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GENETIC ANALYSIS OF SOME PHYSIOLOGICAL CHARACTERS IN RELATION TO PLANT DEVELOPMENT OF A SUNFLOWER (*Helianthus annuus L.*) DIALLEL CROSS.

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SUMMARY

A complete set of diallel crosses between four inbred lines of sunflower has been used to study genetic variability of the following characters: duration of phenological phases, dry matter production in each phase considered, leaf area per plant, seed yield and harvest index. The results obtained indicate that, while the additive genetic component is consistent for the characters collected during the first phases of plant development, the unfixable component of variation is the major part of genetic variability for the characters collected at the end of the onthogenetic cycle, as seed yield and harvest index.

The genetic correlations between seed yield and physiological characters as dry matter production and leaf area, are discussed in relation to the possibility of their use in sunflower breeding programs.

INTRODUCTION

Development of improved inbred lines for hybrid production is one of the most important objectives of sunflower breeding programs. Achene yield is the primary target trait of genetic improvement, but, as in other crops, it is a complex character which depends on many factors and greatly varies with environment (Fick, 1978). Many authors have found the variability for yield production to be dependent on both additive and non-additive gene actions (Stoyanova, 1978; Cecconi et al., 1987; Miller et al., 1980). Genotype-environment interactions also may be important for genetic improvement when particular environments are considered (Dominiques Gimenez et al., 1987).

Several simple plant traits, as leaf area per plant, total dry matter and harvest index have been found to be correlated with achene yield (Škorić, 1974, 1985; Pathak, 1974; Lakshmanrao et al., 1985; Cheervet and Vear, 1990), but few information are available on the genetic control of these characters during the growth of the plant.

The objective of this papaer was to evaluate, within four elite inbred lines of sunflower, the genetic variability of some physiological traits in relation to plant development and to analyze the phenotypic and genetic correlations among them, seed yield and phenological phases.

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MATERIALS AND METHODS

Experimental material was constituted of four inbred lines of sunflower from which a complete diallel set of crosses was obtained. Crosses were made in a greenhouse during the winter 1988, using continuous white-light treatment to induce male sterility (Pistolesi et al., 1986). On April 1988, parents and hybrid combinations including reciprocals were sown at the experiment station of the University of Pisa in three randomized blocks. The experimental unit was a plot of four rows five meters long, the distance between rows was 0.5 meters and plant interval 0.3 meters resulting in a plant density of about seven plants per square meter. Data were collected on the two central rows using a minimum of three plants for each plot.

According to Shneiter and Miller (1981), phenological phases were defined as follows:

V-R1: days from emergence to visible head.

R1-R5: days from visible head to the beginning of flowering.

R5-R9: days from flowering to physiological maturity of seeds.

For each phase the characters analyzed were:

i) Air dry matter production per plant calculated as a difference between data collected at the end and data collected at the beginning of each phase (for identification purpose, in tables are reported D.M1, D.M2 and D.M3, which identify dry matter production in the first, second and third phase).

ii) Leaf area per plant determined by Haiashi Denko electronic planimeter model AAM7 (in tables L.a1 and L.a2 identify leaf area developed at the end of the first and second phase).

Finally seed yield per plant was determined and harvest index calculated.

Statistical analysis of data was done according to the model of Hayman (1954a, 1954b, 1958), the relationships between the variance (Vr) and parent-offspring covariance (Wr) of members of the same half-sib family (array) were used to test the assumptions of the additive-dominance model of gene actions. When the model fits the data collected the regression coefficient of Wr on Vr must be not different from unity and the variance of Wr-Vr values over arrays must be non-significant when compared with the variance over replicate blocks. If both tests were satisfied, the genetic components of variance, the degree of dominance (H/D) and narrow sense heritability (h) were calculated (Mather and Jinks, 1971).

Genetic and phenotypic correlations between characters were calculated using the analysis of covariance (Falconer, 1967).

RESULTS AND DISCUSSION

Genetic variability as it results from the analysis of variance reported in Table 1, is consistent for all the characters considered (significance of "a" and/or "b"). It is interesing to notice that genetic control depends on the developmental stage at which the character is monitored.

Table.1 - Analysis of variance of diallel tables (for legend see Materials and Methods)

Source	d.f.	Mean squares				
		U1-R1	L.A1	D.M1	R1-R5	L.A2
a	3	103.4**	594.6**	2506.1**	32.1**	1305.2*
b	6	5.1	96.3**	286.3**	0.7	1312.7**
b1	1	0.4	248.6*	783.2*	0.8	4889.3*
b2	3	7.7	61.3	249.2**	1.7	446.3**
b3	2	3.7	72.8	93.4	0.1	824.1
c	3	0.6	12.1	11.3	1.4	226.9
d	3	4.9	24.2	86.5	2.3	34.8
Blocks	2	10.5*	19.7	34.3	2.4*	44.1
Bxa	6	2.3	15.8	84.8	1.4	244.5
Bxb	12	2.4	12.6	33.6	0.6	68.8
Bxb1	2	2.5	3.3	21.5	0.3	98.3
Bxb2	6	2.6	5.8	24.3	0.9	21.7
Bxb3	4	2.1	27.4	53.7	0.2	124.6
Bxc	6	1.5	4.5	38.3	0.1	173.6
Bxd	6	3.2	10.7	38.5	0.4	102.7
BI inter.	30	2.4	11.2	45.7	0.6	131.7

Table.1 - (continued)

Source	d.f.	Mean squares				
		D.M2	R5-R9	D.M3	S.YL	H.IN
a	3	4648.7**	28.2	75.6	3764.3**	65.5
b	6	1593.7**	75.3**	237.9**	5932.9**	120.6**
b1	1	5340.1*	182.7*	895.5*	33422.9**	335.2**
b2	3	350.5	87.7*	99.9	511.1	42.4
b3	2	1585.4*	3.2	116.2	320.9	130.5*
c	3	444.7	0.9	29.6	33.4	24.5
d	3	18.0	0.4	64.7	320.9	189.3
Blocks	2	23.9	47.3**	65.2	605.9	35.4
Bxa	6	454.9	3.7	24.9	110.3	60.5
Bxb	12	146.6	10.0	42.6	170.2	21.0
Bxb1	2	182.3	4.0	28.1	38.3	1.8
Bxb2	6	146.1	14.9	51.2	272.6	30.2
Bxb3	4	129.5	5.6	37.0	82.4	16.6
Bxc	6	294.8	7.6	15.4	275.1	14.0
Bxd	6	14.6	4.3	32.4	252.9	86.8
BI inter.	30	237.8	7.1	31.6	195.7	40.6

* Significant at 5%
** Significant at 1%

Duration of phenological phases

The results synthetized in Table 1 indicate that the genetic variability for the duration of the phase of vegetative growth (V-R1) and the phase of flower differentiation (R1-R5) is consistent and determined by the additive genetic effects (significance of "a"), while the genetic control of the duration of grain filling (R5-R9) is based on the dominance effects of allelic interactions (significance of "b"). The relationships between Wr and Vr (Table 2 and Table 3) satisfy the assumptions of the genetic model (see Materials and Methods) for the three characters considered. Genetic components (Table 4) show that heritability is very high for the first two phases which is in agreement with the importance of additive effects, and which indicate the presence of overdominance for the duration of the third phase (H/D > 1).

Table.2 - Analysis of variance of (Wr-Vr) and (Wr+Vr) values

Source	d.f.	Mean squares									
		U1-R1	L.A1	D.M1	R1-R5	L.A2	D.M2	R5-R9	D.M3	S.YL	H.IN
(Wr+Vr)											
Arrays	3	78.53	3931.91	11459	4.82	337352**	275908**	4940**	435828*	29582**	8650*
Replicates	8	26.42	1272.12	38956	1.48	31809	31643	617	106752	2771	2023
(Wr-Vr)											
Arrays	3	1.65	359.71	4062	0.032	16761	4010	71.02	173428**	1237	180
Replicates	8	2.89	132.92	5879	0.212	8510	6136	73.49	32852	786	565

Leaf area

Development of leaf area during the onthogenetic cycle is another important character. The analysis of variance for the data collected at the end of the first phase (Table 1) shows the significance of "a" and "b", furthermore, since the significance of "b" is not confirmed by heterogeneity in the Wr+Vr analysis, additive genetic effects comprise the major source of genetic variability (Table 4). At flowering dominance effects of allelic interactions are the most important source of genetic variability, a similar result has been found by Škorić (1985). The relationships between Wr and Vr are in agreement with the importance of dominance deviations (heterogeneity of Wr+Vr analysis in Table 2) and indicate the adequacy of the genetic model as it results from the homogeneity of Wr-Vr analysis (Table 2) and from the regression coefficient of Wr on Vr significantly different from zero and not different from unity (Table 3).

The analysis of the component of variation reported in Table 4 indicate that phenotypic selection may be useful in improving the development of leaf area at the stage of visible head (heritability of 65%) but this method cannot be used for the same character at flowering when heritability is very poor. However considering that directional dominance effect seems to be significant ("b1" in Table 1) other informations may be obtained: the correlation between Wr+Vr values of half sib families with the phenotypic values of common parents reflects the direction of the dominance; in this case the value is -0.94 (data not reported) indicating that the dominant alleles increase the character.

Air-dry matter production

The variability observed at the end of the first phase is significant only for half sib families ("a" in Table 1), dominance deviations become consistent at flowering as they result from the significance of "b" in Table 1 and from the heterogeneity of Wr+Vr analysis in Table 2. At the end of the onthogenetic cycle, the character shows a variability that does not fit the additive-dominance model of inheritance, the regression coefficient of Wr on Vr is in fact significantly different from unity (Table 3). These results indicate, in agreement with the heritability which is high only when the first two phases of plant development are considered, that the genetic control of the air dry matter production is more complex at the end of the onthogenetic cycle when other sources of variability become consistent. In this case the interactions between genetic sources of variability and blocks (error variances) are homogeneous, indicating the absence of genotype-environment interactions.

Seed yield and harvest index

Considering first seed yield, both additive and non-additive variance appear to be important (significance of "a" and "b" in Table 1). The results reported in Table 2 indicate that the non-additive source of variation is determined by dominance effect of allelic interactions (homogeneity of Wr-Vr analysis and heterogenity of Wr+Vr analysis); this is not different from unity (Table 3). The degree of dominance is 2.69 indicating the presence of overdominance, while heritability is 0.19 (Table 4) which is not very high, but high enough to select lines for general combining ability.

The ratio between seed yield and total air dry matter, is an important index known as harvest index which reflects the assimilation and translocation efficiency of plants. The analysis of data shows a light presence of non-additive genetic variance, the significance of "b" in Table 1 is confirmed by the heterogeneity of Wr+Vr analysis only for $p=0.5$ (Table 2). The absence of non-allelic interaction is in agreement with the Wr on Vr regression coefficient, the result of which is not different from unity (Table 3).

Genetic and phenotypic correlations

The results synthetized in Table 5 indicate that seed yield is positively and strongly correlated with leaf area development and dry matter production in the first and second phase of the onthogenetic cycle. It is interesting to notice also that the genetic correlation with the increment of dry matter production during grain filling is negative. It seems that the photosynthetic activity during the first two phases, when it is setting flower differentiation, is more important than the activity after flowering even if in the third phase the grain filling is realized. This result may be explained by taking into account that grain filling is realized by both redistribution of assimilates from storage sites and by assimilation after flowering (Blanchet and Merrien, 1982; Hall et al., 1989; Dubbelde et al., 1985). The discrimination of these two physiological processes and the relative importance under different environments and different genetic backgrounds are at present a matter of investigation.

Table.3 - "t" test of Wr on Vr joint regression coefficient (b)

	Mean squares									
	U1-R1	L.A1	D.M1	R1-R5	L.A2	D.M2	R5-R9	D.M3	S.YL	H.IN
b	0.783	0.791	1.343	0.772	0.837	0.966	0.923	0.327	0.663	0.836
S.E.	0.126	0.121	0.128	0.134	0.102	0.172	0.134	0.103	0.122	0.165
t (0)	6.190**	6.528**	10.468**	5.746**	8.137**	5.616**	6.889**	3.184	5.434**	5.066**
t (1)	1.742	1.735	-2.656	1.692	1.663	0.197	0.569	6.488**	2.747	0.984

Table.4 - Estimates of variation components

	U1-R1	L.A1	D.M1	R1-R5	L.A2	D.M2	R5-R9	S.YL	H.IN
D	8.07	109.2	601.7	4.95	92.2	5607	24.84	533.4	13.1
H1	2.89	65.1	220.3	0.22	719.3	7706	65.41	3868.9	23.8
H2	2.22	59.9	184.2	0.11	720.1	8121	50.26	3815.1	32.1
F	3.76	17.1	321.2	0.36	25.2	1585	38.52	45.3	0.8
E	2.41	11.3	49.1	0.63	131.7	2378	7.15	195.7	40.6
H1/D	0.59	0.77	0.61	0.21	2.72	1.17	1.62	2.69	1.34
h^2	0.73	0.65	0.63	0.80	0.25	0.47	0.03	0.19	0.05

Table.5 - Phenotypic (upper triangle) and genetic (lower triangle) correlatios

	U1-R1	L.A1	D.M1	R1-R5	L.A2	D.M2	R5-R9	D.M3	S.YL	H.IN
U1-R1	-	0.52	0.35	0.39	0.47	0.53	-0.10	-0.11	0.43	0.48
L.A1	0.51	-	0.90**	0.76*	0.66*	0.66*	0.21	-0.16	0.74*	0.35
D.M1	0.39	0.98**	-	0.80**	0.64*	0.68*	0.32	-0.05	0.67*	0.05
R1-R5	0.36	0.88**	0.92**	-	0.62*	0.67*	-0.02	-0.30	0.50	0.22
L.A2	0.076*	0.94**	0.89**	0.86**	-	0.97**	0.39	0.19	0.88**	0.45
D.M2	0.79*	0.91**	0.87**	0.85**	0.98**	-	0.23	0.11	0.83**	0.38
R5-R9	-0.06	0.21	0.14	-0.26	0.01	-0.04	-	0.58	0.49	0.30
D.M3	-0.10	-0.59	-0.35	-0.29	-0.42	-069	-0.10	-	0.47	0.29
S.YL	0.75*	0.95**	0.90**	0.81**	0.97**	0.98**	0.15	-0.52	-	0.55
H.IN	0.69	0.44	0.33	0.38	0.72*	0.75*	-0.19	0.04	0.69	-

CONCLUSIONS

The results obtained indicate that genetic variability is consistent for all the characters analyzed. As far as the genetic control is concerned, it becomes more complex approaching the end of the onthogenetic cycle when the unfixable component of variation becomes the major part of genetic variability. This is the case with seed yield, dry matter production during the phase of grain filling and harvest index.

The high genetic correlations between seed yield and physiological traits as leaf area development and dry matter production indicate that these characters are important limiting factors by which the efficiency of plant assimilation and translocation may be evaluated. Considering the high heritability of these characters especially during the first phases of plant development, their use in early screening may be useful and economically convenient when a large amount of hybrid combinations are included in selection programs.

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ANALYSE GÉNÉTIQUE DE QUELQUES CARACTÉRES PIIYSIOLOGIQUES EN RELATION AVEC LE DÉVELOPPEMENT DES PLANTES DE TOURNESOL (*Helianthus annuus* L.) ISSUES DE CROISEMENTS DIALELLIQUES

RÉSUMÉ

Un plan complet de croisement diallelique entre quatre lignées de tournesol a été utilisé pour étudier la variablité des caractéres suivants: durée des phases phénologiques, surface foliaire par plante, production de matière séche au cours de chaque phase du développement des plantes. D'aprés les résultats obtenus les composantes génétiques additives sont constantes pendant les premières phases du développement des plantes, des composantes variables constituent la principale part de la variation génétique pour les caractéres étudiés à la fin de la phase ontogénique tel que le rendement en grain et l'index de récolte. La corrélation génétique entre le rendement en grain et les caractéres physiologiques tels que production de matière séche et surface foliaire sont discutés en fonction des possibilités de leurs utilisations dans des programmes de sélection du tournesol.

ANALISIS GENETICO DE ALGUNOS CARACTERES FISIOLOGICOS EN RELACION AL DESARROLLO DE LA PLANTA EN UN CRUCE DIALILO EN GIRASOL (*Helianthus annuus* L.)

RESUMEN

Un dialelo completo entre cuatro líneas de girasol ha sido usado para estudiar la variabilidad genética de los siguientes caracteres: duración de las fases fenológicas, producción de materia seca en cada fase considerada, area foliar por planta, rendimiento e indice de cosecha. Los resultados obtenidos indican que, mientras que el componente genético aditivo es consistente para los caracteres determinados durante las primeras fases del desarrollo de la planta, el componente de variación no fijable constituye la mayor parte de la variabilidad genética para los caracteres determinados al finas del ciclo como rendimiento e indice de cosecha.

Las correlaciones genéticas entre rendimientos y caracteres fisiológicos como produción de materia seca y area foliar, se discuten en relación con la posibilidad de ser utilizados en programas de mejora.