GENETIC ANALYSIS FOR SOME AGRONOMICAL CHARACTERS OF A SUNFLOWER *(HELIANTHUS ANNUUS* L.) DIALLEL CROSS

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INTRODUCTION

In spite of successful selection for high oil content, the main current problem in sunflower — as pointed out by Morozov (1971) – is the improvement of productivity by increasing seed yield. Anaschenko (1974), when comparing the combining ability of source populations found high heritability (from 60 to 86%) for yield. In a diallel cross of seven lines, Rao and Singh (1978) found significant additive genetic variance for capitulum diameter, 1 000-seed (achene) weight and oil percentage. Dua and Yadava (1984) found significant both the dominance and the additive component of genetic variance for plant height, stem diameter, number of leaves and seed yield per plant in a diallel cross of 12 lines and 61 F_1.

The present study was conducted to gain information on genetic control of characters concerning plant development and their correlations with seed yield.

MATERIALS AND METHODS

Seven lines of sunflower, after 5 to 6 generations of selfing, were included in a diallel cross. The number given to each line in Table 1 is used also in graphics for identification purposes. Selfing and crosses were carried out in a growth chamber using the continuous white-light treatment and nutrient stress method (Pistolesi et al., 1986).

A full diallel scheme was set up in three randomized blocks of 980 plants each (20 plants per cross). Randomization was carried out per plot with the aid of random number tables.

The separation between rows was 0.7 m and each row contained 10 plants at 0.2 m intervals. The data collected on each plant following Schneiter and Miller (1981) were :

- *V* : duration (days) of vegetative stage that begins with emergence of the seedling and ends with visual appearance of the inflorescence ;
- $R_1 — R_5$: duration (days) of reproductive stage from visual appearance of the inflorescence to the beginning of anthesis ;
- $R_5 — R_9$: duration (days) of reproductive stage from the beginning of anthesis to the physiological maturity of seeds ;
- *HV* : plant height (cm) at the end of vegetative stage ;
- *HR* : increase in plant height (cm) from the end of vegetative stage to the end of reproductive stage ;

Capitulum diameter (cm) ;

Seed weight per capitulum (g).

The analyses of data were made according to the techniques of Hayman (1954 a ; 1958). For the analysis of the diallel, we used the model proposed by Hayman (1954 b). If maternal and/or reciprocal effects were significant, additive and/or dominance effects were respectively compared with those (a/c and/or b/d) (Mather and Jinks, 1971). Parameters for testing epistasis were estimated according to the model of Mather and Jinks (1971).

Assuming that the parents are homozygous, that there is diploid segregation to prove the independent distribution of genes in the parents, the variance analysis of (Wr — Vr), (Wr + Vr) and the regression of Wr on Vr have been made. If it was possible, the complete diallel analysis of Mather and Jinks (1971) were used to obtain the genetic parameters and Wr/Vr graphs were drawn. Phenotypic and genetic correlations have been calculated following one way analysis of covariance.

RESULTS AND DISCUSSION

In table 1, the average for the measured characters in the parental lines are reported showing that the differences in performance for all seven characters were considerable. In table 2, the results of the analysis of variance are described, from which the following conclusions can be drawn :

Table 1

Mean performance of the seven lines included in the diallel analysis (For legend see Material and Methods)

Lines	Plant development			Plant height		Capitulum diameter (cm)	Seed weight per capitulum, (g)
	V (days)	$R_1 - R_2$ (days)	$R_5 - R_9$ (days)	HV (cm)	HR (cm)		
1. GF	46.27	23.23	47.21	47.67	123.74	19.35	77.58
2. GL	42.27	27.24	53.35	39.50	125.67	21.70	89.73
3. GB	44.33	23.67	47.88	23.00	77.44	16.19	36.53
4. GA	42.71	25.52	47.00	21.11	77.11	17.16	47.24
5. GE	41.52	22,24	52.90	20.01	104.58	17.15	36.59
6. GG	43.04	26.25	48.83	12.49	50.94	15.70	20.52
7. GC	37.00	22.54	42.46	10.72	40.72	14.38	18.52

Table 2

Analysis of variance of a diallel table (For legend see Material and Methods)

Source	D.F.	Mean squares						
		Plant development			Plant height		Capitulum diameter	Seed weight per capitulum
		V	$R_1 - R_5$	$R_5 - R_9$	HV	HR		
a	6	85.25 **	31.05 **	37.32 **	1 544.61 **	10 321.10 **	30.32 **	4 047.58 **
b	21	7.88	2.08	41.20 **	137.39	1 507.94 **	62.85 **	4 610.41 **
b1	1	2.36	9.57	369.39 *	631.29	15 058.50 **	752.88 **	60 864.08 **
b2	6	5.90	1.29	66.18 **	36.18	356.23	10.02	425.94 **
b3	14	9.12	1.88	7.6	145.48	1 033.63	36.20	2 384.92
c	6	3.54	1.16	10.77	22.24	885.61 **	3.92	408.85
d	15	4.88 *	2.00	4.32	79.88 **	263.54 **	14.27 **	818.32 **
t	48							
B	2	31.77 **	1.05	94.61	236.62 **	375.29 **	367.91 **	384.02 *
Ba	12	1.84	1.83	1.33	19.90	45.95	1.18	213.90
Bb	42	1.79	1.92	5.67	7.04	61.77	1.57	180.91
Bb1	2	1.08	0.60	20.79	4.74	19.18	4.38	395.43
Bb2	12	1.76	4.0	8.37	6.27	52.53	0.77	149.24
Bb3	28	1.86	1.10	3.43	7.54	68.77	1.67	179.16
Bc	12	1.60	0.92	4.09	11.73	46.16	1.91	168.49
Bd	30	2.01	0.67	3.84	9.28	44.65	1.90	224.66
Bt	96	1.84	1.39	4.36	9.93	52.49	1.66	197.16
tot.	146							

* Significant at 5% level
** Significant at 1% level

1. The mean squares for *a*, which are equivalent to the mean squares among parents, were significant for all seven characters, thereby illustrating the importance of additive effects.

2. Mean squares values for *b* were significant for the duration of reproductive stage $R_5 - R_9$, for the increase in plant height during the reproductive stage (HR), for the capitulum diameter and for seed weight per plant indicating the presence of dominance.

3. The character "increase in plant" (HR) during the reproductive stage shows the mean square value for *c* (maternal effect) to be significant and all traits except the duration of reproductive phases ($R_1 - R_5$ and $R_5 - R_9$), show the residual from the reciprocal effect *d* to be significant.

The adequacy of the additive-dominance (no epistasis) model of gene action, which is distributed independently in the parent lines was tested by the analysis of variance of (Wr + Vr) and (Wr — Vr) (Table 3) and joint regression analysis of Wr/Vr. The first test, showing homogeneity of both (Wr + Vr) and (Wr — Vr) over arrays for the duration of reproductive

Table 3

Heterogeneity test for (Wr + Vr) and (Wr — Vr) estimates
(For legend see Material and Methods)

Source	D.F.	Mean squares						
		Plant development			Plant height		Capitulum diameter	Seed weight per capitulum
		V	$R_1 - R_5$	$R_5 - R_9$	HV	HR		
Wr + Vr (array)	6	40.55 **	11.47	569.34 **	2 678.96	681 043.00 **	176.94 **	1 372 430.00 **
Wr + Vr (replicates)	14	4.35	7.70	118.98	2 660.23	39 035.10	14.03	55 555.10
Wr — Vr (array)	6	1.01	0.56	29.04	222.01	16 469.70	33.35 **	147 530.00 *
Wr — Vr (replicates)	14	3.12	0.42	14.71	136.08	10 711.00	4.35	42 843.40

stage ($R_1 - R_5$) and plant height at the end of vegetative stage, suggests the existence of a significant additive gene action only.

Furthemore the test shows for duration of vegetative stage (V), duration of reproductive stage ($R_5 - R_9$) and increase in plant height (HR) heterogeneity of (Wr + Vr) and homogeneity of (Wr — Vr) over arrays suggesting the existence of a significant non additive gene action due to dominance gene effects. Finally capitulum diameter and seed weight per capitulum, showing heterogeneity of both (Wr + Vr) and (Wr — Vr) over arrays, indicate the failure of one or more assumptions. The second test shows significant joint regression and non significant heterogeneity of regression for all characters (data not presented), suggesting consistency of regression over the replications. The joint regression coefficients (Table 3) are not significantly different from unity, indicating the absence of epistasis for all characters except capitulum diameter and seed weight per capitulum, where the joint regression coefficients *b* are significantly different from zero as well from unity (data not presented).

a) Duration of vegetative stage (V) and duration of reproductive stage ($R_1 - R_5$)

Table 4 shows that WR/Vr slopes are not different from one. The analysis of variance indicates only additive variation. The estimates of genetic parameters (Table 5) show only *D* to be significant for both characters and the

Table 4

Signification test of joint regression coefficients (b)
(For legend see Material and Methods)

	Plant development			Plant height		Capitulum diameter	Seed weight per capitulum
	V	$R_1 - R_5$	$R_5 - R_9$	HV	HR		
b	0.725	0.906	0.812	1.024	0.828	0.402	0.548
S.E.	0.161	0.101	0.109	0.118	0.091	0.061	0.109
t test #1	1.705	0.928	1.717	—0.199	1.878	9.854 **	4.145 **

Table 5

Estimates of genetic parameters
(For legend see Material and Methods)

	Plant development			Plant height	
	V	$R_1 - R_5$	$R_5 - R_9$	HV	HR
D	7.45 **	4.24 **	13.48 **	184.67 **	1 103.21 **
H1	4.51	2.41	42.94 **	85.62 *	1 055.01 **
H2	3.63	1.22	26.49 **	81.52 *	984.81 **
F	0.51	2.58	27.55	41.12	198.83
E	2.01	1.39	4.36	9.93	52.49
H/D	0.79	0.75	1.78 **	0.68 *	0.98 **
F/DH	0.10	0.57	0.92 **	0.75 **	0.65 **
r	—0.27	0.11	0.79 **	0.38	—0.82 **
Heritability					
Broad sense	0.71 **	0.55 **	0.64 **	0.90 **	0.93 **
Narrow sense	0.57 **	0.46 **	0.10	0.71 **	0.62 **

heritabilities are rather high, in agreement with the important additive effects. The conclusion could be intermediate inheritance (no dominance) for both characters or a very slight partial dominance for duration of vegetative stage (V) because of the significance of Wr + Vr analysis in Table 3 and because dominance *b* was not significant only when compared to reciprocal effects.

The results are similar to those reported by Fick (1978) for flowering dates of several hybrids that have been found intermediate to the two parents, while Unrau (1974) and Putt (1966) suggest that early flowering was dominant over late flowering.

b) **Duration of reproductive stage** (R_5 — R_9)

The second phase of reproductive stage shows a good agreement with the basic assumptions for applying the analysis. The dominant components (*H 1* and *H 2*) were larger than the additive value *D*, indicating the former as the major part of genetic variance as shown by the analysis of variance where b_1 and b_2 are significant.

The regression coefficient *b* of Wr or Vr doesn't differ significantly from unity. The position of the regression line was to the right of origin. This indicates the presence of overdominance, which is in accordance with the result detected from the parameter *H 1/D* reported in Table 5. The graphical analysis of Wr/Vr (Fig. 1) shows that the parent 7 behaved as having the most of recessive alleles as indicated by its position at the end of regression line. Furthemore, the correlation of allelic distribution (Wr + Vr) with phenotypic values of parental lines being negative shows that recessive alleles are of negative sense.

c) **Plant height**

1. Plant height at the end of vegetative stage (HV).

Table 4 shows that the Wr/Vr slope is not different from unity. The analysis of variance indicated additive variation and significant reciprocal effects. Heritability is rather high in accordance with the important additive effects. The conclusion could be no dominance (intermediate inheritance).

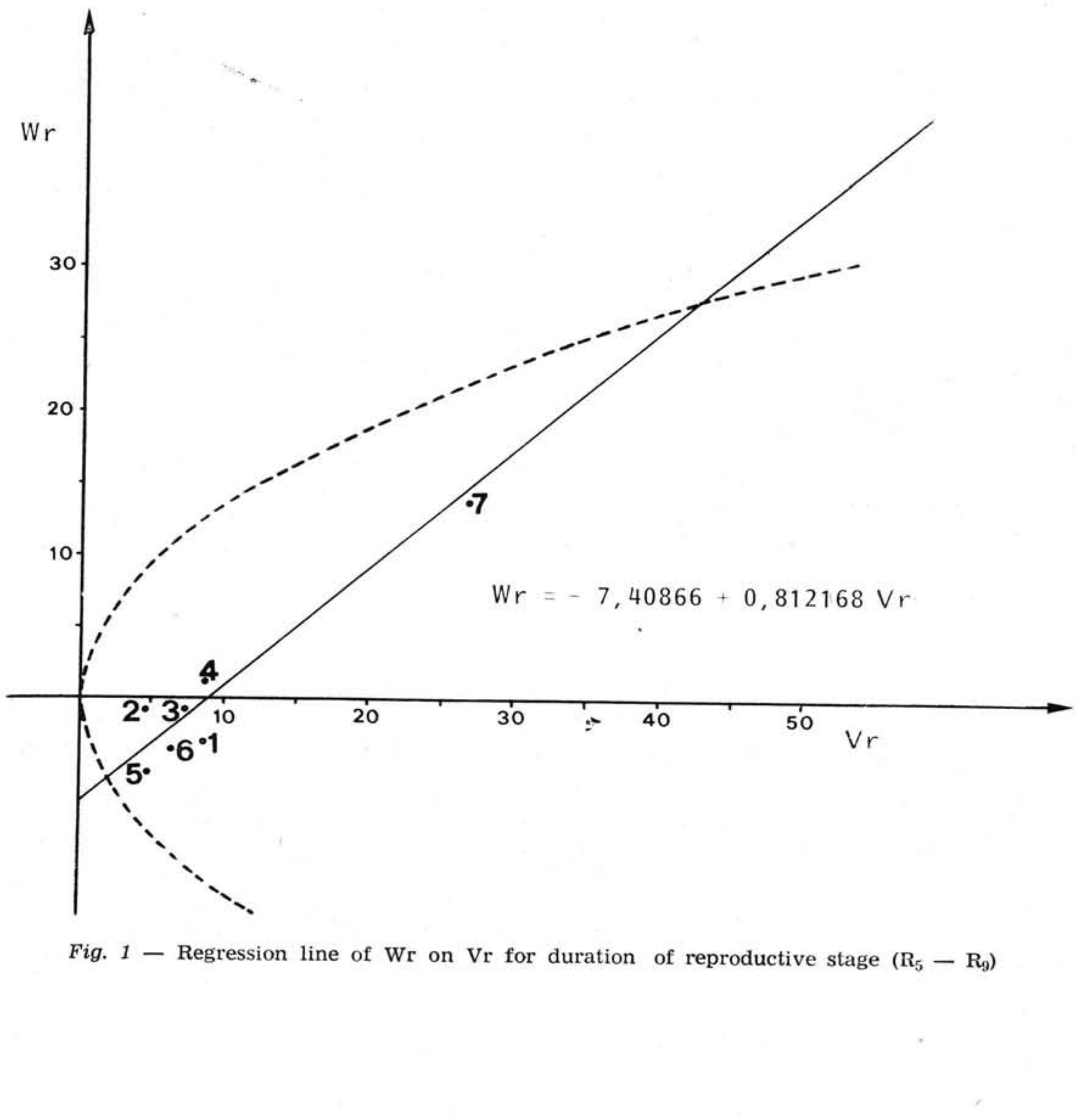

Fig. 1 — Regression line of Wr on Vr for duration of reproductive stage (R_5 — R_9)

2. Increase in plant height from the end of vegetative stage to the end of reproductive stage (HR)

Additivity is again the most important effect. Directional component of the dominance, maternal and reciprocal effects are also significant. Fig. 2 shows the Wr/Vr graph in which the largest values of the character (parents *1*, *2*) are in the zone of dominants confirming partial dominance of positive sense (r = —0.816). Our data are in contrast with many studies (Putt, 1966 ; Berger and Miller, 1984 ; Brigham and Yang, 1985) where the F_1 hybrids were taller than the tallest parent suggesting that heterosis for plant height is common. Furthemore, Fick (1978) reported estimates of narrow sense heritability ranging from 20.4% to 37.5% with an average of 29.6%, whereas we found higher estimates (71%, 62%) for height at the different stages considered.

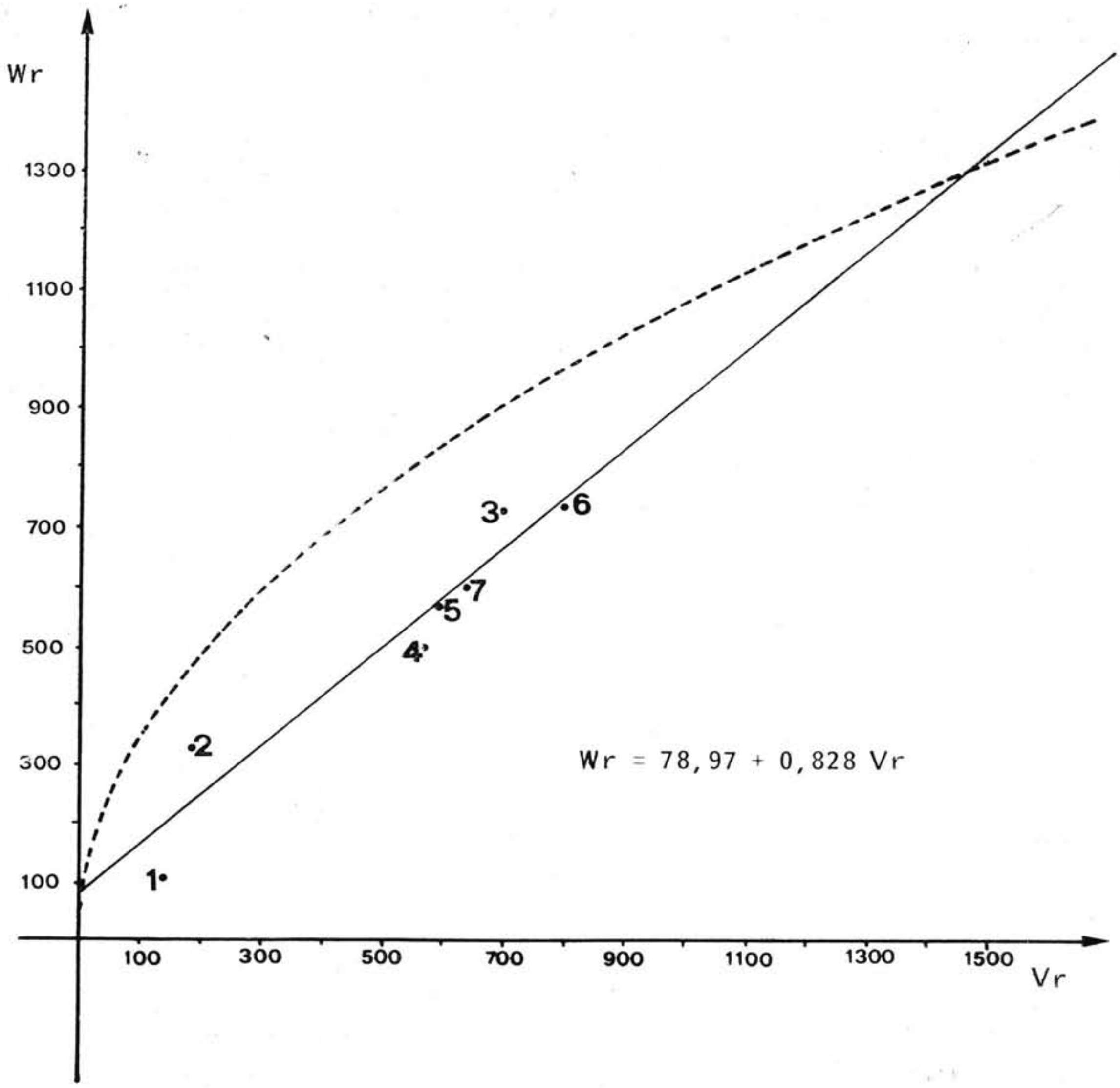

Fig. 2 — Regression line of Wr on Vr for the increase in plant height (HR)

d) **Capitulum diameter and seed weight per capitulum**

Both characters show a similar genetic control based on additivity, dominance effects (Table 2) and a non allelic genetic interaction as resulting from Wr — Vr analysis (Table 3) and from regression coefficients that are significantly different from unity (Table 4).

e) **Phenotypic and genetic correlations**

Table 6 shows that seed weight per capitulum is positively correlated with the duration of vegetative stage, with the duration of reproductive stage ($R_5 — R_9$) corresponding to the grain filling period, with plant height at the end of vegetative stage, with the increase in plant height during the reproductive stage

Table 6

Phenotypic (upper triangle) and genetic (below triangle) correlations

	V	$R_1 - R_5$	$R_5 - R_9$	HV	HR	Capitulum diameter	Seed weight per capitulum
V	—	0.21	0.22	0.62 **	0.55 **	0.44 *	0.51 **
$R_1 - R_5$	0.37	—	—0.08	—0.16	—0.23	0.01	—0.06
$R_5 - R_9$	0.40	0.11	—	0.38	0.64 **	0.64 **	0.47 **
HV	0.67 **	—0.14	0.37	—	0.89 **	0.86 **	0.95 **
HR	0.58 **	—0.27	0.73 **	0.90 **	—	0.89 **	0.89 **
Capitulum diameter	0.49 **	0.03	0.70 **	0.88 **	0.92 **	—	0.93 **
Seed weight per capitulum	0.58 **	—0.05	0.46 **	0.97 **	0.92 **	0.96 **	—

and with capitulum diameter. From the genetic correlations it seems that tall plants would tend to have a greater biomass than short plants and that the amount of biomass might be expected to be correlated with productive potential and final yield. These correlations are contrary to the breeders' aim of short plants (resistant to lodging) with high yield. Furthermore, our results show, as for other crops, that in sunflower the genetic control of the analysed characters depends on the developmental stage being the characters strictly correlated with an agronomic benefit (i.e. seed yield) the most difficult to select for. Therefore, a breeding method to increase seed yield could be the exploitation of allelic and non allelic interactions (the major components of genetic variability for capitulum diameter and seed weight per plant) by hybridization of short statured inbred lines that combine improved tolerance to lodging and stalk breakage with relatively dense planting.

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ANALYSE GÉNÉTIQUE DE QUELQUES CARACTÈRES AGRONOMIQUES DE CROISEMENT DIALLÈLE EN TOURNESOL (*HELIANTHUS ANNUUS* L.)

Résumé

Sept lignées autofécondées de tournesol ont été croisées dans un système diallèle complet afin d'étudier les types d'action génique pour les caractères suivants : hauteur de la plante à la fin des phases phénologiques, la durée des phases phénologiques, le diamètre du capitule et le poids des grains par plante.

Les deux effets additifs et non additifs ont été responsables de variation génétique dans la population diallèle. Cependant, la variation due à la dominance a été plus importante par rapport à la variation additive dans les caractères étudiés pendant la période reproductive. Pour les caractères observés pendant la phase végétative, la variation additive était plus importante. Quant au rendement en graines, les interactions alléliques et non alléliques étaient la majeure partie de la variation. Corrélations phénotypiques et génétiques ont été trouvées et les résultats ont été analysés en relation au stade de développement des plantes. Quelques indications sur les méthodes d'amélioration génétique pour accroître le rendement en graines par unité de surface sont discutées.

ANALISIS GENETICA DE ALGUNOS CARACTERES AGRONOMICOS DE ENCRUCE DIALLELICO EN GIRASOL (*HELIANTUS ANNUUS* L.)

Resúmen

De siete lineas consanquineas de girasol se han efectuado una serie completa de cruces dialelas para estudiar los tipos de accion genica en los caracteres siguientes : altura de la planta al final de las fases fenologicas, duracion de las fases fenologicas, capitulum diametro y peso de la semilla por planta.

Ambos efectos aditivo y no aditivo han sido responsables de variacion genetica en la poblacion dialela. Sin embargo, la variacion de la dominacion fueron mas importantes de la variacion aditiva en los caracteres estudiados durante el periodo reproductivo. Para los caracteres analizados durante la fase vegetativa, la variacion aditiva ha sido mas importante. En cuanto a la produccion de semilla, las interacciones allelicas y no allelicas fueran la mayor parte de la variacion. Correlaciones fenotipicas y geneticas han sido encontradas y los resultados fueron analizados en relacion a la fase de desarrollo de las plantas. Algunas indicaciones sobre los metodos de mejora son discutidos para incrementar la produccion de semilla por unidad de superficie.