INHERITANCE OF THE FLOWERING TIME IN MAIZE
I. DIALLEL ANALYSIS[1]

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ABSTRACT - In order to determine the inheritance of the number of days necessary to flowering in maize, four inbred lines in a complete diallel cross were used. It was observed that this trait is controlled by at least three genes or blocks of genes. The number of days necessary for flowering in the early and late blooming lines was 85.3 and 95.3, respectively. Of the inbred lines tested, L-352 presented the greatest number of earliness alleles and L-142 the greatest number of lateness flowering alleles. Both additive and dominant effects are involved in the control of this character, while maternal inheritance is not. Estimated narrow heritability was low (37.67%), indicating that selection based on phenotype is little effective, under the conditions of this test.

Index terms: *Zea mays*, maize, flowering time, inheritance, diallel crosses.

HERANÇA DO NÚMERO DE DIAS PARA FLORAÇÃO EM MILHO
I. ANÁLISE DIALÉLICA

RESUMO - Visando obter informações a respeito da herança do número de dias para a floração do milho, quatro linhagens, num dialelo completo, foram usadas. Verificou-se que este caráter é controlado por pelo menos três genes, ou blocos gênicos, sobredominantes. O número de dias predito para a floração de linhagens tendo somente alelos para precocidade (dominantes) e somente alelos para floração tardia (recessivos) foram, respectivamente, 85,3 e 95,3 dias. Das quatro linhagens estudadas, a L-352 foi a que apresentou maior número de alelos para precocidade, e a linhagem L-142, o maior número de alelos para floração tardia. Tanto os efeitos aditivos quanto os desvios da dominância estão envolvidos no controle do caráter, mas não os efeitos maternos. A estimativa de herdabilidade no sentido restrito foi relativamente baixa (37,67%), o que indica que seleção com base no fenótipo, nas condições deste ensaio, seria pouco eficaz.

Termos para indexação: *Zea mays*, milho, floração, herança, cruzamentos dialélicos.

INTRODUCTION

Development of early maturing maize hybrids is essential for successful production in short growing season areas and in crop rotation systems. Success of this activity depends on the knowledge of the inheritance of the number of days to flowering in the breeding population. However, few published papers contain information on this matter using Brazilian populations.

Studies in other countries have shown that earliness in maize may be either partially dominant (Bonaparte, 1977; Rood & Major, 1981), or completely dominant (Jones, 1952; Mohamed, 1959) or overdominant (Rood & Major, 1981). Additive (Hallauer, 1965; Bonaparte, 1977; Casañas et al., 1989; Ajala, 1992) and dominant effects (Bonaparte, 1977; Casañas et al., 1989) have been reported to account for a high proportion of the genetic variation in different populations.

Varying number of genes are reported to be involved in the control of the flowering time in maize. Giesbrecht (1960) reviewing the literature found reports of two to nineteen genes with most of them

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reporting four to six genes controlling the flowering time in maize. Rood & Major (1981) reported one gene influencing this trait; Yang (1949) and Mohamed (1959), two genes; Hallauer (1965), three genes; Bonaparte (1977), Bianchi & Maliani (1954), and Giesbrecht (1960), four to five genes; and Jones (1952), as much as five to nineteen genes. Narrow heritability estimates have ranged from 11% to 95% (Warner, 1952; Jones, 1952; Bonaparte, 1977; Rood & Major, 1981; Casañas et al., 1989).

Selection for early flowering in maize has been practiced. Troyer and colleagues (Troyer & Brown, 1972, 1976; Troyer & Larkins, 1985; Troyer, 1986) obtained genetical gains ranging from 0.6 to 2.0 days per cycle, for two to eleven selection cycles, in different populations of maize.

The inheritance of the flowering time in maize is investigated in this paper using Hayman's procedure (Hayman, 1954a, 1954b) for diallel analysis.

MATERIALS AND METHODS

A complete diallel cross involving four maize S_7 inbred lines (L-142, L-352, L-929, L-966) belonging to the maize germplasm collection from the Federal University of Viçosa was employed in this study. The inbred lines L-142 and L-929 have Flint kernel and were derived from a Flint composite formed from several populations with flint, white, and yellow endosperm originally from Central America, Colombia and Brazil. The lines L-352 and L-966 have Dent kernel and were derived from a Dent composite obtained by crossing samples of white and yellow endosperm maize from Mexico, and Central and South Americas.

The progenies were grown randomly in 25 plant row plots, replicated in two blocks in the Agronomy Field at the Federal University of Viçosa, from March to July/1986. Spacing was 0.20 m within rows 1.00 m apart.

Flowering time, characterized by number of days between the planting and the first exposition of anthers from glumes, was recorded for individual plants, such as used by Rood & Major (1981).

The data analysis were based on the diallel cross method outlined by Hayman (1954a, 1954b). This method makes the following assumptions that must be satisfied: a) homozygous parents; b) diploid segregation; c)no reciprocal differences; d) no epistasis; e) no multiple alleles; and f) uncorrelated gene distributions (Hayman, 1954b). According to Hayman (1954b), the difference Wr-Vr is constant in the several arrays when the method assumptions do not fail. A consequence of this is that the regression coefficient of Wr on Vr is equal to 1. Thus, the assumptions can be tested by testing this coefficient (Hayman, 1954b).

The Hayman's procedure permits valuable genetic information to be drawn not only from the analysis of variance (Hayman, 1954a), but also from graphical analysis and relationships among the parameters D, H_1, H_2, h^2 and F (Hayman, 1954b). Estimates of heritability at broad and narrow sense were obtained according to the procedures described by Mather & Jinks (1982, p.277).

The analysis of variance proposed by Hayman (1954a) permits the quantification of the relevance of additive, dominant and maternal effects in the control of the target character.

In the graphical analysis the regression of Wr (Covariance parent-line) on Vr (Variance within line) permits quantify the degree of dominance as well as the proportion of dominant/recessive alleles in each parent (Hayman, 1954b). The completely recessive parents correspond to points at the upper end of the regression line, and completely dominant parents to points at the lower end where it cuts the limiting parabola (Fig. 1). With no dominance (H_1=0), the regression line will be tangent to the parabola (Fig. 1); with complete dominance (H_1=D),

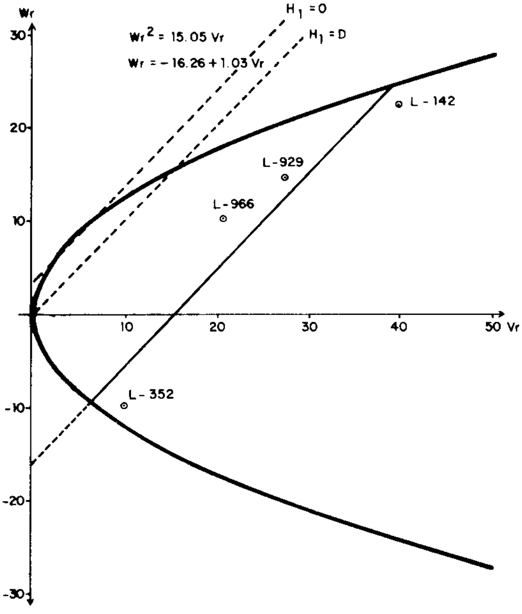

FIG. 1. Wr on Vr graphs and distribution of inbred line points of flowering time in maize.

this line will intercept the Wr axis at the origin; with partial dominance the regression line will intercept the Wr axis above the origin and, with overdominance, below the origin.

From the estimates of the parameters D, H_1, H_2, h^2 and F (Hayman, 1954b), the following genetical information can be obtained:

$(H_1/D)^{1/2}$ - the average dominance degree.

$H_2/4H_1$ - the frequency of positive (late flowering) and negative (early flowering) alleles in the parents. This proportion has a maximum value of 0.25, which occurs when positive and negative alleles are symmetrically distributed in the parents.

$[(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F]$ - the proportion of dominant/recessive alleles in the parents.

h^2/H_2 - the number of genes with some dominance degree.

$(D + H_1 - 0.5H_2 - F)/(D + H_1 - 0.5H_2 - F + 2E)$ - the broad sense heritability.

$(D + H_1 - H_2 - F)/(D + H_1 - 0.5H_2 - F + 2E)$ - the narrow sense heritability.

The Hayman's analysis (Hayman, 1954b) also permits verification of the dominance of positive alleles. This information can be obtained from the correlation coefficient between Wr+Vr and Yr (number of days to flowering). If this coefficient is high and negative, positive alleles are mainly dominant; if positive, alleles are mainly recessive. On the other hand, if this correlation is small, a proportion of positive alleles is dominant and other proportion recessive.

Theoretical selection limits can be obtained substituting the Wr/Vr points of the parents with all recessive alleles (intersection of the parabola with the upper extremity of the regression line) and with all dominant alleles (intersection of the parabola with the lower extremity of the regression line) in the regression equation of Yr on Wr+Vr.

RESULTS AND DISCUSSION

Among the four inbred lines studied, L-352 flowered earlier, while L-142 flowered last (Table 1). The other two, L-966 and L-929, performed intermediately. The F_1's normally flowered earlier than the earliest parent. This finding of heterosis for earliness was also observed by Bonaparte (1977).

Zea mays is a diploid species (Randolph, 1928); the parental lines were homozygous (at least seven selfing generations) and reciprocal differences were not significant (kr^{ns} and krs^{ns}; Table 2) for flowering time. Multiple allelism, correlated gene distributions and epistasis can not be tested individually. The regression coefficient of Wr on Vr (1.03±0.24) differed statistically from zero, but not from 1. Thus, these assumptions are valid and the discussion presented below is acceptable.

The results from the ANOVA presented in Table 2 show that the genetic control of the flowering time in maize is primarily due to additive (jr^{**}) and

TABLE 1. Averages of flowering time in a diallel cross involving four inbred lines of maize. Viçosa, MG, 1986.

Female parents	Male parents			
	L-142	L-352	L-929	L-966
L-142	94.54	80.13	86.67	88.07
l-352	78.17	85.73	80.14	78.95
L-929	84.24	80.89	92.96	84.97
L-966	85.15	79.24	83.21	89.93

TABLE 2. Analysis of variance of the flowering time in a diallel cross involving four inbred lines of maize according to Hayman (1954a). Viçosa, MG, 1986.

Source of variation	Degrees of freedom	Mean square	F^2
Treatment	15	49.72	9.93**
jr	3	90.23	18.02**
jrs	6	75.52	15.08**
l	1	413.85	82.64**
lr	3	7.90	1.58^{ns}
lrs	2	7.80	1.56^{ns}
kr	3	6.79	1.36^{ns}
krs	3	0.53	0.06^{ns}
Error	16	5.01	

[1] jr - mean deviation from the grand mean due to the r^{th} parent.
jrs - remaining discrepancy in the reciprocal sum.
l - mean dominance deviation.
lr - further dominance deviation due to the r^{th} parent.
lrs - remaining discrepancy in the r^{st} reciprocal sum.
2kr - difference between the effects of the r^{th} parental line used as male parent and as female parent.
2krs - remaining discrepancy in the rs^{th} reciprocal difference.

[2] ** - significant at 1% level by F test.
ns - not significant by F test

dominant effects (jrs^{**}). This is in agreement with previous results reported by Hallauer (1965), Bonaparte (1977), Casañas et al.(1989) and Ajala (1992). But dominant effects accounted for a major part of the genotypic variability compared with additive effects (H_1 and $H_2 > D$) (Table 3). This dominance is unidirectional (l^{**}) (Table 1) and the dominant alleles are acting in the direction of earliness and the recessive alleles in the direction of lateness ($r_{(Wr+Vr,Yr)}$=+0.98) (Table 4), such as found by other authors (Jones, 1952; Mohamed, 1959; Bonaparte, 1977; Rood & Major, 1981).

Overdominance is present in the genetic control of flowering time as indicated by the negative intercept of regression line on the Wr axis (Fig. 1) and also by the dominance ratio $H_1/D > 1$ (Table 4). Similar results were also observed by Rood & Major (1981) in other maize populations. In the parents, positive (late flowering) and negative (early flowering) alleles are distributed symmetrically (lrs^{ns} and $H_1/4H_2$=0.25) (Tables 2 and 4). But the proportion of dominant/recessive alleles was 3:4 (Table 4). These apparently contradictory results are possible since the correlation coefficient between dominance and means of the parents, $r_{(Wr+Vr,Yr)}$, was not exactly equal to 1 (Table 4).

As a consequence of the predominance of recessive alleles in the diallel, the majority of the parents on the Wr/Vr graph lies closer to the recessive end (upper extremity) (Fig. 1). Therefore, it is still possible to increase the concentration of dominant (early flowering) alleles in these parents by using appropriate breeding procedures. However, since $r_{(Wr+Vr,Yr)}$ was not exactly equal to 1 (Table 4), some few recessive alleles also contribute towards early flowering and then a procedure that increases the frequency of recessive and dominant alleles, with negative effects, should also be practiced.

TABLE 3. Statistical and genetical parameters estimated in a diallel cross of maize inbred lines of the flowering time. Viçosa, MG, 1986.

Parameter	Estimate
VoLo	15.05
WoLo1	8.91
V1L1	24.52
VoL1	5.64
$(m_{L1} - m_{L0})^2$	38.80
D	12.54 ± 3.33*
H_1	71.24 ± 9.67**
H_2	70.51 ± 8.93**
h^2	153.32 ± 6.05**
F	-8.04 ± 8.55ns
E	2.51 ± 1.49**

ns = not significant by t test.
* = significant at 5% level by t test.
** = significant at 1% level by t test.

TABLE 4. Genetic information concerning the flowering time in inbred lines of maize. Viçosa, MG, 1986.

Genetic information		Estimate
Mean degree of dominance	$(H_1/D)^{1/2}$	2.38
Distribution of early/late flowering alleles in the parents	$H_2/4H_1$	0.25
Distribution of dominant/recessive alleles in the parents	$[(4DH_1)^{1/2} + F]/$ $[(4DH_1)^{1/2} - F])$	3:4
Number of genes	$h2/H2$	2.17
Dominance of late flowering alleles	$r_{(Wr + Vr,Yr)}$	0.98
Limits of selection: - early flowering	Y_D	85.34
- late flowering	Y_R	95.32
Heritability: - broad sense	h_b^2	91.87
- narrow sense	h_n^2	37.67

The number of days for the lines studied to flower is controlled by at least three genes or gene blocks (h^2/H_2=2.17) overdominants (Table 4), in agreement with other authors (Mohamed, 1959; Troyer & Brown, 1972; Rood & Major, 1981).

Theoretically, an inbred line which has only dominant alleles towards early flowering is expected to flower at 85.3 days, while the one with only recessive alleles should flower at 95.3 days after planting. The L-352 inbred line is very close to the earliest flowering extreme, then it is difficult to have lines with earlier flowering than this.

It must be stressed that the selection limit is predicted for parents of maximum homozygosis for dominant or recessive alleles. The fact of certain hybrid populations, namely crosses involving L-142, flower near to 80 days (Table 1) is attributed to the heterosis conditioned by dominant effects, which are not expressed in the inbred lines obtained from the F_2. Then one could not expect lines extracted from F_2 progenies to flower in less than 80 days.

Considering all the diallel crosses, the narrow heritability estimate is low (37.67%) (Table 4). This agrees with the results of other studies (Yang, 1949; Rood & Major, 1981) and indicates that phenotypic selection would be little effective under the conditions of this test.

CONCLUSIONS

1. The number of days necessary to flowering in four inbred lines of maize was observed to be controlled by at least three genes or blocks of genes.
2. Among the inbred lines tested, L-352 presented the greatest number of earliness alleles, and L-142 the greatest number of lateness flowering alleles.
3. Both additive and dominant effects are involved in the control of this character, while maternal inheritance is not.
4. Estimated narrow heritability was low (37.6%), indicating that selection based on the phenotype is little effective, under the conditions of this test.

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