Fick attributed the differing results of various attempts to define genetic effects of flowering date to the different parental lines involved (3), and our results support this

explanation.

These results suggest that selection for early flowering sunflower lines under short-day conditions would be at least moderately successful. The degree of success would depend on the specific selection of parental lines. Selection for moderate — to late —flowering lines could be more difficult, particularly if one or more of the parental lines responded to long-day photoperiod.

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EPISTATIC GENE ACTION IN SUNFLOWER — A CAUTION TO SUNFLOWER GENETICISTS AND BREEDERS.

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ABSTRACT

The three epistatic types of gene action viz., additive x additive (i), additive x dominance (j) and dominance x dominance (1) are usually involved to a lesser extent than the additive (d) and dominance (h) types of gene action in the inheritance of quantitative characters. But, an investigation into the genetics of 12 quantative characters in sunflower involving seed yield, its components and vegetative characters, by a 10×10 diallel analysis (Hayman, 1954) and six generation mean analysis (Jinks and Jones, 1958) of 25 crosses revealed a different trend. For all the characters, the former method indicated epistasis while the latter showed '1' as the most important type of gene action. Though 'h' was next in the order of merit, the other two epistatic components 'i' and 'j' were observed to have been involved to a greater extent than 'd' for seven to eight characters. Thus, it appears safer for the geneticists and breeders meddling with sunflower to make room for epistasis in planning their experiments.

INTRODUCTION

Even a cursory glance at the sunflower literature reveals a strange fact that though the progress in sunflower breeding has been satisfactory, there is not much information accumulated on the genetics of the crop. There is thus, need in sunflower, for methods of genetic analysis that would provide ample information on genetics in a minimum time possible, so that, any breeding programme could be given a proper orientation in the initial stages itself depending on the genetic architecture of the base material. Diallel analysis which requires only parents and their all possible F1s is one such method. But it works only under certain assumptions with regard to the genetic constitution of the material under study; one of the important assumptions being 'absence of epistatic gene action'. Theoretically speaking (Falconer, 1975) epistasis is not much involved in comparison with additive and

dominance types of gene action in quantitative genetics and consequently the diallel analysis should usually work. This investigation was hence planned to know the applicability of diallel analysis to sunflower. In planning so, care was taken to carry the material forward to further generations to estimate epistasis, in case the diallel analysis were to reveal such a type of gene action.

MATERIALS AND METHODS

Ten inbred lines with wide genetic diversity were crossed in all possible combinations to get the 45 F₁s. For 25 of these 45 F₁s, seeds for the F₂, B₁ and B₂ generations were also obtained by selfing and back crossing. These 25 crosses involved all the ten parents. This experimental material was grown in a randomized block design with three replications.

Observations were recorded on twelve characters viz., number of leaves, leaf length, leaf breadth, petiole length, stem girth, plant height, head diameter, head weight (dry), number of seeds per head, hundred seed weight, seed yield and S/H estimate (proportion of seed yield to head weight) on five randomly selected plants in case of parents and F₁s and on all the plants in case of F₂s, B₁s and B₂s. Measurements of the leaf length, leaf breadth and petiole length were to be recorded after blooming so as to allow maximum growth of the leaves. By then, most of the lower leaves were dried up, hence seventh leaf from the top which had not yet dried in any

of the plants was used for recording these three observations. Analysis of variance (ANOVA) was carried out by the method of Panse and Sukhatme (1961) while the method of Hayman (1954) was followed for diallel analysis. The components of means using the data from six generations i.e., Parent 1 (P1) Parent 2 (P2), F1, F2, B1 and B2 of 25 crosses were estimated by the generation mean method of links and were estimated by the generation mean method of Jinks and Jones (1958) and Hayman (1958).

RESULTS AND DISCUSSION

The ANOVA is presented in Table 1. The 'treatments' were further partitioned in to all possible sources but only the information required for this paper is given in the table. The mean sum of squares due to parents and due to F1s were significant for all the twelve characters confirming the genetic diversity among the parents and consequently their suitability for a genetic study.

Table 1. Analysis of variance for twelve quantitative characters in sunflower⁺.

Source of variation	Degrees of freedom	Mean sum of squares					
		Number of leaves	Leaf length	Leaf breadth	Petiole length	Stem girth	Plant height
Replications Treatments Parents Direct F ₁ s Error	2 194 9 44 388	64.67** 25.26** 22.96** 29.39** 3.47	22.38** 42.66** 20.36** 27.57** 2.96	7.58 50.74** 17.62** 32.83** 3.55	2.27 13.62** 14.69** 16.87** 2.81	0.36** 0.44** 0.17** 0.22** 0.04	110.07 1184.88** 1255.47** 719.74** 346.20
Table 1. Contd	l .						
Source of variation	Degrees	Mean sum of squares					
	of freedom	Head diameter	Head weight	Number of seeds	Hundred seed weight	Seed yield	S/H estimate
Replications Treatments Parents Direct F ₁ s Error	2 194 9 44 388	13.54** 28.51** 10.35** 14.76** 2.07	103.02** 1449.07** 344.32** 1246.96** 16.73	10668.93* 161071.64** 20433.22** 197465.88** 2545.90**	0.87** 3.86** 3.48** 2.40** 0.09	122.67** 797.62** 116.62** 801.99** 8.43	0.01** 0.02** 0.01** 0.14** 0.00

The regressions (b) of W_r (Covariance of parents and their offspring in the rth array) values on V_r (variance of rth array) values computed for different characters in the diallel analysis are given in Table 2. For all the characters, the b values were significantly away from unity revealing the involvement of epistatic gene action.

Table 2. Regresson (b) of V_r values of W_r values for twelve quantitative characters in a diallel analysis of sunflower.

Character	$v(V_r, W_r)$	Characters	$b(V_r, W_r)$
Number of leaves	0.59 ± 0.18 0.29 ± 0.21	Head diameter	0.22 ± 0.18
Leaf length Leaf breadth	0.29 ± 0.21 0.16 ± 0.20	Head weight Number of seeds	0.08 ± 0.03 -0.01 \pm 0.03
Petiole length	0.49 ± 0.18	Hundred seed weight	0.34 ± 0.26
Stem girth Plant height	$0.44 \pm 0.24 \\ 0.17 \pm 0.26$	Seed yield S/H estimate	-0.05 ± 0.02 -0.12 ± 0.14

The A, B, C scaling tests of generation mean analysis also revealed the operation of epistasis for all the characters. *The gene effects (components of means) i.e., the effects of additive (a), dominance (h), additive x additive (i), additive x dominance (j) and dominance x dominance (l) types of gene action for different characters are summarised in Table 3. The number of crosses for which a particular gene effect was significant and the magnitudes of gene effects in different crosses revealed the relative importance of different types of gene action. Based on these two criteria, the sequence of gene effects in the decreasing order of their importance were as follows for different characters:

characters. : l - h - j - i - d: l - h - i - j and d+: l - h - d - i - j: h - l - i - j - d: l - h - i - d - jNumber of leaves Leaf length Leaf breadth Petiole length Stem girth

Plant height Head diameter Head weight : h - l - i - j - d : h - l - i - j - d : l - h - d - i - j Number of seeds : l - h - d - i - jHundred seed weight: l - h - j - d - iSeed yield : h - l - i - j and : h - l - i - j and d+: l - h - j - i - d S/H estimate

*The details are not given as it needs a lot of space to cover the A, B and C values of 25 crosses for 12 characters. + j and d were of equal importance

Thus, in general, dominance x dominance (1) epistasis was most important, dominance (h) occupying the second rank. The third and fourth in importance were again the epistatic components additive x additive (i) and additive x dominance (j), additive gene action (d) being placed in the last position.

⁺ Sources of variation required for the present discussion only are given.

^{*} Significant at five per cent level of probability. ** Significant at one per cent level of probability.

Table 3. Summary of genetic components of means in 25 crosses of sunflower for twelve quantitative characters.

Character	First row Second row	: Number	component of crosses of crosses	in whic	h significa	nt de is highest
	đ	h	i	j	1	
Number of leaves	10	12	9	13	12	
	Nil	8	2	2	13	
Leaf length	11	20	12	11	19	
-	Nil	8	Nil	Nil	17	
Leaf breadth	14	18	13	11	19	
	Nil	10	Nil	Nil .	15	
Petiole length	10	21	13	10	11	
	Nil	11	.2	2	11	
Stem girth	10	19	12	5	16	
	Nil	8	Nil	Nil	17	
Plant height	16	21	12	15	16	
	Nil	12	Nil	3	10	
Head diameter	9	22	15	9	12	
	Nil	18	Nil	3	4	
Head weight	8	21	15	13	19	
	Nil	13	1	2	9	
Number of seeds	16	21	15	12	18	
	Nil	8	Nil	Nil	17	
Hundred seed weigh		20	12	20	19	
~	Nil	7	Nil	2	16	
Seed yield	9	23	12	9	14	*
G/TT	Nil	14	1	Nil	10	
S/H estimate	12	11	10	12	11	
	Nil	5	1	1	18	

As mentioned earlier, there are not many attempts in sunflower to study genetics exclusively. The breeding programmes might have involved the estimation of general and specific combining abilities which do not provide a clear Velkov, 1970; Rao and Singh, 1977 and Dua, 1980), only additive and dominance types of gene action were reported for some characters. But, in the present study, the epistasis indicated by the diallel analysis was confirmed by generation mean analysis. So, one suggestion is that until a large number of studies are reported on the genetics of the crop to provide a general idea about its genetic architecture, it is necessary to plan any future genetic study with methods capable of estimating epistasis in addition to additive and dominance estimates. The alternative suggestion possible is to carry out diallel analysis involving parents selected at random (random effects model) from the world germplasm of sunflower so that the results are applicable to the whole germplasm. Though this sounds nice theoretically, its practicability is not definite; the former suggestion hence seems to be appropriate. If the future breeding programmes are preceded by such genetic studies to follow the appropriate breeding procedures depending on the relative importance of additive, dominance and epistatic types of gene action, the new achievements in sunflower breeding could be made faster than in the past.

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