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THE GENETICS OF FLOWERING TIME IN *RAPHANUS SATIVUS* L.
II. GENOTYPE-ENVIRONMENT INTERACTION

AHSAN A. VAHIDY* AND RICHARD W. HARTMANN

Department of Horticulture, University of Hawaii, Hanolulu, Hawaii, U.S.A.

Abstract

The genotype-environment interaction for flowering time in *Raphanus sativus* was studied by growing 10 Early, 2 Check, and 10 Late lines in a Randomized Complete Block Design at two locations during two times of year. Data on 50 percent flowering time were found to be significantly heterogeneous for the four plantings. However, the data became homogeneous after transformation based on the performance of Check lines in the individual plantings. The effects of the transformation are described and justification for such a transformation is discussed. Breeding lines were grouped, based on their pedigrees, in four different ways. Analyses of variance of transformed data were done for each type of grouping, separately for the individual plantings as well as combined for all four plantings.

The magnitudes of the various variance components were quite different for Early and Late lines. The combined analyses of variance for Early and Late lines nullified some effects that were quite significant in the separate analyses. An attempt has been made to identify the possible causes of significance of the various effects.

Estimations of the heritability of mean flowering time of the Check line were possible after certain assumptions on the causes of variability in the selected lines were made. The estimation from the data of three of the plantings were similar as reported by Vahidy and Hartmann (1971). The skewed distribution of the flowering time of the Check lines in the fourth planting was postulated to be the cause of the somewhat higher values of heritability from that planting.

Introduction

The literature on genotype-environment interaction is very large. In the opinion of Allard & Bradshaw (1964), "Probably no one has the competence to review this literature in its entirety. . .". Here, the review shall be restricted to the literature pertaining to flowering time only.

Fisher (1918) was probably the first to separate genetic variance into three components: additive variance, dominance variance, and epistatic variance. Charles & Smith (1939) and Powers (1942) separated genetic from total variance by use of estimates of environmental variance based on non-segregating populations. Robinson, Comstock & Harvey (1949) used a method to measure heritability that involved the estimation of components of variance through the study of biparental progenies. Warner (1952) utilized two inbred lines and their F , F_2, and back cross progenies to estimate heritability. He found it to be 32 percent for the date of silking in corn.

Jinks (1954) has studied the flowering time in *Nicotiana rustica*, utilizing diallel crosses. He developed a method of analyzing the data based on partitioning of

* Present Address: Department of Genetics, University of Karachi, Karachi-32, Pakistan.

variances and covariances. The regression of array covariance on variance was expected to have a slope of one. The data of flowering time were in agreement with this theoretical expectation.

Allard (1956) has demonstrated the use of diallel crosses to find genotype-environment interactions. Utilizing Jink's data of eight varieties of *Nicotiana rustica*, he showed that the intervarietal hybrids had unimportant epistatic interaction for date of flowering. The additive genetic effects were found to be comparatively stable, but the dominance effects appeared quite unstable in different environments.

Jinks (1956) has extended the studies on the flowering of *Nictotiana*, using the data of F and back cross generations derived from a diallel set of crosses. He found in *Nicotiana rustica* varieties significant differences in the genetical control of flowering time in the two seasons. These differences involved not only variation in the magnitude of the components of variation but also the presence of duplicate gene interactions in one of the two seasons. Also, linkage involving at least four factors was detected in one of two seasons.

Perkins & Jinks (1968 a) have shown that a significant proportion of the genotype-environment interaction component of variation is a linear function of the additive environmental component. However, quite often there is a significant remainder that is non-linear. In another report (1968 b) the nature of the non-linear component of variation was studied by separating the lines into groups on the basis of significant positive and negative correlations for deviations from the linear regression. A reduction in the non-linear portion of the variation due to genotype-environment interaction was observed from grouping the lines. However, a significant non-linear portion of interaction was left even after grouping.

Lindsey, *et al* (1962) utilized half sib families of two open pollinated varieties of corn. The experiments were conducted at two locations in two years. A meaningless negative value was found for the dominance variance for the date of flowering in the first planting. New half-sib families were made for the second planting. The dominance variance, though still negative, was much higher for the date of flowering for this planting. The authors hypothesized that the meaningless negative value for dominance variance might have been due to a degree of assortative mating, since individual plants would be more likely to mate with others which flowered at the same time. The degree of assortative mating was apparently somewhat reduced in the second planting.

Goodman (1965) utilized full-sib and half sib families of Corn Belt Composite and West Indian Composite corn grown in Iowa and North Carolina. The estimates of genotypic variance, additive genetic variance, and interactions of these two factors with location were higher in West Indian Composite than in the Corn Belt Composite.

da Silva & Lonnquist (1968) used Robinson and Comstock's Design I to study differences in genetic variances for flowering time in two populations, resulting from two selection systems in corn. The population developed from one selection system had a significant Female X Year interaction variance for flowering time. The variance components due to Males and Females in Males were significant in both populations.

Liang & Walter (1968) worked with three crosses of grain sorghum. They evaluated the parental lines and their F_1, F and back crosses. They were able to partition epistatic variance into additive X additive epistatic effects for the half blooming day. F-tests showed that the dominance X dominance variance was significant in all three crosses, the additive X dominance variance was significant in one cross, and the additive X additive variance was significant in two crosses. From these results they concluded that Genetic models assuming negligible epistasis may be somewhat biased.

The issue of genotype-environment interaction has become more complicated with the discovery of environmentally-induced heritable changes (transmutations). Hill (1965, 1967), and Hill & Perkins (1969) have reported transmutation of flowering time in an inbred variety of *Nicotiana rustica*. This variety was treated with all the eight possible combinations of presence or absence of Nitrogen, Phosphorus, and Potassium fertilizers. The progeny of these eight treatment lines differed in mean flowering time, even after five generations of selfing. The plants of a particular generation were treated alike after the initial treatment. It was found that the differences in the flowering time were mainly due to Potassium treatment. The variance due to selected vs. unselected lines for early flowering was found to be highly significant. This further suggested that the change (transmutation) was heritable. The variance due to selected vs. unselected lines for late flowering was nonsignificant. However, the variance due to selected vs. unselected X environment interaction was highly significant, and this probably masked the response to selection for lateness.

Materials and Methods

To conduct this research 10 early flowering, 2 check and 10 late flowering breeding lines of *Raphanus sativus* were selected. These lines were labelled as E-1 to E-10 for early flowering lines, Ck-1 and Ck-2 for check lines, and L-1 to -L-10 for late flowering lines. Pedigrees of these lines are given in Table I and further information is provided in another report Vahidy & Hartmann (1971).

These 22 lines were grown in a Randomized Complete Block Design, with 4 replications at two farms, during two times of year. Independent randomization

Table 1. Pedigrees of Lines.

Line Number	Pedigree	Group of Lines
E-1	U[a]-100-E[b]-5-1-3-B[c]	
E-2	U-100-E-5-1-6-B	Eearly group 1
E-3	U-100-E-5-2-1-B	
E-4	U-100-E-5-2-2-B	
E-5	C[d]-25-L[b]-7-E-2-1-3-B	
E-6	C-25-L-7-E-2-1-3-B	Early group 2
E-7	C-25-L-8-E-2-4-4-B	
E-8	C-25-L-11-E-4-1-1-B	
E-9	C-26-L-8-2-E-1-2-1-B	Early group 3
E-10	C-26-L-8-2-E-1-2-2-B	
Ck-1	unselected original seeds	Check group
Ck-2	unselected original seeds	
L-1	C-30-L-5-3-1-3-2-B	
L-2	C-30-L-5-3-5-3-2-B	
L-3	C-30-L-5-3-5-4-1-B	Late group 1
L-4	C-30-L-5-3-5-5-1-B	
L-9	C-30-L-5-3-1-1-2-B	
L-10	C-30-L-5-3-5-3-4-B	
L-5	C-31-L-3-3-5-1-1-B	Late group 2
L-6	C-31-L-3-3-5-3-2-B	
L-7	C-33-L-4-2-3-1-1-B	Late group 3
L-8	C-42-L-5-4-4-3-2-B	Late group 4

[a]Not treated with colchicine.
[b]Early or late selection in generations following the symbol.
[c]Seeds of the selected plants bulked within line.
[d]Colchicine treated.

was done for each of the four plantings. Replications, farms, and times of year were considered as random effects while the breeding lines as fixed effect.

The two farms were Poamoho and Waimanalo Experimental Farms on the island of Oahu (Hawaii, U.S.A.), while the two times of the year were Fall of 1968 (October 1968 to January 1969) and Spring of 1969 (February 1969 to May 1969). The average maximum and minimum temperatures during the Fall, 1968, period were 79.8 and 66.1 degrees Fahrenheit at Poamoho, and 81.6 and 69.7 degrees Fahrenheit at Waimanalo Experimental Farms. The average maximum and minimum temperatures during the Spring, 1969 period were 77.1 and 64.7 degrees Fahrenheit at Poamoho, and 78.9 and 69.6 degrees Fahrenheit at Waimanalo. The rainfall during these periods was 37.17 inches at Poamoho, Fall; 37.32 inches at Waimanalo, Fall; 9.46 inches at Poamoho, Spring; and 12.93 inches at Waimanalo, Spring. From these figures it can be seen that Waimanalo was generally somewhat warmer, but there was little difference in rainfall.

The dates when 50 percent of the plants had flowered were recorded. For analyses of variance the lines were grouped in 4 ways, namely, 10 Early vs. 10 Late lines; 3 Early vs. 1 Check vs. 4 Late groups of lines; 1 Check vs. 3 Early groups of lines; and 1 Check vs. 4 Late groups of lines. The three Early groups were made on the basis of whether they had been selected for lateness for 0, 1, or 2 generations, while the grouping of Late lines was based on their origin tracing back to a single seed (see Table 1). For the analyses of groups of lines, the data used were the mean 50 percent flowering days of lines in each particular group.

For each of the four types of groupings the heterogeneity of the error variances of the four plantings was tested by Bartlett's test of heterogeneity. The Chi-square had significantly large values for all the four types of analyses and thefrore, the data of the four plantings could not be pooled.

It was possible to obtain homogeneous error variances by utilizing the following method of transformation. The mean 100 percent flowering day of the two Check lines (four replications each) was computed for each planting. The individual flowering dates were then expressed as percentages of the mean 100 percent flowering day of the Check lines. Transformed data were analyzed separately for each planting.

The sources of variation and degrees of freedom for the combined analysis of variance for four plantings are given in Table 2. The expectations of mean squares for each source of variation are given in Figure 1. Figure 2 gives the formulas for calculation of the expectations of mean square.

SOURCE OF VARIATION	CALCULATED MEAN SQUARE	EXPECTATIONS OF MEAN SQUARE
Farms (F)	M_1	$\sigma^2 + b\sigma^2_R + r\sigma^2_{BFT} + rt\sigma^2_{BF} + rb\sigma^2_{FT} + rbt\sigma^2_F$
Times of year (T)	M_2	$\sigma^2 + b\sigma^2_R + r\sigma^2_{BFT} + rf\sigma^2_{BT} + rb\sigma^2_{FT} + rbf\sigma^2_T$
F × T	M_3	$\sigma^2 + b\sigma^2_R + r\sigma^2_{BFT} + rb\sigma^2_{FT}$
Breeding lines (B)	M_4	$\sigma^2 + r\sigma^2_{BFT} + rt\sigma^2_{BF} + rf\sigma^2_{BT} + rtf\sigma^2_B$
B × F	M_5	$\sigma^2 + r\sigma^2_{BFT} + rt\sigma^2_{BF}$
B × T	M_6	$\sigma^2 + r\sigma^2_{BFT} + rf\sigma^2_{BT}$
B × F × T	M_7	$\sigma^2 + r\sigma^2_{BFT}$
Reps. in F & T	M_8	$\sigma^2 + b\sigma^2_R$
B × reps in F & T	M_9	σ^2

σ^2	=	Error Variance
σ^2_R	=	Component of Variance due to replications in F & T
σ^2_F	=	Component of Variance due to farms
σ^2_T	=	Component of Variance due to times of year
σ^2_B	=	Component of Variance due to breeding lines
σ^2_{FT}	=	Interaction Variance of farm effects with times of year
σ^2_{BF}	=	Interaction Variance of breeding lines effects with farms
σ^2_{BT}	=	Interaction Variance of breeding lines effects with times of year
σ^2_{BFT}	–	Second order interaction variance of breeding line effects with farms & times of year
b,r,t,f		Number of breeding lines, replications, times of year, farms respectively

Fig. 1. Sources of variation and expectations of mean square for the combined analysis of variance.

$$\sigma^2_{BFT} = (M_7 - M_9)/r$$

$$\sigma^2_{BT} = (M_6 - M_7)/rf$$

$$\sigma^2_{BF} = (M_5 - M_7)/rt$$

$$\sigma^2_B = [(M_4 + M_9) - (M_7 + M_8)]/rtf$$

$$\sigma^2_{FT} = [(M_3 + M_9) - (M_7 + M_8)]/rb$$

$$\sigma^2_T = [(M_2 + M_7) - (M_3 + M_6)]/rbf$$

$$^{2} = [(M_1 + M_7) - (M_3 + M_5)]/rbt$$

Fig. 2. Formulas to calculate variance components from the expectations of mean square.

F-tests for main effects as well as for interaction effects are described at the bottom of Table 11, except the F-test for breeding lines effect. This test was done as suggested by Cochran & Cox (1955).

Estimates of heritabilities of mean flowering time of Check lines were possible by assuming certain late flowering lines (L-2, L-3, L-6, L-7, and L-10) to be homozygous. These lines were selected at random from those Late lines that had rather low coefficients of variation (see Tables 3 to 6). Since the variance of

Table 2. Sources of variation and degrees of freedom for combined analysis of variance.

Source of variation	Degrees of freedom
Farm (F)	(f-1)
Time (T)	(t-1)
F x T	(f-1) (t-1)
Error (a)	(tf) (r-1)
Replication over Experiments (R)	(rft)-1
Breeding Line (B)	(b-1)
B x F	(b-1) (f-1)
B x T	(b-1) (t-1)
B x T x F	(b-1) (t-1) (f-1)
Error (b)	(tf) (r-1) (b-1)
Total:	(rbtf)-1

f = number of farms.

t = number of times of year.

r = number of replications per experiment.

b = number of breeding lines.

Table 3. Variance, standard deviation, mean, and coefficient of variation of flowering time; Poamoho-Fall, 1968.

Line	Variance	Standard deviation	Mean	Coefficient of variation in %
E-1	24.09	4.91	47.25	10.39
E-2	23.14	4.81	46.95	10.24
E-3	25.77	5.07	46.79	10.83
E-4	25.59	5.06	45.66	11.08
E-5	20-36	4.51	46.48	9.70
E-6	24.05	4.90	46.48	10.54
E-7	24.52	4.95	47.46	10.42
E-8	24.79	4.98	49.00	10.16
E-9	26.32	5.13	48.43	10.59
E-10	22.61	4.76	47.88	9.94
Ck-1	44.06	6.64	61.90	10.72
Ck-2	47.67	6.90	61.97	11.13
L-1	57.86	7.61	78.31	9.71
L-2	55.65	7.47	76.69	9.72
L-3	48.27	6.95	77.77	8.93
L-4	68.97	8.30	80.07	10.36
L-5	47.04	6.86	79.28	8.65
L-6	38.52	6.21	77.78	7.98
L-7	48.57	6.97	80.87	8.61
L-8	51.25	7.16	83.89	8.53
L-9	114.10	10.68	79.24	13.47
L-10	40.75	6.38	80.66	7.90

Table 4. Variance, standard deviation, mean, and coefficient of variation of flowering time; Poamoho—Spring, 1969.

Line	Variance	Standard deviation	Mean	Coefficient of variation in %
E-1	24.97	5.00	36.04	13.87
E-2	33.63	5.80	33.48	17.32
E-3	29.03	5.39	35.08	15.36
E-4	29.58	5.44	33.99	16.00
E-5	28.51	5.34	34.87	15.31
E-6	32.56	5.71	33.61	16.98
E-7	19.33	4.40	37.36	11.77
E-8	28.17	5.31	35.34	15.02
E-9	16.81	4.11	37.04	11.09
E-10	23.93	4.89	36.72	13.31
Ck-1	28.72	5.36	44.61	12.01
Ck-2	28.21	5.31	45.23	11.73
L-1	29.92	5.47	56.35	9.70
L-2	33.34	5.77	58.97	9.78
L-3	24.32	4.93	56.96	8.65
L-4	47.93	6.92	59.46	11.63
L-5	30.54	5.53	56.73	9.74
L-6	25.61	5.16	56.98	9.05
L-7	32.74	5.72	58.11	9.84
L-8	49.01	7.00	60.08	11.65
L-9	25.03	5.00	58.24	8.58
L-10	31.75	5.63	57.85	9.73

Table 5. Variance, standard deviation, mean, and coefficient of variation of flowering time; Waimanalo-Fall, 1968.

Line	Variance	Standard deviation	Mean	Coefficient of variation in %
E-1	29.74	5.45	52.15	10.45
E-2	20.55	4.53	51.98	8.71
E-3	18.60	4.32	52.06	8.29
E-4	20.26	4.50	50.39	8.93
E-5	29.01	5.39	52,54	10.25
E-6	37.52	6.13	54.27	11.29
E-7	39.06	6.25	52.45	11.91
E-8	42.62	6.53	55.69	11.72
E-9	35.51	5.96	54.99	10.83
E-10	35.39	5.95	54.38	10.94
Ck-1	71.95	8.48	64.65	13.11
Ck-2	70.01	8.37	66.59	12.56
L-1	76.73	8.76	88.95	9.84
L-2	85.54	9.25	85.20	10.85
L-3	43.80	6.62	85.54	7.73
L-4	71.95	8.48	87.71	9.66
L-5	69.67	8.35	87.85	9.50
L-6	37.63	6.13	86.79	7.06
L-7	47.09	6.86	89.14	7.69
L-8	53.18	7.29	89.50	8.14
L-9	46.94	6.85	89.79	7.62
L-10	43.69	6.61	90.38	7.31

Table 6. Variance, standard deviation, mean, and coefficient of variation of flowering time; Waimanalo—Spring, 1969.

Line	Variance	Standard deviation	Mean	Coefficient of variation in %
E-1	26.91	5.19	36.91	14.06
E-2	21.09	5.57	36.93	15.08
E-3	30.13	5.49	37.57	14.61
E-4	24.64	4.96	36.68	13.90
L-5	32.86	5.73	36.34	15.76
L-6	34.31	5.86	36.32	16.13
L-7	21.07	4.59	38.90	11.79
L-8	34.95	5.91	37.53	15.74
L-9	25.05	5.01	38.65	12.96
L-10	29.76	5.45	37.44	14.55
Ck-1	32.97	5.74	49.06	11.69
Ck-2	31.68	5.63	49.79	11.30
L-1	36.46	6.04	64.47	9.36
L-2	42.07	6.49	67.71	9.58
L-3	35.70	5.98	67.10	8.91
L-4	58.23	7.63	66.98	11.39
L-5	51.48	7.17	64.65	11.09
L-6	33.61	5.80	66.10	8.77
L-7	44.37	6.66	68.86	9.67
L-8	36.12	6.01	67.39	8.91
L-9	45.32	6.73	66.71	10.08
L-10	41.09	6.41	66.67	9.61

flowering time increases with an increase in mean flowering time even though the relative variability is the same, the coefficient of variation, rather than the variance, was used for comparison of lines with different means. The following method was employed to estimate the heritability of the Check lines:

Phenotypic variance of Check line = 45.86 (mean variance of 2 Check lines, see Table 3).
Environmental variance of Check line:

Coefficient of variation of L-2 .0972 (Table 3).

Assumption: Coefficient of variation of Check line due to environment would also be .0972.

Mean of Check line = 61.93 (mean of 2 Check lines, see Table 3).

Calculated variance of Check line due to environment = $(61.93 \text{ x } .0972)^2$ 36.04.
Genotypic variance of Check line 45.86—36.04 = 9.82.
Heritability of Check line - 9.82/45.86 = 21.41 percent.

Results and Discussion

The data of the four plantings at the two farms at two different times were found to be heterogeneous. The data of 10 Early, 1 Check, and 10 Late lines gave a value of 39.3 for heterogeneity Chi-square. When the lines were grouped into 3 Early, 1 Check, and 4 Late groups of lines, heterogeneity Chi-square was 28.0. Both these values are highly significant (P less than 0.01) for 3 degrees of foreedom. When the data of the four plantings for 10 Early, 1 Check, and 10 Late lines were pooled and analyzed anyway, the main effects, first degree interactions and second degree interaction were all highly significant. This was not surprising, since pooling heterogeneous data may lead to significance even when it is not actually present. In other words, a Type I statistical error may be committed by pooling data with heterogeneous variances. In order to preform a statistically legitimate analysis, the data was transformed in the following way so that the variances were homogeneous.

The transformation used was to express all flowering dates as a percentage of a particular reference point within the individual planting. The reference point which was chosen as the most constant point from one planting to the next was the mean 100 percent flowering date of the Check lines. The reason why the mean 100 percent flowering day of the Check lines was chosen, rather than the mean 50 percent flowering day is that the frequency distribution of Check lines in the Waimanalo-Fall, 1968 planting was somewhat skewed towards earliness in flowering. If the 50 percent day of Check lines were used, the data for this planting showed a pattern of distribution which was distinctly different from that of other three plantings.

Mathematically the data were coded by multiplying with a particular constant, different for each of the four plantings. Statistically, such coding of data is not permissible, as it will change not only the mean but also the variances. Furthermore, there is a possibility of committing a statistical error of Type II, in which the results may show nonsignificance for certain effects which are actually significant. Although it is obvious that the transformation will change the Farm and Time effects, it is assumed that it would not make any significant change in the other effects.

The transformation applied, however, is a type often used by plant breeders, who are interested in expressing the results in comparison to a certain "Check". Since it was observed in the earlier experiments that the time of planting has a great effects on the flowering time in radish, Vahidy and Hartmann (1971), it was necessary to use a separate transformation for each individual planting. Reliance on the performance of Check lines seems appropriate on the grounds that (a) these are unselected lines and thus are probably better representatives than the selected lines of a constant level of performance; and (b) the two Check lines were identical thus has double the accuracy than any other line in a planting.

Since the transformation was "percent of mean 100 percent flowering of Check", it may seem desirable to apply a logarithmic or arc-sine transformation to the transformed data. However, it was not necessary because the use of "percent of Check" is not causing skewness in any direction. Such a transformation might have been necessary if the data were expressed as the "percent of Late" or the "percent of Early" lines, since these might have caused skewness in the distribution.

Table 7 shows the results of analyses of variance for 10 Early and 10 Late lines for the four plantings separately. For each planting the lines effects was highly significant. The lines effect was also highly significant in the analyses of 3 Early, 1 Check and 4 Late groups of lines (Table 8).

In the analyses of variance for 1 Check and 3 Early groups of lines, the groups of lines effect was separated into two parts, viz., Early vs. Check, and within Early.

Table 9 shows that not only the effects due to groups of lines, but also the effects due to Early vs. Check were highly significant in all four plantings. However, within Early effects were found to be non-significant.

In the analyses of variance for 1 Check and 4 Late groups of lines, the groups of lines effects was also separated into two parts, viz., Late vs. Check, and within Late. The results are shown in Table 10. The groups of lines effects and Late vs. Check effects were highly significant in all four plantings. However, within Late effects were highly significant in the two plantings of Poamoho Experimental Farm, significant for the Waimanalo-Spring plantings, and nonsignificant for the Waimanalo-Fall planting.

The error variances for the four methods of comparing the Early, Check, and Late lines were tested for heterogeneity. Since the Chi-Square values were nonsignificant for all these tests, the data for the four plantings were pooled and analyzed as one combined experiment.

Table 7. Tables of analyses of variance for ten Early and ten Late lines.

Source of Variation	df	Poamoho-Fall S.S.	Poamoho-Fall M.S.	Poamoho-Spring S.S.	Poamoho-Spring M.S.	Waimanalo-Fall S.S.	Waimanalo-Fall M.S.	Waimanalo-Spring S.S.	Waimanalo-Spring M.S.
Replication	3	15.93	5.31	11.76	3.92	1.46	0.48	18.08	6.02
Lines	19	36,791.24	1,936.38**	29,351.76	1,544.82**	37,288.07	1,962.53**	43,851.14	2307.95**
Error	57	279.87	4.91	261.26	4.58	386.47	6.78	355.86	6.24
Total	79	37,087.04	469.45	29,624.78	374.99	37,676.00	476.91	44,225.08	559.81

* Significance at .01 level of probability.

Table 8. Tables of analyses of variance for three Early, one Check, and four Late groups of lines.

Source of Variation	df	Poamoho-Fall S.S.	Poamoho-Fall M.S.	Poamoho-Spring S.S.	Poamoho-Spring M.S.	Waimanalo-Fall S.S.	Waimanalo-Fall M.S.	Waimanalo-Spring S.S.	Waimanalo-Spring M.S.
Replication	3	12.50	4.16	0.72	0.24	4.12	1.37	5.18	1.72
Groups of Lines	7	13,296.69	1,899.52**	10,209.53	1,458.50 *	13,271.85	1,895.97 *	15,455.52	2,207.93**
Error	21	69.23	3.29	26.88	1.28	92.51	4.40	62.02	2.95
Total	31	13,378.42	431.56	10,237.13	330.23	13,368.48	431.24	15,522.72	500.73

* Significance at .01 level of probability.

Table 9. **Tables of analyses of variance for one Check and three Early groups of lines.**

Source of Variation	df	Poamoho-Fall S.S.	Poamoho-Fall M.S.	Poamoho-Spring S.S.	Poamoho-Spring M.S.	Waimanalo-Fall S.S.	Waimanalo-Fall M.S.	Waimanalo-Spring S.S.	Waimanalo-Spring M.S.
Replication	3	8.81	2.93	2.88	0.96	34.39	11.46	0.04	0.01
Groups of Lines	3	1,098.24	366.08**	638.86	212.95 *	582.85	194.28**	1,162.42	387.47**
Early vs. Check	(1)	(1,087.47)	(1,037.47)	(629.23)	(629.23*)	(560.60	(560.60**)	1,158.27)	(1,158.27**
Within Early	([illegible])	(10.77)	(5.38$^{n.s.}$)	(9.63)	(4.81$^{n.s.}$)	(22.25)	(1.12$^{n.s.}$)	(4.15)	(2.07$^{n.s.}$)
Error	9	24.73	2.47	18.71	2.07	21.49	2.38	4.84	0.53
Total	15	1,131.78	75.45	660.45	44.03	638.73	42.58	1,167.30	77.82

* Significance at .01 level of probability.
n.s. Nonsignificant.

Table 10. **Tables of analyses of variance for one Check and four Late groups of lines.**

Source of Variation	df	Poamoho-Fall S.S.	Poamoho-Fall M.S.	Poamoho-Spring S.S.	Poamoho-Spring M.S.	Waimanalo-Fall S.S.	Waimanalo-Fall M.S.	Wamanalo-Spring S.S.	Wamanalo-Spring M.S.
Replication	3	16.63	5.54	2.21	0.73	2.41	0.80	9.38	3.12
Groups of Lines	4	2,036.31	509.07**	1,825.19	456.29**	2,812.69	703.17 *	2 460.83	615.20**
Late vs. Check	(1)	(1,938.48)	(1,938.48)	(1,792.39)	(1,792.39*)	(2,792.83)	(2,792.83**)	(2,413.18)	(2,413.18*)
Within Late	(3)	(97.83)	(32.61 *)	(32.80)	(10.93*)	(19.86)	(6.62$^{n.s.}$)	(47.65	(15.88)
Error	12	61.62	5.13	19.23	1.60	74.40	6.20	53.43	4.45
Total	19	2,114.56	111.29	1,846.63	97.19	2,889.50	152.07	2,523.64	132.82

* Significance at .05 level of probability.
** Significance at .01 level of probability.
n.s. Nonsignificant.

The combined analyses of variance for 10 Early and 10 Late lines and for 3 Early, 1 Check, and 4 Late groups of lines are given in Tables 11 and 12 respectively. In both of these combined analyses lines and the second degree interaction were highly significant. All the main effects (except lines), and the first degree interactions were nonsignificant in both the combined analyses.

The combined analysis for 1 Check and 3 Early groups of lines is given in Table 13. Here, besides lines and the second degree interaction, Farms, Early vs. Check, and within Early effects were also found to be highly significant. Only one first degree interaction, Farms, X Times, was significant. Although the within Early effect was nonsignificant in all the four individual analyses of variance, it was found to be highly significant in the combined analysis. This might be due to the fact that the means of three Early groups of lines had slight, nonsignificant differences and occurred in the same sequence in all four plantings. In the combined analysis these small, constant differences evidently became highly significant. The mean

Table 11. Combined analysis of variance for ten Early and ten Late lines.

Source of Variation		df	S.S.	M.S.
Farms	(F)	1	87.09	87.09 n.s.
Times	(T)	1	15.31	15.31 n.s.
F X T		1	10.23	10.23 n.s.
Error (a)		12	47.24	3.91
Reps. over Experiments		15	159.87	10.65
Lines	(B)	19	146,133.51	7,691.23**
B x F		19	467.07	24.58 n.s.
B x T		19	293.80	15.46 n.s.
B. x F x T		19	387.83	20.41**
Error (b)		228	1,283.44	5.62
Total		319	148,725.52	466.22

n.s. Nonsignificant.

**Significant at .01 level of probability.

F-tests:

Farms	tested against B x F
Times	tested against B x T
F x T	tested against Error (a)
B	tested by an indirect test
B x F	tested against B x F x T
B x T	tested against B x F x T
B x F x T	tested against Error (b)

Table 12. Combined analysis of variance for three Early, one Check and four Late Groups of lines.

Source of Variation		df	S.S.	M.S.
Farms	(F)	1	28.37	28.37 n.s.
Times	(T)	1	2.12	2.12 n.s.
F x T		1	7.77	7.77 n.s.
Error (a)		12	22.52	1.87
Reps. over Experiments		15	60.78	4.05
Lines	(B)	7	51,845.68	7,406.52**
B x F		7	170.86	24.40 n.s.
B x T		7	31.46	4.49 n.s.
B x F x T		7	185.59	26.51**
Error (b)		84	250.63	2.98
Total		127	52,545.00	413.74

n.s. Nonsignificant.

** Significant at .01 level of probability.

F-tests same as in Table 11.

Table 13. Combined analysis of variance for one Check and three Early groups of lines.

Source of Variation		df	S.S.	M.S.
Farms	(F)	1	23.10	23.10**
Times	(T)	1	8.92	8.92 n.s.
F x T		1	22.98	22.98*
Error (a)		12	46.12	3.84
Reps. over Experiments		15	101.12	6.74
Lines	(B)	3	3,392.82	1,130.94**
Early vs. Check		(1)	(3,350.77)	(3,350.77**)
Within early		(2)	(42.05)	(21.02**)
B x F		3	0.69	0.23 n.s.
B x T		3	4.24	1.41 n.s.
B x F x T		3	84.62	28.20**
Error (b)		36	69.76	1.93
Total		63	3,653.25	57.98

n.s. Nonsignificant.

*Significance at .05 level of probability.

**Significance at .01 level of probability.

F-tests same as in Table 11.

Table 14. Combined analysis of variance for one Check and four Late groups of lines.

Source of Variation		df	S.S.	M.S.
Farms	(F)	1	97.88	97.88 n.s.
Times	(T)	1	0.09	0.09 n.s.
F x T		1	105.64	105.64*
Error (a)		12	30.63	2.55
Reps. over Experiments		15	234.24	15.61
Lines	(B)	4	9,013.62	2,253.40**
Late vs. Check		(1)	(8,867.62)	(8,867.62**)
Within Late		(3)	(146.00)	(48.66 n.s.)
B x F		4	84.09	21.02*
B x T		4	26.88	6.72 n.s.
B x F x T		4	10.43	2.60 n.s.
Error (b)		48	208.67	4.34
Total		79	9,577.93	121.23

n.s. Nonsignificant.
*Significant at .05 level of probability.
**Significant at .01 level of probability.

F-tests same as in Table 11.

flowering time was earliest in the first group of lines, slightly later in the second group, and latest in the third group. The pedigrees show that these three groups of lines had previously been selected for late flowering for 0, 1, and 2 generations. These results show that in spite of the great influence of environment on the time of flowering, selection was effective.

Table 14 shows the results of the combined analysis of variance for 1 Check and 4 Late groups of lines. Among the main effect Lines and Late vs. Check were highly significant, while among the interactions Farms X Times and Lines X Farms were highly significant and significant, respectively. Although significance was observed for the within Late effect in three out of four plantings, in the combined analysis this effect was nonsignificant. This probably was due to inconsistency in the ranking of the four groups of lines in different plantings. The results suggest that the original four seeds, from which the four groups of Late lines were developed, were probably not different genetically from each other and that the response to selection in these groups of lines was probably also alike.

The variance components obtained from the combined analyses are given in Table 15. This table shows the magnitude of the variance components in four different types of analyses. From this table it seems probable that the cause of the second degree interaction component is the Early lines. Furthermore, this table shows that the behavior of the Early and Late lines is quite different. Some of the effects that are significant in one are nonsignificant in the other and *vice versa.* When the Early and Late "populations" were grouped, they nullified some of the significant effects of each other.

The Farms and Times effects were nonsignificant in the four combined analyses, although from the raw data, it seems that these effects should be significant. This, of course, is due to expressing the data relative to the performance of the Checks. Two planned comparisons to check the significance of Farms and Times were made with the non-transformed data. The results, given in table 16, show that both the effects were highly significant in all the four types of grouping of the lines.

In Figures 3 and 4, Early, Check, and Late represent the means of all the Early, Check and Late lines respectively. The ordinates of these figures give the cumulative percentages of flowering time of the Early and Late lines expressed as deviations from the Check for the respective classes on the abscissa. At the earliest dates flowering had started in the Early lines, while there was no flowering in the Check. Thus to get the deviations from the Check (ordinate values) a value of zero was given to the Check, similarly, at the latest dates flowering had finished in the Check lines, while the Late lines were still blooming. Thus to get the deviations from the Check a value of 100 was given to the Check. These Figures show that the maximum cumulative difference of the Late lines from the Check lines was the same in the two plantings of Fall, 1968. This reflects the similar performance of the Late population in the two plantings of Fall, 1968. Similarly the maximum cumulative differences of the Late lines from the Check lines are not very different in the two plantings of Spring, 1969. Furthermore, in the Late populations the relation between Poamoho and Waimanalo plantings of Fall, 1968 is very similar to the relation between the Poamoho and Waimanalo plantings of Spring, 1969. The maximum cumulative differences of the Early lines from the Check lines are quite different in the two plantings of Fall, 1968 (Figure 3). This shows that the performance of the Early populations in the two plantings was different. The differences are also noted in the two plantings of Spring, 1969 (Figure 4). It can also be noted that while the maximum deviation of Early lines from the Check was higher in Poamoho in the Fall, 1968 plantings, the maximum deviation was higher in Waimanalo, for the Spring, 1969 plantings. These discrepancies noted in the Early lines, particularly in 1968, and not in the Late lines explain the significant second degree interaction for Early population, and the nonsignificant interaction for the Late population.

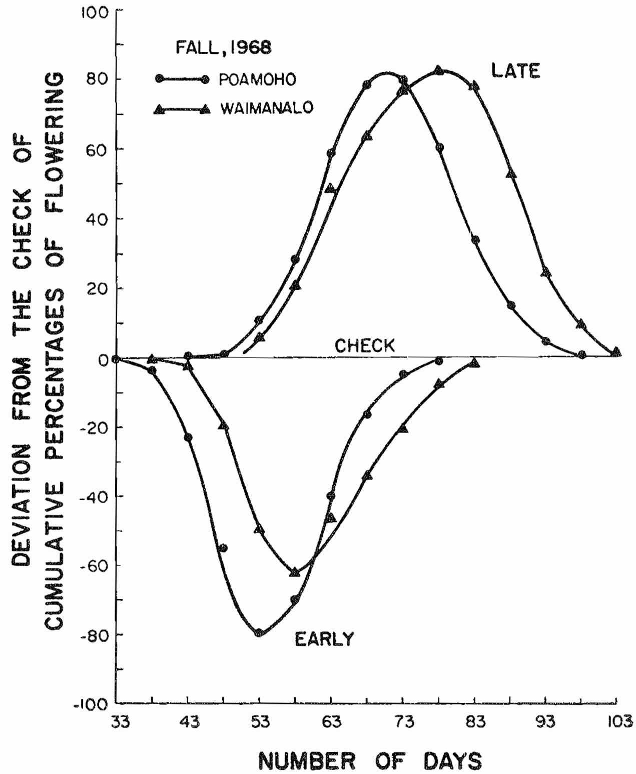

Figure 3. Deviations from the Check of cumulative percentages of flowering for the Early and Late populations in the two Plantings of Fall, 1968.

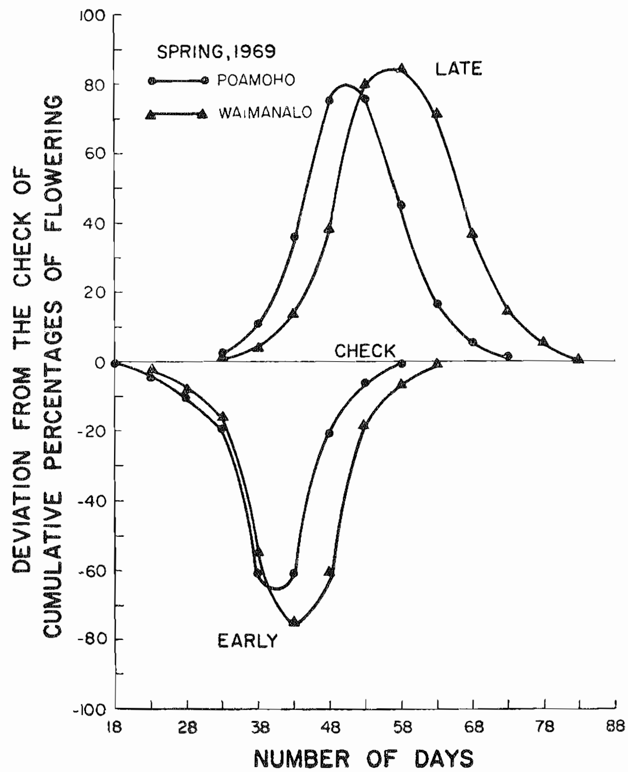

Figure 4. Deviations from the Check of cumulative percentages of flowering for the Early and Late populations in the two Plantings of Spring, 1969.

Table 15. Variance component estimates from combined analyses of variance.

Variance Components[a]	10 Early & 10 Late Lines	3 Early, 1 Check & 4 Late Groups of Lines	1 Check & 3 Early Groups of Lines	1 Check & 4 Late Groups of Lines
$\bar{O}^{2}_{BFT}$	3.6975**	5.8825**	6.5675**	0.0000[b]
$\bar{O}^{2}_{BT}$	0.0000[b]	0.0000[b]	0.0000[b]	0.5150 n.s.
$\bar{O}^{2}_{BF}$	0.5212 n.s.	0.0000[b]	0.0000[b]	2.3025*
$\bar{O}^{2}_{B}$	479.5318**	461.3200**	68.8018**	140.7868**
$\bar{O}^{2}_{FT}$	0.0000[b]	0.0000[b]	0.0000[b]	5.2415**
$\bar{O}^{2}_{T}$	0.0626 n.s.	0.2557 n.s.	0.3978 n.s.	0.0000[b]
$\bar{O}^{2}_{F}$	0.4543 n.s.	0.3548 n.s.	0.8849**	0.0000[b]
$\bar{O}^{2}$	5.6200	2.9800	1.9300	4.3400

[a] For description see Fig. 1.
[b] Negative estimates for which the most reasonable value is zero.
n.s. Nonsignificant.
*Significant at .05 level of probability.
**Significant at .01 level of probability.

Table 16. Effects of location and planting time on flowering.

	10 Early & 10 Late Lines	3 Early, 1 Check & 4 Late Groups of Lines	1 Check & 3 Early Groups of Lines	1 Check & 4 Late Groups of Lines
Location:				
Mean differences	5.91	5.89	3.44	7.42
Variance of differences	7.38	7.24	0.04	4.92
St. dev. of differences	2.72	2.69	0.20	2.22
St. Error of differences	0.61	0.95	0.10	0.99
t-Value	9.85**	6.20**	34.40**	7.49**
Planting Time:				
Mean differences	17.45	18.06	13.72	21.08
Variance of differences	23.58	22.90	2.15	9.49
St. dev. of differences	4.86	4.79	1.47	3.08
St. Error of differences	1.08	1.69	0.73	1.37
t-Value	16.15**	10.68**	18.79**	15.38**

**Significance at .01 level of probability.

Estimates of heritability of the mean flowering time of the Check line were made, assuming that (a) lines L-2, L-3, L-6, L-7, and L-10 are homozygous, and thus the variance of flowering time in these lines is a valid estimate of the environmental variance, and (b) the variation due to the environment of the Check line is of the same magnitude as that of the Late lines in a particular planting. The estimates obtained from the Waimanalo-Fall planting were considerably higher than those of the other planting (Table 17). The reason for this is the skewed distribution of the Check line in that planting. The skewed distribution yielded considerably higher variance of the Check lines in this planting. The higher variance of the Check line is expected to give higher estimates of heritability.

Table 17. Estimates of heritabilities of mean flowering times of Check Line, considering L-2, L-3, L-6, L-7, and L-10 as homozygous lines.

Homozygous lines	Poamoho		Waimanalo	
	Fall	Spring	Fall	Spring
L-2	21.41	32.29	28.58	30.78
L-3	33.31	46.83	63.79	40.09
L-6	46.79	41.81	69.79	41.98
L-7	38.05	31.34	64.07	29.30
L-10	47.86	32.88	67.54	30.19

The variance due to the breeding lines was not used as an estimate of the total genetic variance, because the breeding lines had been selected in opposite directions and thus had a higher variance than would be expected from unselected families or from and F population. A heritability estimate calculated from this variance would be expected to have a high positive bias when the breeding lines had been selected in opposite directions.

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