorded as types 2, 3, 4, and 4+, the type 2 flowers being the most pistillate while type 4+ flowers are the most staminate of the hermaphroditic papaya flowers.

Significantly greater percentages of carpellic flowers (types 2 and 3) were produced by plants at either Kainaliu or Makawao over plants at Honolulu. These differences associated with locality must be primarily the result of differences in minimum temperature, since day-lengths are essentially the same at all localities.

When the carpellic flowers are broken down into types 2 and 3, greater percentages of type 2 flowers are indicated from plants at Kainaliu than at Makawao in spite of the lower minimum temperature at the latter location. This appears to be due to a relationship between carpellicity and growth rate.

The sterile type of flowers (type 4+) was produced in great quantities during October, November, and December by plants growing at Honolulu but no flowers of this type were produced by plants at Kainaliu and Makawao.

The data and statistical analyses indicate that the percentage of carpellic flowers is significantly correlated with minimum temperature and growth rate of the plants.

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