INHERITANCE OF FLOWERING IN MAIZE¹

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Received February 23, 1965

KNOWLEDGE about the mode of inheritance of flowering date of corn is useful in the development of inbred lines for possible use in hybrids. The complexity of the inheritance of flowering varies, but, generally, selection has been more effective for flowering date than for yield. EMERSON and EAST (1913) explained the inheritance of flowering in corn by the multiple-factor hypothesis and GIESBRECHT (1960a) found in the literature reports of 2 to 19 genetic factors influencing flowering date, with most authors reporting 4 to 6. From a genetic analysis of the progeny of two crosses, GIESBRECHT (1960a, b) postulated that the inbreds differed by 4 to 5 factors for flowering date. Heritability percentages were obtained in two years and ranged from 59.0 to 75.9 for one cross and — 26.6 to — 0.5 for the second. The author (1960a) interpreted the negative estimates obtained in the second cross as a result of high interallelic interaction, whereas the formulas used in calculating heritabilities were based on the assumption that the gene effects accumulate additively. WARNER (1952) reported a heritability of 32% for days to silking. From a study of six early × late crosses, JONES (1952) obtained heritabilities ranging from 11 to 48%.

Because of the varying number of genetic factors estimated as effecting time of flowering and the differences in the relative magnitude of the estimates of heritability, it appears that time of flowering may be controlled by several factors and is influenced, to a large extent, by the environment (SHAW 1955). If one assumes the parents differ by four allelic pairs, the smallest perfect F_2 population would have 256 individuals with 81 different possible genotypes (assuming coupling and repulsion heterozygotes to be equivalent). If a larger number of allelic pairs is involved in the expression of time of silking, as has been postulated by some studies, the number of different kinds of genotypes possible in the F_2 generation increases exponentially. Therefore, it appears days to flowering is a trait that is amenable to biometrical analysis.

The inheritance of time of flowering was investigated by the procedures outlined by MATHER (1949) and the results are reported in this paper. Time of flowering was defined as the time silks were first visible on the top female inflorescence.

¹ Contribution from the Iowa Agricultural and Home Economics Experiment Station, Ames, and the Crops Research Division, Agricultural Research Service, U.S. Department of Agriculture cooperating. Journal Paper No. J-5042 of the Iowa Agriculture and Home Economics Experiment Station Project No. 1335.

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MATERIALS AND METHODS

The material used to study the inheritance of time of flowering in corn was formed by crossing B14 and Oh45. The two inbred lines are relatively early (Oh45) and late (B14) for time of flowering, with Oh45 flowering approximately 10 to 12 days earlier than B14. The F_1 cross of the two lines was selfed and backcrossed to both parents. Self-pollinations were made on the F_2 and backcross plants to produce the F_3 and selfed backcross progenies. At maturity, ears were harvested from 57 F_2 , 81 B14 backcross, and 57 Oh45 backcross plants. Therefore, the material available for study included the two inbred lines, B14 (P_1) and Oh45 (P_2), the F_1 , and 57 F_3 , 81 selfed B14 backcross (BS_1), and 57 selfed Oh45 backcross (BS_2) progenies.

Time of flowering was recorded in 1957, 1958, and 1959 at the Agronomy Farm, Ames, Iowa. The 1957 experiment included 3 P_1 , 3 P_2 , 3 F_1 , 57 F_3 , 81 BS_1 , and 57 BS_2 entries; whereas, the 1958 and 1959 experiments included 1 P_1 , 1 P_2 , and 1 F_1 , and 20 entries selected at random from the F_3 , BS_1 , and BS_2 entries included in 1957. Each year the experiment was grown in a randomized complete block design with four replications. A plot (assuming a perfect stand) consisted of 25 plants, spaced approximately 13 inches apart within rows 40 inches apart. To avoid differential competition between the inbred line plots and the more vigorous entries, the inbred plots were bordered with the appropriate inbred.

Except for two BS_1 entries, plant stands were good each year with the average number of plants per row for all entries being 21.0, 22.2, and 21.2 in 1957, 1958, and 1959, respectively. Each plot was checked daily after the initiation of flowering in the early entries and a tag (indicating the date when silks were first visible from the uppermost shoot) was attached to each plant. Each plot was checked until all plants had silked. After the cessation of silking, an inventory was made for each plot. The inventory indicated the time of silk for each plant within the plot and formed the data that were used in the subsequent analysis for the inheritance of time of silking.

Analyses of variance were computed which included all entries within a year, for the F_3 , BS_1 , and BS_2 progenies within each year, and a combined analysis across years for all entries and the F_3 , BS_1 , and BS_2 progenies. These analyses were computed on a plot mean basis. Also, a pooled within-plot variance was calculated for each entry. In the analysis of variance, the degrees of freedom and sums of squares were pooled to obtain the total within-plot variation for all entries and for the F_3 , BS_1 , and BS_2 progenies.

The within-plot sums of squares of the P_1 , P_2 , and F_1 were pooled to obtain an estimate of the variation attributable to environmental effects (E_w). This estimate may be biased (BYRD 1955; SHANK and ADAMS 1960), but an alternative method for estimating the environmental effects was not available. The environmental effects obtained for each of the P_1 , P_2 , and F_1 entries within each of the years, combined for years, and combined for the three entries within each year are presented in Table 1; the latter were used for the estimation of E_w for each year. The amount of variation that existed among the entries within each year and among years for the same entry is indicated in Table 1, also. The combined estimates for each entry across years indicated the F_1 had less plant-to-plant variation than either of the parents. However, the P_2 and F_1 entries exhibited more variation among years than the P_1 . In 1958, the estimates of E_w were larger for the P_2 and F_1 entries and were indicative of the sensitivity of time of silking to

TABLE 1

Within-plot variance (E_w) obtained from the nonsegregating, B14, Oh45, and F_1 , entries in 1957, 1958, and 1959

Year	P_1 (B14)	P_2 (Oh45)	F_1	Combined
1957	2.71	2.71	1.21	2.16
1958	1.77	7.89	5.34	5.00
1959	1.68	0.85	0.71	1.05
Combined	2.29	3.25	1.94	2.49

the vicissitudes of the environment (SHAW 1955). The P_2 and F_1 entries silked earlier than the P_1 entry and had a bimodal distribution in 1958 because a portion of the plants silked prior to a hot, dry period and completed silking after a subsequent rain. Bartlett's test for homogeneity of variance indicated the estimates of E_w were significantly different among entries within each year and among years for each entry. The combined estimates of E_w among years for all entries and among entries over years were significantly different also.

Estimates of additive genetic variance (D) and variance due to dominance deviations (H) were obtained in each year and for the data combined over years. Prior to the analyses, scaling tests of the F_3 , BS_1 , and BS_2 progeny means indicated the data were amenable to this type of analysis. Scaling tests of the F_3 , BS_1 , and BS_2 means for 1957, 1958, 1959, and combined indicated only three comparisons had differences larger than two standard deviations; these were for BS_2 in 1957 and 1958 and BS_1 in 1959.

Estimates of the genetic components of variance were obtained for days to silk by utilizing the variance components obtained from the analysis of variance for each of the F_3 , BS_1 , and BS_2 populations. The expectations of the genetic components for the variance of F_3 means, mean F_3 variance, variance of reciprocal backcross means, and mean backcross variance were recorded by MATHER (1949). By extension, the variance of the BS_1 and BS_2 means and the mean variance of the BS_1 and BS_2 can be obtained and, by utilizing multiple regression analyses, can be used in conjunction with the variance of F_3 means and mean F_3 variance to obtain estimates of D and H .

The associated errors (E_1 and E_3) of the F_3 , BS_1 , and BS_2 means were obtained from the analyses of variance. The error (E_2) for the mean F_3 , BS_1 , and BS_2 variances was obtained from the combined within plot variance of the P_1 , P_2 , and F_1 (Table 1). Eight basic equations were then available for the estimation of D , H , E_1 , E_2 , and E_3 and these, when equated to their observed values, would be as follows:

$$\begin{aligned} V_{F_3} &= \frac{1}{2} D + \frac{1}{16} H + E_1 = Y_1 \\ \bar{V}_{F_3} &= \frac{1}{4} D + \frac{1}{8} H + E_2 = Y_2 \\ V_{BS_1} + V_{BS_2} &= \frac{1}{2} D + \frac{1}{8} H + 2 E_3 = Y_3 \\ \bar{V}_{BS_1} &= \frac{1}{4} D + \frac{1}{8} H + E_2 = Y_4 \\ \bar{V}_{BS_2} &= \frac{1}{4} D + \frac{1}{8} H + E_2 = Y_5 \\ E_1 &= Y_6 \\ E_2 &= Y_7 \\ E_3 &= Y_8. \end{aligned}$$

These eight basic equations were combined to give the five normal equations to solve for the five components of variation. The five normal equations were as follows:

$$\begin{aligned} .6875 D + .1875 H + .5000 E_1 + .7500 E_2 + 1.0000 E_3 &= Q_1 \\ .1875 D + .0664 H + .0625 E_1 + .3750 E_2 + .2500 E_3 &= Q_2 \\ .5000 D + .0625 H + 2.0000 E_1 &= Q_3 \\ .7500 D + .3750 H + &4.0000 E_2 = Q_4 \\ 1.0000 D + .2500 H + &5.0000 E_3 = Q_5. \end{aligned}$$

The normal equations were then solved to obtain estimates of the five parameters. Five degrees of freedom were used in the estimation of the five parameters, D , H , E_1 , E_2 , and E_3 , leaving only three for deviations. The deviation sum of squares was obtained by comparing the expected and observed values for the F_3 , BS_1 , and BS_2 populations. Thus, the deviation mean square was obtained by dividing the deviation sum of squares by three. The standard errors for each of the five estimated parameters were obtained by multiplying the deviation mean square by their respective diagonal elements of the inverse or variance-covariance matrix.

Estimates of the number of effective factors controlling date of silking were obtained by the procedures outlined by MATHER (1949). When the estimate of the effective factors was obtained as the ratio of the square of half of the parental difference to $\bar{D}$, it was designated as K_1 . If use was made of the h increments instead of the d 's, the estimate of the number of effective factors

was designated as K'_1 . The latter estimate was calculated as the ratio of the square of half the parental difference to $\bar{H}$. Also, an estimate designated as K_2 was obtained by the ratio of ${}_H\bar{V}_{F_3}$ to ${}_HV_{VF_3}$ where ${}_H\bar{V}_{F_3}$ is the heritable mean variance of the F_3 progenies and ${}_HV_{VF_3}$ is the variance of the F_3 variances. The K_2 estimate overcomes the difficulties of incomplete concentration and incomplete reinforcement which is tantamount in the estimates of K_1 and K'_1 .

RESULTS AND DISCUSSION

Differences were obtained among entries in each of the years and across years at the 1% level of probability. Also, the differences among years and the first order interaction of years $\times$ entries were significant at the 1% level. However, for purposes of this study, the primary interest was in the groups of entries that were used to obtain estimates of genetic variances. The differences for date of silking among the F_3 , BS_1 , and BS_2 progenies within each of the three groups were significant at the 1% level within each year. The range for time of silk averaged 8.3, 7.2, and 6.4 days for the F_3 , BS_1 , and BS_2 progenies, respectively, for the three years.

A combined analysis of each of the three groups of progenies was calculated for the 20 entries included for the three years. The combined analysis indicated highly significant differences (1% level of probability) for time of silk among the three years for each of the three groups of progenies. The differences among entries were highly significant in the combined analyses, but the differences were not consistent among years because the years $\times$ entries interaction was highly significant for each of the three groups of progenies. The significant years $\times$ entries interaction indicates that the relative ranking for time of silk of the progenies varied among years.

The data are summarized in Table 2. The extremes for the interval from planting to date of silk ranged from 78.8 days for the F_1 in 1959 to 91.6 for B14 in 1957; a difference of approximately 13 days. The interval from planting to date of silk is quite variable and this interval varies both among years and among different genetic material (SHAW 1955). Thus, the more realistic comparisons would be made within a particular year. The differences for date of silk between the two inbred parents were 8.9, 9.8, 7.0, and 8.6 days for 1957, 1958, 1959, and years combined, respectively, with Oh45 being the earlier parent.

The F_1 hybrid silked at approximately the same time as the early parent, Oh45, indicating nearly complete dominance for earliness in this particular cross. In 1957, the time of silk of the F_1 was 82.4 compared to 82.7 days for the early parent. In 1958, the F_1 was two days later than Oh45, whereas, in 1959, the F_1 was approximately two days earlier than Oh45. The data, when combined over years, resulted in the F_1 and Oh45 inbred having nearly identical silking dates. The amount of heterosis for earliness ranged from 3.5% in 1958 to 6.4% in 1959 with a heterotic expression for earliness of 5.2% when combined over years.

The amount of inbreeding depression was calculated by using the mean silking date of all F_3 progenies in comparison with the F_1 . The amount of inbreeding depression ranged from 3.7% in 1958 and 1959 to 5.1% in 1957 with the combined data indicating a depression of 4.0% from earliness for silking. In all cases,

TABLE 2

Summary of data obtained for the entries in 1957, 1958, 1959, and combined across years

Entry	Year	No. of plants	C.V.* percent	Interval†	Standard error	Within-plot variance	Heterosis‡	Inbreeding depression§	Range
B14	1957	253	..	91.6	0.22	2.71	..	..	
	1958	93	..	88.8	0.58	1.77	..	..	
	1959	92	..	87.7	0.24	1.68	..	..	
Combined		438	..	89.4	0.60	2.29	..	..	
Oh45	1957	215	..	82.7	0.22	2.71	..	..	
	1958	93	..	79.0	0.58	7.89	..	..	
	1959	131	..	80.7	0.24	0.85	..	..	
Combined		439	..	80.8	0.60	3.25	..	..	
F ₁	1957	276	..	82.4	0.22	1.21	5.5%	..	
	1958	92	..	81.0	0.58	5.34	3.5	..	
	1959	95	..	78.8	0.24	0.71	6.4	..	
Combined		463	..	80.7	0.60	1.94	5.2	..	
F ₃	1957	4871	3.6	86.6	0.46	5.74	..	5.1%	82.9-90.5
	1958	1818	5.6	84.1	0.65	7.24	..	3.7	78.9-88.3
	1959	1699	3.5	81.8	0.37	4.49	..	3.7	78.1-86.0
Combined		8388	4.3	84.1	0.62	5.84	..	4.0	80.4-88.2
BS ₁	1957	6379	3.5	88.6	0.48	5.59	..	..	84.1-92.0
	1958	1707	4.5	88.2	0.56	6.31	..	..	82.6-89.5
	1959	1605	3.8	85.7	0.43	5.54	..	..	79.8-86.7
Combined		9691	3.6	87.6	0.43	5.81	..	..	82.2-89.0
BS ₂	1957	4882	3.7	85.2	0.45	5.84	..	..	82.9-88.9
	1958	1783	5.3	83.1	0.58	8.10	..	..	79.5-86.0
	1959	1715	8.9	80.8	0.88	4.55	..	..	77.0-83.6
Combined		8380	6.0	82.5	0.46	6.46	..	..	80.6-86.0

* Coefficient of variability.

† Number of days from planting to silk.

‡ Heterosis = $[(MP - F_1)/MP] \times 100$, where MP is the midparent value.§ Inbreeding depression = $[(F_3 - F_1)/F_1] \times 100$, where F_3 is the mean of all F_3 progenies.

the mean date of silking of the F_3 progenies has increased and is similar to the mid-parent value. A comparison of the F_3 progeny means and mid-parent values shows that the mean of the F_3 progenies was 0.6 day earlier in 1957, 0.2 day later in 1958, and 2.6 days earlier in 1959 than the mid-parent values.

Transgressive segregation was not indicated by the range of the F_3 progeny means (last column Table 2). In 1957, the range of the 57 F_3 progeny means for time of silk extended from the early silking parent (Oh45) to the late silking (B14). The same trend was observed for 1958 and 1959 although only 20 of the 57 entries compared in 1957 were included in 1958 and 1959.

The components of variance for the F_3 , BS_1 , and BS_2 progenies (Table 3) exhibit some variation among years, the most notable differences having been obtained in 1958. The variation among F_3 means was approximately twice as large as those obtained in 1957 and 1959, whereas, the mean F_3 variance was smaller. Also, as indicated previously, the within plot environmental variance (E_2) was considerably larger in 1958. The same relationship was not exhibited for the components obtained from the BS_1 and BS_2 progenies because the variance of

TABLE 3

Variance components obtained from the analysis of variance of the F₂, BS₁, and BS₂ progenies grown in 1957, 1958, 1959, and combined over years

Year	Variance components								
	$\sigma^2_{F_2}$	E_1	$\sigma^2_{BS_1}$	E_2	$\sigma^2_{BS_1}^*$	$\sigma^2_{BS_2}^*$	E_3	$\sigma^2_{BS_1}$	$\sigma^2_{BS_2}$
1957	3.6605	0.2105	3.5742	2.1636	2.7973	3.5596	0.2195	3.4224	3.6723
1958	7.0750	0.4200	2.2360	5.0019	3.4650	3.1800	0.3294	1.3054	3.0977
1959	3.9418	0.1374	3.4433	1.0474	3.5752	1.4975	0.4782	4.4948	3.5010
Combined	4.2137	0.3860	3.3521	2.4891	3.4397	3.6786	0.1991	3.3202	3.9659

* $\sigma^2_{BS_1}$ and $\sigma^2_{BS_2}$ components were combined for estimating D and H .

means was not consistently larger than those in 1957 and 1959, and the mean BS₁ and BS₂ variances were smaller; the greatest decrease in magnitude having been obtained from the BS₁ progenies. Again, this was probably the result of the environmental conditions because of the BS₁ population's having been developed by backcrossing to the late parent, B14; it was not affected to the same extent as the earlier flowering progenies.

The variance components (Table 3) were used in conjunction with their genetic expectations to obtain estimates of the additive (D) and dominance (H) variance (Table 4) that were present in the F₂ population. The estimates of D were all positive, and the 1957, 1958, and combined estimates indicate that a significant amount of additive variance was present. Considerable variation existed among years for the D values; but the greatest discrepancy, the estimate obtained in 1958, was 2½ to 3½ times larger than the estimates obtained in 1957 and 1959. A comparison of the combined estimate of D with the average of the estimates obtained in 1957, 1958, and 1959 indicates that the interaction of D with years was not large.

Greater variation was obtained for the H estimates, and the standard errors on the estimates were considerably larger than those for D . The magnitude of the estimates ranged from -64.0 in 1958 to 9.1 in 1959; the 1957 and combined estimates having been negative, but not significantly different from zero. With the exception of H in 1958, all estimates indicate that the amount of variance due to

TABLE 4

Estimates of components of genetic and environmental variation and their associated standard errors for 1957, 1958, 1959, combined for years, and average for years

Components	1957	1958	1959	Combined	Average*
D	8.3273 ± 2.5490	22.7315 ± 4.2237	6.3600 ± 4.3674	10.0671 ± 3.1004	12.4729
H	-2.5641 ± 9.2661	-64.0790 ± 15.3530	9.1188 ± 15.8756	-7.8851 ± 11.2705	-19.1748
E_1	-0.0662 ± 0.6201	0.0671 ± 1.0275	0.1647 ± 1.0625	0.0295 ± 0.7543	0.0553
E_2	1.8872 ± 0.6203	4.6555 ± 1.0278	1.0743 ± 1.0628	2.1335 ± 0.7545	2.5390
E_3	1.0494 ± 0.3976	1.3815 ± 0.6587	0.3968 ± 0.6812	1.2680 ± 0.4836	0.9426

* Average values obtained by using the algebraic sum of 1957, 1958, and 1959.

dominance deviations was very small. Since $\hat{H}$ was obtained by squaring deviations, the estimates obtained are presumably estimates of zero or some small positive value with no apparent interpretation of the 1958 estimate. Except for the 1958 estimate, all estimates of H are within one standard deviation of zero. Also, a comparison of the average and combined $\hat{H}$'s indicates that there was variation among years for $\hat{H}$; however, the large negative estimate obtained in 1958 would inflate the average value.

The data afford no means for test of linkage, because neither the F_2 or back-cross plants were included in the study. Therefore, no test was available to test the homogeneity of D and H over F_2 and F_3 to determine the extent the estimates of D and H may be influenced by linkage bias. As indicated by MATHER (1949), regardless of the phase of linkage, the H value will have a positive bias, assuming that the effects at the different loci are reinforcing in their physiological effects. The $\hat{H}$ values obtained indicate that the bias due to linkage was not large, or that the effects were opposing, because the estimates of H indicated that H was zero or very small.

Contrary to the estimates of H , the estimates of D may be biased up or down according to the phase of linkage. The parents used to make the original cross were quite dissimilar for date of silking, and it appeared logical to assume that the parents would be in opposition for factors influencing date of silk; B14 for lateness of silking and Oh45 for earliness. The F_2 population, involving these two lines, would have been produced from coupling phase gametes, if linkage is present, for earliness and lateness of flowering. If this were true, the estimates of D would be biased upward, due to the coupling phase of linkage. The presence and amount of linkage bias on the $\hat{D}$ value are unknown at the present, but the presence of linkage could be detected if estimates were also obtained in populations that have allowed for further genetic recombination. Therefore, on the basis of the $\hat{D}$ and $\hat{H}$ values obtained in this study for this particular population, it appears that most of the genetic variation was of the additive type, and that selection for early or late flowering types should be effective; however, it is realized that linkage may be biasing the estimates of D in a positive but unknown amount.

It was suggested previously, on the basis of the parental and F_1 means in Table 2, that early silking was completely dominant to late, because the F_1 hybrid silked at approximately the same time as the early inbred. The values of $\hat{D}$ and $\hat{H}$ did not, however, indicate that the dominance variance was the major type of genetic variation. Scaling tests performed prior to the analysis of the data indicated that the genic effects were on the average additive among loci. Apparently the earliness of flowering in the F_1 was associated, at least in part, with the phenomenon of heterosis, because the distribution of the mean date of silk of the F_3 progenies, combined over the years, was not bimodal. Distributions of the combined means for the BS_1 and BS_2 progenies also indicated equal distribution of the progeny means about the mean of each group. This would suggest that several factors were segregating for date of silk. On the other hand, F_3 entries were obtained that represented the extremes of the parents for time of silk and seemed to indicate that a maximum of three factors was involved for the expression of silking.

TABLE 5

Estimates of the number of effective factors influencing the time of silking in 1957, 1958, and 1959

Year	Estimates			
	K_1	K'_1	K_2	K_2^*
1957	2.38	...†	0.16	0.23
1958	1.06	...	0.01	0.04
1959	1.93	3.20	0.01	0.01

* Estimate of ${}_H\bar{V}_{F_3}$ calculated assuming $H \approx 0$.

† Estimate of H was zero.

The estimates of the number of effective factors influencing date of silking were small (Table 5). The K_1 and K'_1 values were not as high as have been reported for maize (GIESBRECHT 1960a, b; JONES 1952), and indicate that the number of effective factors influencing date of silk for this particular cross is either small, or that the assumptions for the use of the K_1 and K'_1 formulae were not fulfilled, or that linkage is distorting the estimates. Because of the distribution of the F_3 progeny means (Table 2), it appeared that more than one or two factors were influencing the time of silking. The F_3 progeny means ranged from the early to late parent and were about normally distributed. This suggests that the assumptions were not valid or that linkage was responsible for the low estimates. Tests of linkage were not available and, therefore, the effect of linkage is unknown. The assumptions that the segregating factors are not isodirectionally distributed between the two parents, and that they have unequal d or h effects, would both result in an underestimation of the true value.

As an estimate of the number of effective factors, K_2 is superior to K_1 in that it overcomes the difficulty of incomplete concentration of like allelomorphs in the parents. However, the K_2 values were smaller than those obtained for K_1 (Table 5). If the d or h increments were equal, then one would expect the values of K_2 to be greater or equal to the K_1 . The K_2 values were less than the K_1 in all cases. Then it appears that the d and h increments were not equal, and that the estimates of the true value were underestimated (again, recognizing that the presence of linkage may be distorting the results) because of the inequality of the d and h increments. The inequality of the d and h increments will result in a greater variation of K_2 than K_1 , provided the latter are not adversely affected by the incomplete concentration of the like allelomorphs. In either case, one should consider K_1 and K_2 as less than the actual number of factors involved for the expression of a trait. Seven of the ten estimates indicated a maximum of one effective factor influencing the time of silk.

The mean date of silk for all F_3 progenies was 84 days after planting. For the 20 F_3 progenies grown three years the means, combined over years, ranged from 80 to 88 days for time of silk. Three F_3 entries silked 84 days after planting, nine silked less than 84, and eight silked more than 84. Two entries silked 80, or eight days earlier than the one entry that silked 88 days after planting. The entries at

the two extremes were consistent across years and would suggest that selection would be effective for obtaining selections that are quite different for date of silk. To the breeder, this would be especially desirable if the desired traits of the late line could be incorporated with early silking. However, the earliest silking selection was not earlier than the early parent. If one considers both the distribution of the F_3 progenies and the recovery of genotypes representing the extremes of the two parents, it appears that a maximum of three effective factors was influencing date of silk.

SUMMARY

The inheritance of time of silking was studied for the population derived from crossing a relatively early (Oh45) and a relatively late (B14) inbred line. The biometrical procedures outlined by MATHER (1949) were used to obtain estimates of the additive (D) and dominance (H) variance present in the population, and the number of effective factors influencing time of silk.

The estimates of D and H indicate that D was of major importance, and that H was zero (or some very small positive value). However, linkage, if present, could bias the estimates of D positively in an unknown amount. Linkage was not tested.

From two to four effective factors were estimated to influence time of silking. The variation among the estimates suggests that either the assumptions necessary for using the formulae were not fulfilled, or that linkage distorted the estimates and caused an underestimation of the number of factors. The data suggest a maximum of three effective factors influenced time of silking.

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