

QUANTITATIVE INHERITANCE IN SUNFLOWER (*Helianthus annuus* L.)

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SUMMARY

This study was conducted in order to estimate the gene effects which determine the inheritance of certain characters and to search the genetic structure of each group in a 9 x 9 diallel cross group established by crossing inbred lines of sunflower. (1) Significant positive heterotic effects were observed for all the characters studied but for different number of crosses. According to the results obtained, two to three parents were observed to be good general combiners for seed yield and eight hybrids were promising crosses for seed yield and plant height. (2) Both additive and dominance genetic variances were significant for all characters. Also, the overall mean dominance effect of heterozygous loci, h^2 was significant for all characters. It was found that positive and negative alleles at these loci were not in equal proportions in the parents (i.e., $H_1 > H_2$). The average degree of dominance showed overdominance for all characters.

Key words: sunflower, *Helianthus annuus*, heterotic effects, combining ability

INTRODUCTION

Breeding of hybrid and synthetic varieties are the most effective methods in utilizing heterosis in sunflower (Gundaev, 1966; Putt, 1966). In the earlier studies, high heterosis for seed yield and some yield components of sunflower were reported by Pogorletskii (1974), Chaudhary and Anand (1984). Heterotic performance of a hybrid combination depends upon combining ability of its parents. Combining ability studies are frequently used by plant breeders to evaluate parents and crosses for a number of objectives, including the development of superior synthetics or hybrids, assessment of gene action involved in various characters so as to design an efficient breeding plan for further genetic upgrading of the existing material. Many breeders have reported that GCA and SCA variances were significant for all characters in sunflower. However, reports on the ratio of GCA and SCA variances are contradictory suggesting a greater proportion of GCA variance (Sindagi *et al.*, 1979) than SCA variance (Setty and Singh, 1977; Kadkol *et al.*, 1984).

The present study was undertaken to provide information on: (1) heterosis, general and specific combining ability; (2) estimation of genetic parameters in hybrid populations of sunflower.

MATERIALS AND METHODS

Nine parental inbred lines were used in this study as the genetic material. These were: (1) IN 973, (2) IN 991, (3) IN 1022, (4) IN 1182, (5) IN 1212, (6) IN 1241, (7) IN 1091, (8) IN 1112 and (9) IN 1132. The parental inbred lines were crossed in all combinations in 1994 and 36 possible F_1 crosses were obtained. The seeds from the 36 crosses and the nine parents were sown in early April, 1995, in a randomized complete block design with three replicates. The field trials were carried out at Bursa (Turkey). Row spacing was 0.70 m, and plot area was 11.2 m² at harvest.

Data were recorded on an individual plant basis for plant height, head diameter, 1000-seed weight, seed yield per plant and seed yield. Preliminary analysis of variance was conducted with the F_1 and parental data to analyze the genotypic and replication effects. Heterosis for the characters studied was measured by comparing each hybrid with its mid-parent value on a plot-mean basis. LSD values were used to test each hybrid-midparent contrast. General and specific combining ability effects and variances were calculated using Model I, Method 2 of Griffing (1956). Genetic parameters were estimated with a method given by Jinks (1954) and Hayman (1954). Heritabilities of each of the five characters were estimated following Mather and Jinks (1971).

RESULTS AND DISCUSSION

Parental performance

Differences among parents were highly significant ($p < 0.01$) for plant height, head diameter and 1000-seed weight, but not for seed yield per plant and seed yield per decar. Replication effects were also highly significant for head diameter, 1000-seed weight and seed yield per plant. Parents 1 and 8 gave the highest yield while parent 5 yielded the lowest. Also, parent 8 showed the highest plant height, head diameter and 1000-seed weight (Table 1).

Heterotic effects

All hybrids except two, 1 x 4 and 2 x 4, showed significant positive heterotic effects for seed yield (Table 1). Also, most of the hybrids gave significant positive heterotic effects for yield per plant, 1000-seed weight and head diameter. However, the hybrids showed both positive and negative heterotic effects for plant height. Especially, hybrids 1 x 7, 2 x 7, 3 x 4, 3 x 6 and 3 x 7 had highly positive heterotic

Table 1: Parental means, F₁ means and deviations (D) of F₁ from mid-parent

Parent and F ₁ 's	Plant height		Head diameter		1000 seed weight		Seed yield per plant		Seed yield per decar	
	M	D	M	D	M	D	M	D	M	D
1	151.0		10.5		46.5		52.4		171.1	
2	121.5		13.6		51.5		52.7		151.0	
3	154.7		11.2		43.5		37.6		141.2	
4	156.6		12.5		26.9		31.7		121.7	
5	135.5		11.0		52.6		31.6		102.4	
6	147.3		13.2		56.0		44.4		134.4	
7	158.4		16.5		48.2		37.9		128.2	
8	170.0		17.0		61.1		48.7		170.5	
9	140.1		17.2		51.7		35.2		131.7	
1 x 2	171.8	35.6*	17.3	5.3*	51.7	2.7	71.5	19.0*	263.7	102.6*
1 x 3	169.9	17.0*	19.4	8.6*	54.5	9.5*	74.1	29.1*	269.1	113.0*
1 x 4	133.7	-20.1*	16.3	4.8*	56.9	20.2*	34.8	-7.3	111.5	-34.9
1 x 5	151.1	7.8	16.7	6.0*	57.4	7.8	55.8	13.8	208.2	71.4*
1 x 6	160.1	10.9	17.3	5.5*	48.1	-3.1	70.4	22.0*	246.5	93.7*
1 x 7	154.1	-0.6	20.0	6.5*	61.2	13.8*	97.7	52.6*	308.2	154.1*
1 x 8	161.7	1.2	20.7	6.8*	57.8	4.0	79.0	28.5*	271.2	100.4*
1 x 9	162.5	16.9*	19.0	5.2*	50.9	1.8	64.7	20.9*	232.6	81.2*
2 x 3	160.2	22.1*	16.4	4.0*	56.3	8.8	74.1	29.0*	267.8	121.7*
2 x 4	152.1	13.1	16.8	3.8*	65.2	26.0*	42.5	0.3	156.4	20.0
2 x 5	141.5	13.0	18.4	6.1*	57.1	5.0	62.1	20.0*	229.9	103.1*
2 x 6	158.6	24.2*	17.7	4.3*	64.2	10.4*	67.0	18.5*	243.2	100.5*
2 x 7	163.2	23.2*	20.2	5.2*	62.6	12.7*	96.7	51.4*	317.0	177.4*
2 x 8	159.3	13.5	17.7	2.2	65.3	9.0	57.5	6.8	223.9	63.1*
2 x 9	157.7	26.9*	17.7	2.3	64.3	12.7*	69.6	25.7*	244.9	103.5*
3 x 4	171.1	15.4	18.1	6.3*	58.5	23.3*	81.5	46.9*	277.4	145.9*
3 x 5	143.8	-1.3	18.3	7.2*	52.1	4.1	66.5	31.9*	242.0	120.2*
3 x 6	167.2	16.2	17.9	5.7*	53.8	4.1	86.4	45.4*	287.5	149.7*
3 x 7	150.3	-6.2	17.8	4.0*	59.2	13.3*	85.3	47.6*	280.9	146.2*
3 x 8	157.0	-5.3	16.4	2.1	44.3	-8.0	73.8	30.7*	264.9	109.0*
3 x 9	160.8	13.4	21.5	7.3*	60.0	12.4*	63.4	27.0*	235.4	98.9*
4 x 5	128.1	-17.9*	16.1	4.4*	55.0	15.2*	59.0	27.4*	225.2	113.1*
4 x 6	170.7	18.7*	19.2	6.4*	55.4	13.9*	54.8	16.8*	213.8	85.7*
4 x 7	136.8	-20.7*	15.1	0.6	51.5	13.9*	53.3	18.5*	206.3	81.3*
4 x 8	172.3	9.0	18.7	3.8*	51.7	7.7	62.5	22.3*	232.0	85.9*
4 x 9	161.6	13.2	20.5	5.7*	55.4	16.1*	58.2	24.8*	215.7	89.0*
5 x 6	149.1	7.7	18.0	5.9*	59.1	4.8	63.9	25.9*	237.9	119.5*
5 x 7	120.6	-26.3*	16.7	3.0*	58.5	8.1	70.7	36.0*	247.9	132.6*
5 x 8	130.3	-22.4*	16.9	2.7	72.0	15.1*	48.6	8.5	199.9	63.4*
5 x 9	134.1	-3.7	19.8	5.7*	81.1	28.9*	47.4	14.0	208.6	91.5*
6 x 7	151.0	-1.8	17.0	2.2	53.9	1.8	73.1	32.0*	262.1	130.8*
6 x 8	162.4	3.7	17.0	1.7	52.3	-6.2	62.9	16.4	236.0	83.5*
6 x 9	156.0	12.3	19.7	4.5*	58.4	4.5	60.4	20.6*	228.0	94.9*
7 x 8	155.7	-8.5	20.4	3.5*	65.0	10.3*	75.9	32.6*	268.6	119.2*
7 x 9	149.3	0.05	18.9	2.1	55.8	5.8	49.7	13.2	203.5	73.5*
8 x 9	159.2	4.2	20.7	3.4*	70.9	14.5*	70.9	28.9*	258.7	107.6*
LSD P<0.005	16.4		2.9		9.1		16.7		50.9	

effects for seed yield and the other characters. Based on the present experimental material, a hybrid program for sunflower seems feasible. These results agree with those of Sing *et al.* (1984) and Giriraj *et al.* (1986) who reported that a high heterosis was obtained for seed yield and some traits in sunflower.

General and specific combining ability, their variances and effects

Highly significant GCA variances were obtained for all the characters observed. The estimates of SCA variances were also significant for four characters, except plant height but the ratios of the GCA to SCA variance were found to be large in all characters except in seed yield per decar (Table 2). Since GCA and SCA provide an estimate for additive and non-additive gene actions, respectively (Sprague and Tatum, 1942), our results were in good agreement with those of Sindagi *et al.* (1979), and Rao (1980), who found that most of the total genetic variability for a number of agronomic characters in sunflower crosses was due to additive gene effects. Results obtained for seed yield correspond to those of Kadkol *et al.* (1984) and Pathak *et al.* (1985) who reported that greater SCA variance was found for seed yield. Only one parent had significant positive GCA effect for seed yield per decare viz; parent 3 (Table 3). On the other hand, only two parents, 3 and 7, showed significant positive GCA effects for yield per plant. Parents 8 and 9 had significant positive GCA effect for 1000-seed weight, out of which parent 9 showed significant positive effect for head diameter also. Parent 6 gave significant negative GCA effect, while parent 8 showed significant positive GCA effect for plant height (Table 2).

Table 2: Estimates of general combining ability effects of the parents and variances

Parent	General combining ability effects				
	Plant height	Head diameter	1000 seed weight	Seed yield per plant	Seed yield per decar
1	3.45	-0.50	-2.90	3.63	5.27
2	-1.95	-0.34	2.39	3.04	4.86
3	5.53	-0.45	-3.43*	6.13*	19.29*
4	0.97	-0.67	-5.45**	-9.35**	-28.50**
5	-14.48**	-0.93	3.09	-6.87*	-17.35
6	3.71	-0.27	-0.56	1.35	2.60
7	-2.82	0.53	0.06	5.94*	14.15
8	6.27*	0.92	3.46*	1.42	9.17
9	-0.68	1.72**	3.34*	-5.28	-9.49
S.E. (gi)	2.88	0.52	1.60	2.94	8.95
Variances					
GCA	437.9**	8.4*	122.0**	360.1**	2637.6*
SCA	121.8	6.4**	61.2**	245.6**	3022.7**
GCA/SCA+	3.6	1.3	2.0	1.5	0.9

*,** Significant at the 5 and 1 % of the probability levels, respectively

+ GCA/SCA is an estimate of the ratio of additive to non-additive gene effects

Data on specific combining abilities of some promising crosses (Table 3) suggested that the hybrids 1 x 7, 2 x 7 and 3 x 4 had highest significant SCA effects for seed yield per decar and seed yield per plant. Also, SCA effect of hybrid combination 4 x 5 were significant for seed yield per decar. Hybrid combinations 1 x 8, 3 x 6 and 3 x 7 showed significant SCA effects for seed yield per plant. These hybrids had no significant, but highly positive SCA effects for seed yield per decar, also. Significant SCA effects were shown by the hybrids 1 x 3 and 1 x 8 for head diameter and 3 x 4 for 1000-seed weight (Table 3).

In general, it is desired to identify parents and hybrids having positive and significant GCA and SCA effects for yield and yield components in hybrid breeding. But, positive combining ability effects for plant height are not desired because of increasing plant height effects. Parents 3 and 7 were observed to be good general combiners for seed yield (Table 2). Eight hybrids were the promising for seed yield and plant height (Table 3).

Table 3: Specific combining ability effects of some promising crosses

Cross	Plant height	Head diameter	1000-seed weight	Seed yield per plant	Seed yield per decar
1 x 3	8.03	3.04*	4.49	9.96	25.02
1 x 7	0.59	2.65	7.69	34.06**	69.26**
1 x 8	-0.91	2.97*	0.89	20.08*	37.23
2 x 7	15.09	2.69	3.80	26.46**	78.46**
3 x 4	11.71	1.91	11.04*	21.83*	67.10**
3 x 6	5.08	1.31	1.45	21.77*	46.10
3 x 7	-5.29	0.40	6.22	21.45*	27.94
4 x 5	-11.28	0.39	1.01	4.80	51.53*

*,** Significant at the 5 and 1% of the probability levels, respectively

Estimation of genetic parameters

Least squares estimates of the genetic variance components are presented in Table 4. D is the component of variation due to additive effects of genes; H_1 is the component of variation of the dominance effects of genes; H_2 is due to dominance effects corrected for gene distribution; F is the mean variance of additive and dominance effects over all arrays; h^2 is the overall mean dominance effect of heterozygous loci.

In the study, D, H_1 and h^2 were highly significant for all the characters. The mean value of the product of gene frequencies of dominant (u) and recessive alleles (v) at the loci showing dominance may be represented by $uv = H_2 / 4H_1$. If $uv = 0.25$, then $u = v = 0.50$, then $H_1 = H_2$ (i.e., the positive and negative alleles at these loci are in equal proportion in the parents). From Table 4, it was apparent that the positive and negative alleles at these loci were not in equal proportions in the parental lines for all the characters (i.e., $H_1 > H_2$). The asymmetry of the distribution of alleles among parents is to be expected and is a consequence of the signif-

Table 4: Components of genetic variation in the 9 x 9 diallel cross in sunflower

Trait	Genetic component					Proportional values				
	D	F	H ₁	H ₂	h ²	(H ₂ /4H ₁)	(H ₁ /D) ⁰⁵	$\frac{(4D+H_1)^{05}+F}{(4D+H_1)^{05}-F}$	h ² /H ₂	Heritability
Plant height	200±40.9**	262.8±79.8**	704.2±114.9**	451.1±136.1**	23.2±7.3**	0.16	1.87	2.08	0.05	0.49
Head diameter	6.7±0.8**	5.7±1.2**	20.4±9.9*	17.6±10.9	18.4±5.6**	0.22	1.74	1.64	1.04	0.64
1000-seed weight	90.7±6.3**	97.1±32.5**	263.1±17.5**	214.8±24.8**	38.4±7.3**	0.20	1.70	1.92	0.18	0.55
Yield per plant	68.4±12.7**	32.1±26.4	924.8±92.2**	791.3±74.3**	99.2±19.1**	0.21	3.67	1.14	0.12	0.56
Seed yield per decar	490.3±51.4**	228.7±203.6	9797.7±881.4**	8709.3±994.9**	402.0±13.4**	0.22	4.47	1.11	0.05	0.42

icant differences among parental genotypes. The significantly positive F values (Table 4) for plant height, head diameter and 1000-seed weight indicated an excess of positive genes for these characters in the parents.

Degree of dominance

The average degree of dominance was estimated by $(H_1/D)^{1/2}$, which showed complete dominance for plant height, head diameter and 1000-seed weight and overdominance for seed yield per plant and seed yield per decar (Table 4). The ratio of the total number of dominant to recessive genes in all the parents was estimated by $[(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F]$. This ratio ranged from 1.11 for seed yield per decar, to 2.08 for plant height. Thus, it can be assumed that the nine parents included in this research carried more dominant than recessive alleles. The ratio of h^2/H_2 estimates the number of groups which control the character and also exhibit dominance to some degree. This ratio is underestimated if the dominance effects of all genes concerned are not equal in size and direction (e.g., cancelling of effects) or if the distribution of the genes is correlated (Jinks, 1954). As Hayman (1954) had pointed out, the groups of genes as defined here have no connection with Mather's (1949) definition of effective factors. Since all of the h^2/H_2 values were less than one and there is significant dominance variation for all of the 5 characters, it can be assumed that there is at least one group of genes showing dominance.

Heritability

Heritability, defined as the ratio of additive and/or additive x additive genetic variance to total phenotypic variance was estimated as suggested by Matter and Jinks (1971). Heritabilities ranged from 0.42 for seed yield per decar to 0.64 for head diameter (Table 4).

These results showed that heritabilities for yield and yield components in the study were middle and high level. Similar types of results were obtained by Shabana (1974).

The diallel crossing method has been applied successfully for selection according to the general and specific combining abilities of the parents and the crosses in breeding of the hybrid and synthetic varieties. For this objective, it is possible to do realistic estimations by using a method given by Griffing (1956). In this study including the nine inbred lines and their crosses, only parent 3 showed significant and positive GCA effects in both seed yield per plant and seed yield per decar. Parents 7 and 8 followed parent 3 in the second degree. On the other hand, GCA variances were found significant in all characters observed and SCA variances were also significant in the other characters except the plant height. The ratios of GCA to SCA variance were higher than 1 in all characters except seed yield per decar. But this ratio was lower than 1 in the seed yield per decar. This state indicated that the SCA variance was more significant than the GCA variance in the seed yield per decar. According to the results, obtained both additive and dominance effects of

genes were significant for all the characters observed. For that reason, the possibility for obtaining a higher yielding hybrid is very high. The hybrids 1 x 7, 2 x 7 and 3 x 4 showed the highest and positive SCA effects for seed yield per decar and seed per plant.

It is possible to estimate different variance components with a method given by Jinks and Hayman for diallel crossing. In this research, D, H, H_2 , F and h^2 components for all characters were found to be statistically significant. These results confirm the results of Griffing Type Diallel Analysis. The heritabilities ranged from 0.42 for seed yield per decar to 0.64 for head diameter.

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HERENCIA CUANTITATIVA EN GIRASOL (*Helianthus annuus* L.)

RESUMEN

El objetivo de este estudio ha sido determinar los efectos de los genes que controlan la herencia de ciertas características, tanto como de investigar la estructura genética de cada grupo dentro de la serie de cruzamientos dialélicos (9 x 9) entre las líneas consanguíneas de girasol. Los resultados han mostrado lo siguiente: 1) se ha determinado el significativo efecto positivo de heterosis para todas las características investigadas, y el número de cruzamientos varía dependiendo de las características. Para dos a tres líneas parentales, se ha determinado que son buenos combinadores generales para el rendimiento de la semilla, y ocho híbridos se han mostrado con perspectiva para el rendimiento de la semilla y altura de la planta; 2) se ha determinado una significativa variante genética agregada y dominante para todas las características, y el efecto total promedio de dominación para los loci de heterocigotos (h^2), también ha sido significativo. Se ha determinado que los alelos positivos y negativos en dichos loci, no han sido representados equivalentemente en los padres ($H_1 > H_2$). El grado promedio de dominación para todas las características, ha sido la súper dominancia.

L'HERÉDITÉ QUANTITATIVE DANS LE TOURNESOL (*Helianthus annuus* L.)

RÉSUMÉ

Le but de cette étude était d'évaluer les effets des gènes qui déterminent l'hérédité de certaines caractéristiques et d'examiner la structure génétique de chaque groupe dans un croisement diallélique (9 x 9) entre des lignes inbred de tournesol. Les résultats ont été les suivants: 1) un effet significativement positif de l'hétérosis a été confirmé pour toutes les caractéristiques examinées, le nombre de croisements variait selon les caractéristiques. Il a été constaté que de deux à trois parents étaient de bons éléments de combinaison pour le rendement en semences, et que huit hybrides promettaient de bons résultats pour le rendement en semences et la hauteur de la plante; 2) les variances génétiques dominantes et additives étaient toutes les deux significatives pour toutes les caractéristiques. La dominance générale moyenne des locus hétérozygotes h^2 était aussi significative pour toutes les caractéristiques. On a constaté que les allèles positifs et négatifs à ces locus n'étaient pas représentés également chez les parents ($H_1 > H_2$). Le niveau moyen de dominance pour toutes les caractéristiques était une surdominance.

