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GENETIC ARCHITECTURE OF YIELD AND ITS ATTRIBUTES IN SUNFLOWER (*Helianthus annuus* L.)

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SUMMARY

Generation mean analysis of eight quantitative traits: days to 50 percent flowering, plant height, stem diameter, head diameter, percent seed set, seed yield/plant, 100 seed weight and oil content in sunflower revealed that all are predominantly under the control of dominant gene effect. Also, digenic epistatic genetic effect were also found to be important in the inheritance of these traits. Therefore, appropriate breeding methods such as reciprocal recurrent selection and biparental mating methods would be needed to improve these traits.

Key words: Generation mean, digenic, epistasis, gene effects.

INTRODUCTION

In India, sunflower is one of the most important and popular oilsed crops in which heterosis is being exploited to the maximum extent. As a result, many high yielding hybrids were developed and released for commercial cultivation. However, there is a considerable need to further enhance crop productivity. A crop improvement program in any crop depends upon information sush as nature of gene action and choice of suitable breeding method and sunflower is no exception. Several biometrical methods have been designed to assess the breeding behaviour of inbreds for polygenic traits such as factorial methods, diallel analysis (Hayman, 1958 and Jinks, 1954) and generation mean analysis (Jinks and Jones, 1958; Hayman, 1958 and Gamble, 1962). However, the traits like yield and its components are groverned by polygenes with complex gene action, and hence understanding the nature and magnitude of gene action helps in selection of an appropriate breeding method. Therefore, in the present investigated the estimation of gene action using generation means will be used. This method not only provides the estimates of additive and

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Table 1: Generation means with standard errors and variances for different characters in the two sunflower crosses

Generation		Days to flowering			Plant height (cm)			Stem diameter (cm)			Head diameter (cm)		
		Mean ± SE	Variance	Var/n	Mean ± SE	Variance	Var/n	Mean ± SE	Variance	Var/n	Mean ± SE	Variance	Var/n
CROSS-1 (CMS-234 x RHA-274)													
P_1	30	65.13±0.72	15.36	0.51	89.16±2.40	172.63	5.75	0.77±0.03	0.03	0.001	8.07±0.30	2.77	0.09
P_2	30	59.63±0.59	10.51	0.35	96.13±2.41	174.33	5.81	0.83±0.05	0.07	0.0023	7.23±0.18	0.98	0.03
F_1	30	55.37±0.59	10.38	0.35	124.23±2.35	165.15	5.51	1.52±0.05	0.06	0.002	13.05±0.33	3.28	0.11
F_2	195	60.56±0.34	22.57	0.12	119.76±1.34	352.16	1.81	1.11±0.02	0.10	0.0005	10.99±0.21	8.30	0.04
B_1	90	63.11±0.56	27.79	0.31	117.33±2.30	476.88	5.30	0.92±0.03	0.09	0.001	10.36±0.28	6.93	0.08
B_2	90	60.71±0.34	10.14	0.11	126.70±1.58	225.38	2.50	1.25±0.03	0.10	0.001	12.64±0.22	4.43	0.05
CROSS-2 (CMS-234 x 6D-1)													
P_1	30	65.13±0.72	15.36	0.51	89.16±2.40	172.63	5.75	0.77±0.03	0.03	0.001	8.07±0.30	2.77	0.09
P_2	30	68.72±0.56	9.51	0.32	102.50±2.46	182.26	6.08	1.47±0.06	0.11	0.004	8.75±0.23	1.39	0.05
F_1	30	61.97±0.44	5.76	0.19	133.67±1.90	108.02	3.60	1.88±0.07	0.15	0.005	14.77±0.32	3.10	0.10
F_2	195	61.84±0.24	11.10	0.06	122.01±1.06	218.30	1.12	1.64±0.02	0.08	0.0004	12.80±0.18	6.26	0.03
B_1	90	60.78±0.30	8.20	0.09	131.83±1.12	112.79	1.25	1.37±0.04	0.18	0.002	13.33±0.25	5.84	0.06
B_2	90	61.56±0.35	10.88	0.12	125.79±1.37	168.44	1.87	0.91±0.02	0.04	0.0004	11.57±0.23	4.81	0.05
CROSS-1 (CMS-234 x RHA-274)													
P_1	30	85.56±1.04	32.64	1.09	15.67±1.24	46.25	1.54	3.64±0.13	0.51	0.017	37.97±0.52	7.98	0.27
P_2	30	83.32±1.18	42.16	1.41	11.01±0.59	10.41	0.35	3.34±0.11	0.34	0.011	38.22±0.47	6.47	0.22
F_1	30	77.82±2.50	188.22	6.27	36.39±2.26	152.78	5.09	5.34±0.19	1.05	0.035	41.67±0.41	4.98	0.17
F_2	195	80.80±0.75	110.45	0.57	20.80±0.88	152.66	0.78	3.82±0.08	1.34	0.0068	39.28±0.27	14.24	0.07
B_1	90	85.76±0.93	20.72	0.23	31.60±1.16	121.51	1.35	3.87±0.06	0.30	0.0033	38.82±0.35	11.22	0.12
B_2	90	88.50±1.50	9.80	0.11	21.47±0.58	30.46	0.34	3.45±0.03	0.11	0.0012	46.41±0.23	4.91	0.05
CROSS-2 (CMS-234 x 6D-1)													
P_1	30	85.56±1.04	32.64	1.09	15.67±1.24	46.25	1.54	3.64±0.13	0.51	0.017	37.97±0.52	7.98	0.27
P_2	30	83.23±1.73	90.00	3.00	12.13±1.08	35.12	1.17	3.05±0.12	0.46	0.015	44.93±0.46	6.24	0.21
F_1	30	84.75±1.37	55.97	1.86	45.78±2.36	167.63	4.59	5.31±0.14	0.63	0.021	46.46±0.56	9.34	0.31
F_2	195	82.36±0.85	141.12	0.72	25.32±0.93	166.95	0.86	4.36±0.08	1.14	0.0058	45.07±0.25	12.23	0.06
B_1	90	90.13±0.48	20.72	0.23	30.33±1.44	186.38	2.07	4.94±0.09	0.75	0.0083	46.20±0.30	8.37	0.09
B_2	90	90.66±0.33	9.79	0.11	22.87±1.05	99.92	1.11	3.75±0.09	0.71	0.0078	41.18±0.53	25.18	0.28

dominance gene effect but also provides the estimates of magnitude of all three types of digenic epistatic gene effects, additive x additive, additive x dominance and dominance x dominance gene effect. Using such estimates, appropriate breeding procedure can be designed to improve different traits of the sunflower crop.

MATERIALS AND METHODS

The material used for this study comprised of parents (P_1 and P_2) and their F_1, F_2, B_1 (F_1 x P_1) and B_2 (F_1 x P_2) generations of two crosses, CMS-234 x RHA-274 and CMS-234 x RHA-6D-1, designed as cross-1 and cross-2, respectively. The B_1, B_2 and F_2 generations were synthesized using F_1 and parents of the two crosses during 1993-94. The six generations of both crosses were evaluated by following randomized block design in three replications during kharif 1994 at GKVK Campus, University of Agricultural Sciences, Bangalore. The parents and F_1 were sown in three row plots three meter long, B_1 and B_2 in five row plots three meter long, and F_2 in ten-row plots three meter long. A spacing of 60 cm between rows and 30 cm between plants within row was maintaned. Fertilizers were applied at the rate of 60N:90P:60K kg/ha. Recomended cultural practices were followed to raise the crop. Observations were recorded for: days to 50 percent flowering, plant height, stem diameter, head diameter, percent seed set, seed yield/plant, 100-seed weight and oil content on ten randomly selected plants in each replication for P_1, P_2 and F_1. Similar observations were recorded by using 50 plants in each replication for B_1 and B_2 and 100 randomly chosen plants per replication in F_2. The data were subjected to six-generation mean analysis (Jinks and Jones, 1958). The regular notations used to calculate various gene effect in this study were used (Hayman, 1958). Analysis of variance was also estimated (Panse and Sukhatme, 1961).

RESULTS AND DISCUSSION

The mean, standard error of mean and variance of two parents and four generation (F_1, F_2, B_1 and B_2) of the two sunflower crosses, CMS-234 x RHA-274 and CMS-234A x RHA-6D-1, for the respective eight characters is presented in Table 1. It was observed that the hybrids completed flowering earlier than both parents in both crosses. The hybrids exibited superiority over the parents for the rest of the caracters in both crosses, except for percent seed set. The cross CMS-234 x RHA-6D-1 was intermediate to both parents with respect to percent seed set, while the other cross, CMS-234 x RHA-274, was inferior to both parents.

Analysis of variance (Table 2) indicated that the three parents involved in both crosses were significantly different for all the characters, except for head diameter and percent seed set. The two crosses were found to be significant from each other for all the characters, except 100-seed weight. Among the segregating generations, the F_2 generations of both crosses were found to be highly variable for all the characters except

Table 2: Analysis of variance for eight characters in two sunflower crosses

Source of variation	d.f.	Days to flowering	Plant height (cm)	Stem diameter (cm)	Head diameter (cm)	Seed set (%)	Seed yield per plant (g)	100-seed weight (g)	Oil content (%)
I Replication	2	0.36	3.77	0.004	0.27	1.52	1.64	0.02	0.27
II Treatment	10	33.25**	652.88**	0.42**	15.99**	46.30**	334.91**	1.90**	36.67**
(a) Non-segregating		78.46**	1081.18**	0.74**	30.61**	27.43**	754.83**	3.67**	44.29
i)Parents		63.01**	133.43**	0.50**	0.68	5.22	17.73**	0.27**	46.76**
ii)Hybrids (F_1)		65.34**	133.48**	0.19**	4.42	72.10**	132.30**	0.001	34.42**
iii) Parents vs hybrids	1	122.49**	3924.38**	1.78**	116.67**	27.19**	2851.57**	14.15**	49.23**
(b) Segregating	5	2.82**	82.91**	0.24**	4.04**	51.08**	63.68**	0.84**	36.34**
i) F_2s	1	2.45**	7.59	0.43**	4.94**	3.65	30.80**	0.43**	50.35**
ii) Backrosses	3	3.74**	108.30**	0.16**	5.08**	14.48**	79.29**	1.25**	42.52**
iii) F_2s vs backrosses	1	0.47	82.03**	0.28**	0.03	208.30**	49.24**	0.03	3.80**
(c) Non-segregating vs segregating	1	4.51**	1783.53**	0.05**	17.32**	97.88**	11.83**	0.09	7.84**
III Error	20	0.037	10.37	0.002	0.21	2.47	1.80	0.04	0.42
CD at 1%		0.86	4.54	0.07	0.65	2.21	1.89	0.28	1.34
SEm		0.35	1.86	0.03	0.27	0.91	0.78	0.11	0.38
C.V. (%)		0.98	2.75	4.00	4.09	1.85	5.41	4.80	1.54

** $p < 0.01$; * $p < 0.05$

plant height and percent seed set; whereas, the backcross generations of the two crosses significantly differed from each other for all the characters studied.

Table 3: Scaling tests for the eight characters in sunflower crosses

Se.No	Character		Scaling test		
			A	B	C
1.	Days to flowering	C-1	5.72**	6.42**	6.74**
		C-2	-5.54**	-7.59**	-10.46**
2.	Plant height	C-1	21.27**	33.03**	45.27**
		C-2	40.83**	15.41**	29.04**
3.	Stem diameter	C-1	-0.46**	0.15	-0.21
		C-2	0.09	-0.39	4.85**
4.	Head diameter	C-1	-0.41	4.41**	1.94
		C-2	3.83**	-0.39	4.85**
5.	Percent seed set	C-1	8.14**	16.17**	-1.30
		C-2	9.94**	13.33**	-8.84
6.	Seed yield per plant	C-1	11.15**	-4.48	-16.28**
		C-2	-0.78	-12.16**	-18.06**
7.	100-seed weight	C-1	-1.24**	-1.77**	-2.39**
		C-2	0.92**	-0.86**	0.11
8.	Oil content	C-1	-1.99*	12.92**	-2.40
		C-2	7.97**	-9.04**	4.48**

** $p<0.01$ C-1 - CMS-234 x RHA-274
* $p<0.05$ C-2 - CMS-234 x 6D-1

Scaling tests (Table 3) revealed that there is no reason to belive that only additive-dominance model is adequate in explaning the inheritance of all characters as evident from significance of at least one the three scales. This indicated the involvement of other parameters, such as digenic epistatic gene effects, in the inheritance of these traits. Hence, perfect fit solution was used to estimate the magnitude and direction of digenic epistatic effects (Jinks and Jones, 1958). It could be noticed from the gene effects (Table 4) that in the case of the cross-1, both the main genetic effects (additive and dominance) and epistatic genetic effects (additive x additive and dominance x dominance) were involved in the inheritance of days to flowering. Estimates of dominance and dominance x dominance genetic effects observed in the negative direction suggested that the alleles for earliness were more frequent and dominant over the alleles for lateness. Although the estimates of both dominance (h) and dominance x dominance (l) gene effects are in the same direction, all genes for this character complement each other and it could be responsible for the earliness of the hybrid. In cross-2, a significant additive x additive genetic interaction effect in negative direction was recorded despite a non-significant additive genetic effect indicating favorable epistasis among the alleles with additive effects at different loci controlling this character. In addition, this trait also sems to be controlled by dominance and dominance-based gene interaction (dominance x dominance)

Table 4: Gene effects for eight characters in two crosses of sunflower

Se.No.	Character		Gene effect						Type of epistasis
			$\hat{m}$	$\hat{d}$	$\hat{h}$	$\hat{i}$	$\hat{j}$	$\hat{l}$	
1.	Days to flowering	C-1	60.56	2.40**	-1.61**	5.41**	-0.35	-17.55**	Complementary
		C-2	61.84	-0.78	-7.64**	-2.68*	1.02	15.81**	Duplicate
2.	Plant height	C-1	119.76	-9.37**	40.61**	9.03	-5.88	-63.33**	Duplicate
		C-2	122.01	6.04**	65.04**	27.20**	12.71**	-83.45**	Duplicate
3.	Stem diameter	C-1	1.11	-0.33**	0.66**	-0.08	-0.30**	0.39	Complementary
		C-2	1.64	0.46**	-1.26**	-2.02**	0.81**	3.46**	Duplicate
4.	Head diameter	C-1	10.99	-2.29**	7.16**	2.06	-2.41**	-6.06**	Duplicate
		C-2	12.80	1.77**	4.96**	-1.40	2.11**	-2.05	Duplicate
5.	Percent seed set	C-1	80.84	-2.90	18.99**	25.62**	-4.02**	-49.93**	Duplicate
		C-2	82.36	-0.53	32.47**	32.11**	-1.69	-55.39**	Duplicate
6.	Seed yield per plant	C-1	20.79	10.14**	46.00**	22.96**	7.82**	-29.63**	Duplicate
		C-2	25.32	7.46**	36.99**	5.11	5.69**	7.84	Complementary
7.	100-seed weight	C-1	3.82	0.42**	1.23**	-0.62	0.27**	3.63**	Complementary
		C-2	4.36	1.19**	1.91**	-0.06	0.89**	0.01	Complementary
8.	Oil content	C-1	39.28	-7.58**	16.92**	13.34**	-7.46**	-24.27**	Duplicate
		C-2	45.07	5.02**	-0.53	-5.54**	8.50**	6.61**	Duplicate

** p<0.01; *p<0.05

with a greater magnitude than that of additive x additive interaction effects.Thus, days to flowering appeared to be controlled by both additive and dominant genes with a preponderance of dominant gene action. Similar results were also reported (Alba *et al.*, 1985); while additive genes govering this trait were reported by Beretta *et al.*, 1985. Therefore, reciprocal recurrent selection will be more useful for improving this trait as it would exploit both additive and dominance genetic effects.

In both crosses plant height was observed to be predominantly controlled by dominant gene action as evident by the greater magnitude of dominant gene effects compared eith additive gene effects. Further it was noticed that dominance x dominance epistatic gene effect was also important in the inheritance of this trait in both crosses. The results obtained on sunflower by other workers are in accordance with the results of the present study (Lay and Khan, 1985; Singh *et al.*, 1989 and Miller and Hammond, 1991).

Both additive and dominant gene effects were equally important in the inheritance of stem diameter in cross-1. The negative alleles were found to be more frequent than positive alleles as indicated by the estimate of additive gene effects in the negative direction. In contrast to this, positive alleles for stem diameter were found to be more frequent than negative alleles in cross-2.

Predominance of non-fixable genetic effects, dominance and dominance-based epistatic gene effects (additive x dominance and dominance x dominance) were noticed for head diameter in both crosses. However, the preponderance of the additive gene action for this trait in sunflower was reported by Singh *et al.*, 1989.

Non-fixable genetic effects (dominance and dominance x dominance) were found to be prevalent in govering percent seed set. Although the fixable main genetic effects (additive) was non-significant, a significant and higher magnitude of additive x additive gene effects was noted which could have resulted from a favorable interaction among the genes controlling this trait.

Both additive and dominant gene action were involved in the inheritance of 100-seed weight. However, dominant gene action was found to be prevalent as revealed from the greater magnitude of dominant gene effects than additive gene effects in both crosses. Since both dominant and dominance x dominance gene effects are in the same direction, it follows that dominance at individual loci complement each other resulting in an increased manifestation of this trait in the F_1, F_2, B_1 and B_2 generation.

Seed yield per plant also appeared to be predominatly under control of dominant gene effects in both crosses as seen in 100-seed weight. Further, in cross-1, the magnitude of the fixable component of genetic effects (additive and additive x additive) was considerably higher than in cross-2, thus indicating the involvement of both fixable and non-fixable genetic effects. These results are in accordance with the earlier findings of Pathak *et al.*, 1985. In contrast to this, additive genes govering this trait have also been reported (Sheriff and Appadurai, 1985 and Singh *et al.*, 1989). However, in cross-2, the magnitude of fixable component of gene effect was not that pronounced. Therefore, the parents of the cross-1 could be improved by following reciprocal recurrent selection which exploits both additive and non-additive gene effects or through biparental mating method. The parents of cross-2 could be improved through recurent selection for specific combining ability which exploits non-additive gene effects.

Involvement of both additive and dominance gene effect was found to be responsible for the intheritance of oil content in cross-1. However, additive gene effects in the negative direction suggested that the genes responsible for lower oil content seemed to be more frequent. In spite of this, the higher magnitude of dominant gene effects than additive gene effects indicated the predominance of dominant gene action. Dominant gene action govering this trait in sunflower has been reported by Ananda Rao, 1979. Hence, recurrent selection for specific combining ability would be an appropriate breeding method to improve this trait. In contrast to cross-1, fixable effects of genes seemed to control the inheritance of oil content in cross-2. Similar findings have been reported by Sundhakar, 1979. Breeding methods such as mass selection or recurrent selection for general combining ability or biparental mating would lead to the accumulation of favorable alleles controlling this trait.

Thus, it can be concluded that merely the additive-dominance model was not adequate in explaining the differences between various generation means. In addition to the prevalence of dominance gene effect, digenic epistatic effects were also found to be important in the inheritance of all the characters studied.

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ARQUITECTURA GENETICA DEL RENDIMIENTO Y SUS ATRIBUTOS EN GIRASOL *(Helianthus annuus* L.)

RESUMEN

El análisis de generaciones medias de ocho caracteres cuantitativos: días a 50% floración, altura de planta, diámetro del tallo, diámetro del capítulo, porcentaje de semilla llena, rendimiento por planta, peso de 100 semillas, y contenido de aceite en girasol reveló que todos ellos están predominantemente bajo control de efectos génicos dominantes. También fueron encontrados importantes, en la herencia de estos caracteres, los efectos genéticos epistáticos digénicos. Por tanto métodos de mejora apropiados tales como la selección recurrente recíproca y cruces biparentales serían necesarios para mejorar estos caracteres.

FACTEURS GÉNÉTIQUES CONTRÔ1ANT LE RENDEMENT ET SES COMPOSANTES CHEZ LE TOURNESOL (*Helianthus annuus* L.)

RÉSUMÉ

L'analyse des valeurs moyennes de huit variables quantitatives: nombre de jours à 50% de floraison, hauteur de la plante, diamètre de la tige, pourcentage de fructification, production de grains par plante, poids de 100 grains et teneur en huile du tournesol révèlent qu'elles vent principalement contrôlées par des gènes à effets dominants. De même, les effets génétiques épistasiques bi-factoriels se révèlent importants dans le contrôle de l'hérédité de ces caractères. Par conséquent, des méthodes d'amélioration appropriées telles que la sélection récurrente réciproque et les méthodes de reproduction bi-parentales seraient nécessaires pour améliorer ces caractéristiques.