

Breeding to Dissect Genetic Components of Yield and its Contributing Traits in Safflower (*Carthamus tinctorius* L.) through Generation Mean Analysis

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Abstract

Safflower is an oilseed crop with good content of polyunsaturated and monounsaturated fatty acids. Understanding the genetic components of safflower help breeders to decide proper breeding method for improvement of the crop. Six parameters model generation mean analysis was performed for 30 different genotypes consisting of 6P₁, 6P₂, 6F₁, 6F₂, 6BC₁ and 6BC₂. Scaling test was performed for eleven characters of all the six crosses. The result found the presence of non-allelic interaction for almost all the characters studied. Dominance × dominance interaction was found to be mostly dominant for almost all the characters. Higher value of non-fixable gene effect was present as compare to fixable gene indicating the presence of higher contribution of non-additive gene effect suggesting the possibility for improvement of the trait through recurrent selection. The study clearly suggests the effectiveness of heterosis breeding and recurrent selection for improvement of yield and its contributing traits.

Introduction

Safflower is an important oilseed crop which is mostly neglected due to its morphological features. While advanced studies have been done in other major oilseed crops like soybean, groundnut, mustard, etc. more understanding and evaluation of genetic components and inheritance pattern of the qualitative and quantitative characters needs to be done for Safflower (Devi et al. 2022). Presence of high amount of polyunsaturated fatty acid and monounsaturated fatty acid makes the plant a potential oilseed crop. Even with high amount of linoleic and oleic acid content, the cultivation and improvement of safflower is still a long way to go. Proper breeding methods are needed for improvement of the crop. Knowing best method for improvement of the crop is necessary to improve yield and other important characteristics. Study on genetic components like additive and dominance component help in understanding trait gene action for exploiting required breeding method (Singh and Pawar 2005). One way of understanding the genetic components of the crop is through generation mean analysis.

Generation mean analysis (GMA) is a biometrical technique used for estimation of several genetic effects viz. additive, dominance and epistatic (non-allelic interaction) used in quantitative trait (Mather and Jinks 1982; Singh and Singh 1992 and Singh and Pawar 2005). Among the different methods of generation mean analysis, six parameter model was found to show satisfactory result as it involves the estimation based on the back cross study (Kumar et al. 2012). Generation mean analysis is an important tool that helps us choose the best breeding method to choose for development of a variety. The choice of appropriate and best breeding method again depend on type of gene action. Understanding how genes are interacting will give us an idea to determine best breeding method to use and thus optimizing the gene action. Hayman's generation mean analysis divide the gene effect in six different parameters viz., mean [*m*], additive [*d*], dominance [*h*], additive × additive [*i*], additive × dominance [*j*] and dominance × dominance [*l*] gene effects. Besides additive and dominance effect, epistatic or non-allelic interaction also play an important role in genetic trait control (Singh and Pawar, 2005). In some cases, epistatic effects contribute in the expression of hybrid (Kearsey and Pooni, 1996). Several biometrical techniques are available which can be used for estimation of the magnitude of different components of genetic variation.

Materials and Methods

Six elite germplasm accessions including indigenous and exotic (Mexican lines having higher oil content) genotypes were selected to make crosses since they have contrasting traits and wider genetic distance. A total of 6 parents were used to create 6 F₁s in the *rabi* season of 2018–2019. The list of the genotypes and is given in table-1. And a total of 6 BC₁ and 6 BC₂ were created in the next *rabi* season of 2019–2020. The F₁ plants were checked for their purity of hybrid and only the pure F₁ plants were harvested as F₂ plants (Devi et al. 2022). So, a total of six generations were created and grown in replicated trial in *rabi* season of 2020–2021 using RBD design maintaining a spacing of 45cm × 20 cm. The data collected were analysed through generation mean analysis to understand different inter-allelic and intra-allelic interaction. The list of the parents and the F₁s created are given in table no -1.

A total of eleven characters were taken to study genetic components of Safflower. Scaling test for A, B, C and D scales were used to know the adequacy of simple additive-dominance model as suggested by Hayman and Mather (1955) and Mather and Jinks (1971). Several scaling test were combines as one in joint scaling test as suggested by Cavalli (1952) and with the help of χ^2 test it test the adequacy of additive-dominance model. The relationship established between respective generation mean and genetic effects were calculated by weighted least square analysis using reciprocal of the respective variance of the generation means. The generation means were used to estimate digenic interaction of the six genetic parameters viz., *m*, (*d*), (*h*), (*i*), (*j*) and (*l*) which represent mean, additive genetic effect, dominance genetic effect, additive × additive gene interaction effect, additive × dominance interaction effect and dominance × dominance gene effects, respectively with an assumption that there is no linkage and no gene interaction exists.

Table-1: List of the parents and F₁s used in the study

Sl. No.	Parents	Major Characters	Sl. No.	F ₁ 's
1	GMU-1217	High oil and oleic acid content	7	EC 755673 X GMU 6891
2	GMU- 6854	High linoleic acid and lesser oil content	8	EC 755664 X GMU 2830
3	GMU-6891	High linoleic acid content and lesser oil content	9	GMU 6854 X GMU 1217
4	GMU-2830	High linoleic acid content, lesser oil content	10	EC 755673 X GMU 2830
5	EC 755673	Higher oil content, small capitulum, spreading type, more primary branch,	11	EC 755673 X GMU 1217
6	EC755664	Higher oil content Spreading branches,, small capitulum, more primary branch,	12	EC 755664 X GMU 1217

Results and Discussion

Analysis of Variance and Per se Performance

Analysis of Variance was calculated for eleven characters for six different crosses and the analysis of Variance for individual cross and for each character is presented in table-2. The data analysis of all the crosses viz., EC 755673 × GMU-6891, EC-755664 × GMU-2830, EC 755673 × GMU 2830, EC-755673 × GMU-1217, EC-755664 × GMU-1217 and GMU-6854 × GMU-1217 revealed that there was high variability for the characters as the mean sum of squares due to generations was significant except for length of bracts on capitulum and 100 seed weight. Yassein et al. (2020) and Rathod et al. (2021) found significant analysis of variance for all the characters while Dhruw et al. (2021) found significant analysis of variance for all the characters except for the character seed yield per plant and number of seeds per capitulum. Waghmode et al. (2021) found high significant difference for all the characters except for the character days to maturity, 50% flowering and number of branches per plant. The cross EC-755673 × GMU-6891 had highest per se performance for the character plant height and lowest per se performance for the character days to maturity. Highest per se performance of the character number of capitulum/plant, number of seeds per capitulum and oil content was found in cross EC-755664 × GMU-2830. The plants of cross EC-755673 × GMU-2830 had highest per se performance for the characters rosette period, days to 50% flowering while lowest per se performance was obtained for the character plant height. Lowest per se performances of the character rosette period, seed yield per plant was found in cross GMU-1217. The cross EC-755664 × GMU-1217 had highest per se performance for the character days to maturity, number of seeds per capitulum and lowest per se performance was obtained for the characters number of capitulum per plant and 100 seed weight. The characters 100 seed weight and seed yield per plant was found to have highest per se performance in cross GMU-6854 × GMU-1217 and lowest per se performance was found for the characters days to 50% flowering, number of primary branch per plant and oil content.

Table-2 : Cross-wise ANOVA for yield and its components in Safflower

Generations	Source	d.f	Characters								
			Rosette period (days)	Days to 50% flowering	Plant height (cm)	No. of primary branch/pt.	Number of capitulum/pt.	Length Of bracts on capitulum (cm)	Days to maturity	No. of seeds /capitulum	100 seed weight (g)
EC-755673 × GMU 6891	Replication	2	0.329	0.038	14.62	0.82	9.34	0.036	0.985	9.81	0.007
	Treatment	5	63.348**	142.88**	880.69**	65.72**	380.95**	0.54	33.98**	380.95**	2.682
	Error	10	0.1	0.02	7.6	0.42	3.09	0.037	0.25	3.09	0.005
EC-755664× GMU-2830	Replication	2	0.7	1.04	2.68	1.234	6.99	0.128	1.318	1.508	0.001
	Treatment	5	83.97**	98.72**	591.42**	89.52**	507.93**	1.665	78.24**	100.73**	2.567
	Error	10	0.306	0.554	1.737	0.735	3.58	0.034	0.96	1.617	0.004
EC 755673 X GMU 2830	Replication	2	3.239	1.026	0.77	1.76	5.24	0.21	7.603	6.443	0.007
	Treatment	5	23.74**	93.54**	748.79**	61.88**	320.83**	1.709	60.189**	65.872**	1.191
	Error	10	0.908	0.46	8.69	0.514	2.91	0.071	0.975	4.899	0.01
EC-755673×GMU-1217	Replication	2	3.239	1.026	0.77	1.76	5.24	0.21	7.603	6.443	0.007
	Treatment	5	23.747**	93.54**	748.79**	61.88**	320.83**	1.709	60.189**	65.871**	1.191
	Error	10	0.908	0.46	8.69	0.514	2.91	0.071	0.975	4.899	0.01
EC 755664×GMU-1217	Replication	2	3.239	1.026	0.773	1.767	5.24	0.21	7.603	6.44	0.007
	Treatment	5	23.74**	93.54**	748.79**	61.885**	320.83**	1.709	60.189**	65.87**	1.191
	Error	10	0.908	0.463	8.699	0.514	2.916	0.071	0.975	4.899	0.01
GMU-6854×GMU-1217	Replication	2	2.783	0.905	16.022	1.599	3.658	0.021	1.116	10.632	0.005
	Treatment	5	105.41**	83.08**	601.21**	27.37**	323.78**	1.13	73.98**	92.704**	1.373
	Error	10	0.527	0.657	4.44	0.551	1.851	0.043	0.569	3.518	0.011

** significance at 1% level, * significance at 5% level

Scaling test and estimation of gene effects

The mean values of all the six generations viz., F_2 , BC_1 , BC_2 , F_1 , P_2 and P_1 for six different crosses for eleven characters were subjected to generation mean analysis. Testing the adequacy of the scale is necessary to know the presence or absence of gene interaction.

Result:

In this cross, scaling test was performed and all the scales A, B, C and D were found highly significant for the characters like rosette period, plant height, number of capitulum/plant, days to maturity and seed yield indicated presence of non-allelic gene interaction. Both additive and dominance gene effects were significant for rosette period, days to 50% flowering and plant height. Number of capitulum/plant showed negative significance of additive gene effects only, whereas dominant gene effects were found for number of primary branches/plant, number of capitulum/plant, length of bracts on capitulum, days to maturity, number of seeds/ capitulum, seed yield and oil content. Similar result was found by Kotecha and Zimmerman (1978), Golkar et al. (2012), Golkar 2011, Kumar et al. (2012), Mirzahashemi et al. (2013), Mirzahashemi et al. (2014), Shivani and Varaprasad (2016) Waghmode et al. (2021). While significant additive gene effect was observed for the characters days to 50% flowering, plant height, number of capitulum/ plant, oil content and rosette period. Similar result obtained by Manjare and Jambhare (1997), Sabzalian and Saeidi 2007, Golkar 2011, Mirzahashemi et al. (2013), Kumar et al. (2012), Mirzahashemi et al. (2014), Shivani and Varaprasad (2016), Waghmode et al. (2021). Both type of interaction were found significant for days to 50% flowering, plant height and oil content. Epistasis was absent for length of bracts on capitulum, number of seeds/ capitulum and 100 seed weight. Significant additive × additive (i) epistatic gene effect was found for the characters rosette period, days to 50% flowering, primary branch/plant, number of capitulum/plant, days to maturity, seed yield, oil content and length of bract on capitulum. Similar findings were observed by Gupta and Singh (1988), Shahbazi and Saeidi (2007), Golkar 2011, Kumar et al. (2012), Golkar et al. (2012), Mirzahashemi et al. (2014), Waghmode et al. (2021). Significant additive × dominance (j) epistatic gene effect was found for the characters rosette period, days to 50% flowering, number of seeds per capitulum, seed yield, oil content and plant height. Similar findings obtained by Narkhede and Patil, 1987, Kumar et al. (2012), Mirzahashemi et al. (2014), Waghmode et al. (2021). Significant dominant × dominant (l) epistatic gene effect was noted for rosette period, plant height, number of primary branches per plant, number of capitulum per plant, days to maturity, seed yield and oil content. Similar result obtained by Ragab (1991), Mirzahasemi et al. (2013), Mirzahashemi et al. (2014), Waghmode et al. (2021). Duplicate type of gene interaction was obtained for the characters rosette period, number of primary branch/plant, number of capitulum/plant, days to maturity, seed yield and oil content which is in agreement with Kumar et al. (2012), Mirzahashemi et al. (2014), Waghmode et al. (2021) while complementary gene interaction was obtained for the characters days to 50% flowering and plant height which is in agreement with (Prasad et al. 1993; Mirzahashemi et al. 2014). The estimates of scaling test and genetic components are given in table-3.

Table-3 : Estimates of Scaling test and joint test for yield and its components in cross EC-755673 × GMU-6891

Parameters	Characters									
	Rosette period	Days to 50% flowering	Plant height	No. of primary branch/pt.	Number of capitulum/pt.	Length of bracts on capitulum	Days to maturity	No. of seeds /capitulum	100 seed weight	Seed yield
A	-9.3 ± 0.31 **	0.03 ± 0.30	28.20 ± 6.98**	-3.633 ± 1.077**	15.34 ± 3.318**	0.39 ± 0.19	-6.61 ± 0.65**	5.65 ± 2.29**	0.39 ± 0.19	-10.04 ± 4.13
B	-3.66 ± 0.32**	25.86 ± 0.41**	37.00 ± 4.01**	-3.767 ± 2.411	15.56 ± 4.541**	0.74 ± 0.37	-7.53 ± 0.91**	-11.05 ± 2.35**	0.747 ± 0.374	26.38 ± 8.33
C	35.99 ± 0.40**	30.83 ± 0.41**	70.29 ± 7.49**	29.8 ± 1.19**	106.98 ± 6.356**	3.79 ± 0.26**	7.36 ± 0.60**	-4.36 ± 4.48	3.798 ± 0.265	234.6 ± 6.46
D	-24.48 ± 0.22**	-2.46 ± 0.29*	-2.54 ± 3.59	-18.6 ± 1.345**	-38.04 ± 2.192**	-1.33 ± 0.21	-10.75 ± 0.58**	-0.52 ± 2.20	-1.331 ± 0.216	-109.4 ± 4.15
χ ²	15523**	8187.89**	102.15**	720.18**	424.30**	212.55**	417.33**	35.47**	212.55**	1974.4
m	29.16 ± 0.06**	92.03 ± 0.08**	102.22 ± 0.84**	6.067 ± 0.221**	18.987 ± 0.836**	2.71 ± 0.04**	142.06 ± 0.10**	35.57 ± 0.91**	2.718 ± 0.048	31.50 ± 0.69
d	2.00 ± 0.18*	14.53 ± 0.23**	9.00 ± 3.16**	-1.933 ± 1.27	-5.96 ± 1.418**	0.06 ± 0.19	-1.11 ± 0.53	-0.55 ± 1.24	0.06 ± 0.193	-0.66 ± 3.91
h	50.64 ± 0.47**	16.51 ± 0.59**	45.69 ± 7.92**	45.233 ± 2.719**	86.747 ± 5.15**	3.40 ± 0.44**	15.02 ± 1.18**	10.00 ± 4.60**	3.406 ± 0.442	307.8 ± 8.80
i	48.96 ± 0.44**	4.93 ± 0.58**	5.09 ± 7.18	37.2 ± 2.69**	70.08 ± 4.384**	2.66 ± 0.43*	21.51 ± 1.16**	1.04 ± 4.41	2.661 ± 0.432	218.8 ± 8.30
j	5.63 ± 0.40**	25.83 ± 0.49**	8.80 ± 6.71*	-0.133 ± 2.618	0.213 ± 5.098	0.35 ± 0.41	-0.92 ± 1.08	-16.71 ± 2.91**	0.357 ± 0.13	36.38 ± 8.81
l	-61.92 ± 0.84**	20.96 ± 1.03**	60.10 ± 14.71**	-44.6 ± 5.219**	-45.173 ± 8.519**	-1.52 ± 0.81	-35.65 ± 2.23**	-6.44 ± 6.70	-1.525 ± 0.817	-202.16 ± 16.9
Types of interaction	Duplicate	Complementary	Complementary	Duplicate	Duplicate	-	Duplicate	-		Duplicate
** significance at 1% table value, * significance at 5% table value										

Cross-2 (EC-755664 × GMU-2830)

The cross EC-755664 × GMU-2830 found significant scales A, B, C and D for the characters like rosette period, days to 50% flowering, plant height, number of primary branch per plant, days to maturity, seed yield per plant which indicates the presence of non-allelic gene interaction. Rest of the traits viz., number of

capitulum/plant, length of bracts on capitulum, number of seeds per capitulum and 100 seed weight showed significance of any one, two or three scales exhibited the presence of epistasis. Both additive and dominance gene effects were significant for the character plant height, number of capitulum per plant, 100 seed weight, seed yield per plant and oil content while significant dominance gene effect was observed for all the characters. Thus, relative dominance effects were found greater for most of the characters under study. Significant additive gene effect was observed for the characters plant height, number of capitulum/ plant, length of bracts per capitulum, days to maturity, seed yield, oil content and 100 seed weight while significant dominance gene effect was observed for the characters rosette period, days to 50% flowering, plant height, number of primary branch/plant, number of capitulum/plant, length of bracts on capitulum, days to maturity, number of seeds per capitulum, 100 seed weight, seed yield per plant and oil content (%). Same result also reported by Kotecha and Zimmerman (1978), Golkar et al. (2002), Golkar, 2011, Mirzahashemi et al. (2013), Kumar et al. (2012), Mirzahashemi et al. (2014), Shivani and Varaprasad (2016), Waghmode et al. (2021). All types of interaction were found significant for rosette period, days to 50% flowering, plant height, number of capitulum per plant, number of seeds per capitulum, 100 seed weight, seed yield per plant and oil content. Additive × additive type of gene interaction was significant for rosette period, days to 50% flowering, plant height, number of primary branch per plant, number of capitulum per plant,

Table-4 : Estimates of Scaling test and joint test for yield and its components in cross EC-755664× GMU-2830

Parameters	Characters									
	Rosette period	Days to 50% flowering	Plant height	No. of primary branch/pt.	Number of capitulum/pt.	Length of bracts on capitulum	Days to maturity	No. of seeds /capitulum	100 seed weight	Seed yield
A	-7.83 ± 0.75**	17.08 ± 2.35**	28.46 ± 4.22**	-13.167 ± 2.314**	16.278 ± 2.701**	0.06 ± 0.24	-15.88 ± 0.46**	18.11 ± 2.03**	4.20 ± 0.05**	-8.618 ± 7
B	-12.85 ± 0.99**	5.46 ± 0.49**	21.50 ± 2.31**	-12.6 ± 1.485**	-1.389 ± 2.362	-1.19 ± 0.16	-17.46 ± 0.42**	8.97 ± 1.91**	0.14 ± 0.07	69.20 ± 4
C	26.81 ± 0.48**	38.97 ± 0.34**	-11.63 ± 3.9**	18.393 ± 1.521**	72.507 ± 5.189**	4.75 ± 0.42**	5.24 ± 0.89**	0.54 ± 3.58	1.98 ± 0.05*	192.28 ±
D	-23.75 ± 0.59**	-8.20 ± 1.20**	30.80 ± 2.53**	-22.08 ± 1.418**	-28.809 ± 2.145**	-2.94 ± 0.21**	-19.29 ± 0.41**	13.27 ± 1.57 **	1.18 ± 0.04	-65.85 ± 3
χ^2	4757**	12911.17**	191.49**	341.36**	260.72**	244.78**	3302.43**	116.04**	6577.08**	1031.42*
m	29.51 ± 0.04**	93.17 ± 0.05**	108.73 ± 0.68**	7.293 ± 0.281**	22.207 ± 0.956**	2.27 ± 0.09*	142.57 ± 0.17**	36.74 ± 0.64**	4.20 ± 0.00**	28.20 ± 0
d	0.55 ± 0.58	-2.11 ± 1.19	-10.00 ± 2.12**	-0.667 ± 1.302	-6.33 ± 0.97**	-0.30 ± 0.11	1.11 ± 0.22	-1.33 ± 0.91	-2.18 ± 0.04*	35.58 ± 3
h	41.13 ± 1.20**	27.65 ± 2.41**	-31.25 ± 5.25**	52.043 ± 2.882**	89.084 ± 4.634**	7.16 ± 0.44**	31.02 ± 0.88**	-13.84 ± 3.38**	-2.88 ± 0.09**	216.09 ±
i	47.50 ± 1.18**	16.41 ± 2.41**	-61.60 ± 5.06**	44.16 ± 2.836**	57.618 ± 4.289**	5.88 ± 0.43**	38.59 ± 0.83**	-26.54 ± 3.14**	-2.36 ± 0.08*	131.70 ±
j	-5.02 ± 1.22*	-11.62 ± 2.40**	-69.67 ± 4.54**	0.567 ± 2.701	-17.667 ± 3.115**	-1.26 ± 0.27	-1.57 ± 0.55	-9.13 ± 2.46**	-4.06 ± 0.08**	77.81 ± 6
l	-68.19 ± 2.40**	6.13 ± 4.80*	111.56 ± 9.36**	-69.927 ± 5.425**	-42.729 ± 0.479**	-7.01 ± 0.62**	-71.95 ± 1.26**	53.63 ± 5.10**	6.71 ± 0.17**	71.12 ± 1
Types of epistatic interaction	Duplicate	Complementary	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	Complem
** significance at 1% table value, * significance at 5% table value										

length of bracts on capitulum, days to maturity, number of seeds per capitulum, 100 seed weight, seed yield and oil content. Similar findings were observed by Gupta and Singh (1988); Shahbazi and Saeidi (2007); Golkar 2011; Kumar et al. (2012); Golkar et al. (2012); Mirzahashemi et al. (2014); Waghmode et al. (2021). Dominance × dominance gene effects was observed for rosette period, days to 50% flowering, plant height, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, days to maturity, number of seeds per capitulum, 100 seed weight, seed yield per plant and oil content. Similar result obtained by Ragab (1991), Mirzahasemi et al. (2013), Mirzahashemi et al. (2014), Waghmode et al. (2021). Duplicate type of gene interaction was obtained for the characters rosette period, plant height, number of primary branch/plant, number of capitulum/plant, length of bracts on capitulum, days to maturity, number of seeds per capitulum, 100 seed weight and oil content which is in agreement with Kumar et al. (2012), Mirzahashemi et al. (2014), Waghmode et al. (2021). Complementary gene interaction was obtained for the characters days to 50% flowering and seed yield which is in agreement with Prasad et al. (1993), Mirzahashemi et al. (2014). The estimates of scaling test and genetic components are given in table-4.

Cross- 3 (GMU-6854×GMU-1217)

Scaling test A, B, C and D were found highly significant for the cross GMU-6854 × GMU-1217 for the characters rosette period, days to 50% flowering, plant height, number of capitulum per plant, days to maturity and seed yield per plant which indicates the presence of non-allelic gene interaction. Both additive and dominance gene effects were significant for days to 50% flowering, plant height, days to maturity, number of seeds per capitulum and oil content. Significant additive gene effect was observed for the characters plant height, days to maturity and oil content, days to 50% flowering and number of seeds

per capitulum. Similar result obtained by Shahbazi and Saeidi (2007), Golkar (2011), Manjare and Jambhare (1997) Mirzahashemi et al (2013), Kumar et al. (2012), Mirzahashemi et al. (2014), Shivani and Varaprasad (2016), Waghmode et al. (2021). While significant dominance gene effect was observed for the characters rosette period, days to 50% flowering, plant height, number of primary branch/plant, number of capitulum/plant, length of bracts on capitulum, days to maturity, number of seeds per capitulum, 100 seed weight, seed yield per plant and oil content (%). Similar result was found by Kotecha and Zimmerman (1978), Golkar et al. (2002), Golkar (2011), Mirzahashemi et al. (2013), Kumar et al. (2012), Mirzahashemi et al. (2014), Shivani and Varaprasad (2016) Waghmode et al. (2021). Additive $\times$ additive and dominance $\times$ dominance type of gene interaction was significant for all the characters under study. Similar findings were observed by Gupta and Singh (1988), Shahbazi and Saeidi (2007), Golkar (2011), Kumar et al. (2012), Golkar et al. 2012, Mirzahashemi et al. (2014), and Waghmode et al. (2021). Duplicate type of epistasis was observed for rosette period, days to 50% flowering, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, days to maturity, number of seeds per capitulum, 100 seed weight and oil content which is in agreement with Kumar et al. (2012), Mirzahashemi et al. (2014), Waghmode et al. (2021). Complementary type of epistasis was exhibited for plant height and seed yield per plant which is in agreement with (Prasad et al., 1993; Mirzahashemi et al., 2014). The estimates of scaling test and genetic components are given in table-5.

Table-5 : Estimates of Scaling test and joint test for yield and its components in cross GMU-6854 $\times$ GMU-1217

Parameters	Characters									
	Rosette period	Days to 50% flowering	Plant height	No. of primary branch/pt.	Number of capitulum/pt.	Length of bracts on capitulum	Days to maturity	No. of seeds /capitulum	100 seed weight	Seed yie
A	-2.43 $\pm$ 0.39 *	8.47 $\pm$ 0.39**	55.03 $\pm$ 5.09**	-0.356 $\pm$ 1.051	-8.811 $\pm$ 2.609**	0.519 $\pm$ 0.39	-15.77 $\pm$ 0.47**	-3.27 $\pm$ 2.18	-1.77 $\pm$ 0.14	97.35 $\pm$ 1
B	-6.45 $\pm$ 0.39**	5.26 $\pm$ 0.49**	29.31 $\pm$ 2.93 **	1.656 $\pm$ 1.343	-11.767 $\pm$ 2.078**	-2.002 $\pm$ 0.20	-5.04 $\pm$ 0.44**	-14.06 $\pm$ 2.36**	-0.54 $\pm$ 0.12	99.19 $\pm$ 1
C	51.38 $\pm$ 0.35**	32.20 $\pm$ 0.40**	72.48 $\pm$ 3.22**	23.087 $\pm$ 1.199**	66.907 $\pm$ 3.979**	3.786 $\pm$ 0.22**	15.58 $\pm$ 0.84**	-6.68 $\pm$ 2.89**	2.39 $\pm$ 0.06*	269.42 $\pm$ 2
D	-30.13 $\pm$ 0.25**	-9.23 $\pm$ 0.33**	6.32 $\pm$ 3.02**	-10.893 $\pm$ 0.812**	-43.742 $\pm$ 1.978**	-2.63 $\pm$ 0.22*	-18.20 $\pm$ 0.41**	-5.329 $\pm$ 1.78**	-2.35 $\pm$ 0.09*	-36.43 $\pm$ 1
χ^2	30817**	6221.20**	588.06**	443.41**	501.58**	469.22**	2450.07**	36.5**	2027.63**	5610.2**
m	26.48 $\pm$ 0.04**	91.10 $\pm$ 0.07**	90.22 $\pm$ 0.60**	6.387 $\pm$ 0.183**	13.907 $\pm$ 0.792**	2.28 $\pm$ 0.04*	139.45 $\pm$ 0.16**	33.78 $\pm$ 0.54**	3.77 $\pm$ 0.00**	24.99 $\pm$ 0
d	0.22 $\pm$ 0.24	-2.55 $\pm$ 0.29*	-13.44 $\pm$ 2.77**	-0.778 $\pm$ 0.724	0.222 $\pm$ 1.184	-1.08 $\pm$ 0.21	6.00 $\pm$ 0.24 **	-3.77 $\pm$ 1.40*	1.16 $\pm$ 0.09	6.65 $\pm$ 5.
h	60.54 $\pm$ 0.53**	31.01 $\pm$ 0.67**	15.85 $\pm$ 6.14**	26.87 $\pm$ 1.691**	106.08 $\pm$ 4.134**	5.49 $\pm$ 0.45**	27.24 $\pm$ 0.86**	22.64 $\pm$ 3.68**	4.11 $\pm$ 0.18**	188.22 $\pm$ 11.08**
i	60.27 $\pm$ 0.51 **	18.46 $\pm$ 0.66**	-12.65 $\pm$ 6.05**	21.787 $\pm$ 1.623**	87.48 $\pm$ 3.956**	5.26 $\pm$ 0.45**	36.40 $\pm$ 0.81**	10.65 $\pm$ 3.56**	4.70 $\pm$ 0.18**	72.87 $\pm$ 1
j	-4.02 $\pm$ 0.53*	-3.21 $\pm$ 0.62*	-26.52 $\pm$ 5.80**	2.011 $\pm$ 1.678	-2.956 $\pm$ 3.295	-2.52 $\pm$ 0.43	10.73 $\pm$ 0.55**	-10.78 $\pm$ 3.036**	1.22 $\pm$ 0.18	1.83 $\pm$ 11
l	-69.16 $\pm$ 1.03**	-4.71 $\pm$ 1.24**	97.80 $\pm$ 11.57**	-20.487 $\pm$ 3.136**	-108.062 $\pm$ 6.185**	-6.75 $\pm$ 0.87**	-57.23 $\pm$ 1.30**	-28.00 $\pm$ 6.32**	-7.02 $\pm$ 0.36**	123.68 $\pm$ 21.72**
Types of epistatic interaction	Duplicate	Duplicate	Complementary	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	Comple
** Significance at 1% table value and * significance at 5% table value										

Cross-4 (EC 755673 X GMU 2830)

In this cross, scaling test was performed and all the scales A, B, C and D were found highly significant for the characters rosette period, plant height, days to maturity, seed yield per plant and oil content indicated the presence of non-allelic gene interaction. Rest of the traits viz., days to 50% flowering, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, number of seeds per capitulum and 100 seed weight showed significance of any one, two or three scales exhibited the presence of epistasis. Both additive and dominance gene effects were significant for rosette period, days to 50% flowering, days to maturity, seed yield per plant and oil content. Days to 50% flowering and seed yield per plant showed negative significance of additive gene effect whereas significant dominance gene effect was found for rosette period, days to 50% flowering, plant height, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, days to maturity, 100 seed weight, seed yield per plant and oil content. Similar results were also reported by Kotecha and Zimmerman (1978), Golkar et al. (2002), Golkar, (2011), Mirzahashemi et al. (2013), Kumar et al. (2012), Mirzahashemi et al. (2014), Shivani and Varaprasad (2016) and Waghmode et al. (2021). All types of gene interaction was found significant for rosette period, days to 50% flowering, plant height, number of primary branch per plant, number of capitulum per plant, days to maturity and oil content. Additive $\times$ additive type of gene interaction was significant for rosette period, days to 50% flowering, plant height, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, days to maturity, seed yield per plant and oil content. Similar findings obtained by Narkhede and Patil (1987), Kumar et al. (2012),

Mirzahashemi et al. (2014), Waghmode et al. (2021). Dominance × dominance type of gene interaction was significant for rosette period, days to 50% flowering, plant height, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, days to maturity, 100 seed weight and oil content. Epistasis was absent for number of seeds per capitulum. Similar result obtained by Ragab (1991), Mirzahasemi *et al.* (2013), Mirzahashemi et al. (2014), Waghmode et al. (2021). Duplicate type of epistasis was observed for rosette period, days to 50% flowering, plant height, number of primary branch per plant, number of capitulum per plant, length of bracts o capitulum, days to maturity, 100 seed weight and oil content which is in agreement with Kumar et al. (2012), Mirzahashemi et al. (2014), Waghmode et al. (2021). Complementary type of epistasis was absent for all the traits under study. The estimates of scaling test and genetic components are given in table-6.

Table-6 : Estimates of Scaling test and joint test for yield and its components in cross EC 755673 X GMU 2830

Parameters	Characters									
	Rosette period	Days to 50% flowering	Plant height	No. of primary branch/Pt.	Number of capitulum/pt.	Length of bracts on capitulum	Days to maturity	No. of seeds /capitulum	100 seed weight	Seed yield
A	-20.11 ± 0.38**	13.86 ± 0.36**	14.42 ± 3.59**	-6.833 ± 1.387**	13.478 ± 2.389**	-0.36 ± 0.25	-22.60 ± 0.40**	10.47 ± 3.85**	1.58 ± 0.06	46.83 ± 5.00**
B	-14.05 ± 0.39**	2.34 ± 0.83	7.71 ± 2.02**	-1.5 ± 1.718	-1.956 ± 1.851	-1.95 ± 0.18	-2.88 ± 0.55*	-1.98 ± 2.73	1.76 ± 0.08*	35.67 ± 2.95**
C	19.19 ± 0.39**	41.58 ± 0.41**	-19.20 ± 3.80**	29.32 ± 1.168**	77.167 ± 3.909**	4.48 ± 0.22**	10.76 ± 0.64**	8.42 ± 3.12**	2.02 ± 0.05*	163.66 ± 4.98**
D	-26.68 ± 0.28**	12.68 ± 0.47**	20.66 ± 2.10**	-18.827 ± 1.102**	-32.82 ± 1.776**	-3.39 ± 0.16**	-18.12 ± 0.37**	0.031 ± 2.54	0.66 ± 0.05	-40.57 ± 2.53**
χ^2	9155.43**	10219.53**	102.15**	758.24**	469.33**	740.35**	4787.33**	15.06**	1657.25**	1281.21**
m	29.66 ± 0.07**	91.71 ± 0.08**	104.66 ± 0.65**	6.42 ± 0.199**	17.2 ± 0.757**	2.25 ± 0.03 *	140.49 ± 0.11**	32.12 ± 0.62**	4.30 ± 0.00**	32.91 ± 0.56**
d	3.11 ± 0.24**	-4.77 ± 0.44*	-0.88 ± 1.64	1.667 ± 1.027	-1.667 ± 0.926	-0.45 ± 0.13	10.22 ± 0.29**	0.00 ± 2.21	0.15 ± 0.05	-10.74 ± 2.27**
h	49.44 ± 0.58**	40.41 ± 0.95**	-43.73 ± 4.43**	48.22 ± 2.244**	81.994 ± 3.76**	7.86 ± 0.32**	30.34 ± 0.77**	2.47 ± 5.16	-2.07 ± 0.10*	164.36 ± 5.53**
i	53.36 ± 0.57**	25.36 ± 0.94**	-41.33 ± 4.21**	37.653 ± 2.203**	65.644 ± 3.551**	6.79 ± 0.31**	36.24 ± 0.74**	-0.06 ± 5.08	-1.32 ± 0.10	81.15 ± 5.07**
j	6.05 ± 0.52**	-11.52 ± 0.90**	-6.71 ± 3.95**	5.33 ± 2.189**	-15.433 ± 2.955**	-1.59 ± 0.31	19.71 ± 0.61**	-12.46 ± 4.65**	0.17 ± 0.1	-11.15 ± 5.21**
l	-87.52 ± 1.06**	-9.15 ± 1.82**	63.46 ± 7.59**	-45.987 ± 4.154**	-54.122 ± 5.386**	-9.11 ± 0.59**	-61.73 ± 1.34**	8.55 ± 9.37	4.67 ± 0.20**	1.35 ± 10.35
Types of interaction	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	-	Duplicate	-
** Significance at 1% table value and * significance at 5% table value										

Cross- 5 (EC-755673×GMU-1217)

The scaling test was performed and all the scales A, B, C and D were found highly significant for the characters rosette period, days to 50% flowering, plant height, number of capitulum per plant, days to maturity and seed yield per plant depicted the presence of non-allelic gene interaction. Besides these traits, rest of the traits viz., number of primary branch per plant, length of bracts on capitulum, number of seeds per capitulum, and 100 seed weight also showed significance of any one or two or three scales exhibited the presence of epistasis. Both additive and dominance gene effects were significant for number of capitulum per plant and oil content. Dominance gene effect was found greater and significant for most of the characters under study. Significant additive gene effect was observed for the characters number of capitulum/ plant and oil content at 1% table value. Similar result obtained by Shahbazi and Saeidi (2007), Golkar (2011), Manjare and Jambhare (1997) Kumar et al. (2012), Mirzahashemi et al. (2013), Mirzahashemi et al. (2014), Shivani and Varaprasad (2016), Waghmode et al. (2021). While significant dominance gene effect was observed for the characters rosette period, days to 50% flowering, plant height, number of primary branch/plant, number of capitulum/plant, length of bracts on capitulum, days to maturity, number of seeds per capitulum, 100 seed weight, seed yield per plant and oil content (%). Similar result was found by Kotecha and Zimmerman (1978), Golkar et al. (2002), Golkar (2011), Mirzahashemi et al. (2013), Kumar et al. (2012), Mirzahashemi et al. (2014), Shivani and Varaprasad (2016), Waghmode et al. (2021). All types of gene interaction were found significant for number of capitulum per plant, number of seeds per capitulum, 100 seed weight and oil content. Additive × additive type of gene interaction was significant for rosette period, days to 50% flowering, plant height, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, days to maturity, number of seeds per capitulum, 100 seed weight, seed yield per plant and oil content. Similar findings were observed by Gupta and Singh 1988, Shahbazi and Saeidi (2007), Golkar (2011), Kumar et al. (2012), Golkar et al. (2012), Mirzahashemi et al. (2014), Waghmode et al. (2021). Dominance × dominance type of gene interaction was significant for rosette period, days to 50% flowering, plant height, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, days to maturity, number of seeds per capitulum, 100 seed weight and oil content. Similar

result obtained by Ragab (1991), Mirzahasemi et al., (2013), Mirzahashemi et al. (2014), Waghmode et al. (2021). Duplicate type of epistasis was observed for rosette period, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, days to maturity, number of seeds per capitulum, 100 seed weight and oil content which is in agreement with Kumar et al. (2012), Mirzahashemi et al. (2014), Waghmode et al. (2021). Complementary type of epistasis was exhibited for days to 50% flowering and plant height which is in agreement with (Prasad et al., 1993), Mirzahashemi et al. (2014). The estimates of scaling test and genetic components are given in table-7.

Table-7 : Estimates of Scaling test and joint test for yield and its components in cross EC-755673×GMU-1217

Parameters	Characters									
	Rosette period	Days to 50% flowering	Plant height	No. of primary branch/pt.	Number of capitulum/pt.	Length of bracts on capitulum	Days to maturity	No. of seeds /capitulum	100 seed weight	Seed yield
A	-11.66 ± 0.68**	8.93 ± 0.60**	53.35 ± 4.87**	-3.44 ± 1.807	12.044 ± 3.943**	-0.85 ± 0.52	-16.66 ± 0.48**	13.92 ± 4.18**	-0.061 ± 0.11	36.13
B	-10.85 ± 0.72**	8.97 ± 0.56**	47.57 ± 4.35 **	-2.4 ± 1.207	-13.989 ± 2.154**	0.31 ± 0.15	-17.47 ± 0.57**	2.57 ± 3.15	-2.12 ± 0.09*	29.26
C	-14.64 ± 0.38**	24.21 ± 0.45**	113.25 ± 3.79**	31.907 ± 1.226**	75.487 ± 6.021**	5.21 ± 0.23**	-19.32 ± 0.97**	0.82 ± 3.38	3.10 ± 0.07**	13.4 ± 4
D	-3.93 ± 0.50**	-3.15 ± 0.41*	-6.16 ± 3.36**	-18.876 ± 1.062**	-38.716 ± 3.138**	-2.88 ± 0.28*	-7.40 ± 0.59**	7.84 ± 2.81**	-2.65 ± 0.06*	-34.70
χ^2	1690.57**	2800.10**	960.07**	925.54**	281.61**	532.48**	2314.0**	11.79**	3932.40**	87
m	39.25 ± 0.07 **	95.98 ± 0.06**	85.92 ± 0.70**	5.173 ± 0.19**	16.087 ± 1.292**	2.40 ± 0.04*	148.07 ± 0.23**	30.58 ± 0.67**	3.68 ± 0.00**	28.09
d	0.22 ± 0.48	0.88 ± 0.38	1.11 ± 3.05	-1.44 ± 0.992	-5.33 ± 1.781**	0.70 ± 0.26	-0.88 ± 0.36	1.11 ± 2.46	-0.45 ± 0.06	-4.68
h	5.69 ± 1.02**	20.96 ± 0.84**	41.12 ± 6.84**	45.051 ± 2.179**	93.314 ± 6.463**	7.06 ± 0.56**	7.33 ± 1.20**	-16.39 ± 5.71**	4.83 ± 0.14**	13 ± 14
i	7.89 ± 1.01**	6.30 ± 0.84**	12.32 ± 6.72**	37.75 ± 2.125**	77.431 ± 6.276**	5.76 ± 0.56**	14.81 ± 1.19**	-15.68 ± 5.62**	5.30 ± 0.13**	68.14
j	0.81 ± 0.98	0.04 ± 0.79	-5.77 ± 6.45	1.044 ± 2.139	-26.033 ± 4.257**	1.16 ± 0.54	-0.81 ± 0.74	-11.34 ± 5.16**	-2.06 ± 0.14*	-6.13
l	-30.39 ± 1.97**	11.60 ± 1.62**	88.61 ± 12.79**	-43.596 ± 4.154**	-79.376 ± 9.329**	-6.30 ± 1.09**	-48.96 ± 1.75**	32.18 ± 10.41**	-7.49 ± 0.28**	-3.27
Types of epistatic interaction	Duplicate	Complementary	Complementary	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	-
** significance at 1% table value, * significance at 5% table value										

Cross- 6 (EC 755664 X GMU 1217)

Scaling test was performed for this cross and all the scales A, B, C and D were found highly significant for the characters rosette period, plant height, number of capitulum per plant, days to maturity. Seed yield per plant indicated presence of non-allelic gene interaction. Rest of the traits also showed significance of one or two or three scales exhibited the presence of epistasis. Both additive and dominance gene effects were significant for seed yield per plant while dominance gene effect was significant for the characters rosette period, days to 50% flowering, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, days to maturity, seed yield per plant and oil content. Similar results were also reported by Shahbazi and Saeidi (2007), Golkar (2011), Manjare and Jambhare (1997) Mirzahashemi et al. (2013), Kumar et al. (2012), Mirzahashemi et al. (2014), Shivani and Varaprasad (2016), Waghmode et al. (2021). Significant additive gene effect was observed for the character plant height and seed yield per plant. While significant dominance gene effect was observed for the characters rosette period, days to 50% flowering, number of primary branch/plant, number of capitulum/plant, length of bracts on capitulum, days to maturity, seed yield per plant and oil content (%). Therefore, relative dominance effects were found greater for most of the characters under study. All types of interaction were found significant for rosette period, plant height, number of primary branch per plant, days to maturity and seed yield per plant. Additive × additive type of gene interaction was significant for rosette period, days to 50% flowering, plant height, number of primary branch per plant, number of capitulum per plant, days to maturity, 100 seed weight, seed yield per plant and oil content. Similar findings were observed by Gupta and Singh (1988), Shahbazi and Saeidi (2007), Golkar (2011), Kumar et al. (2012), Golkar et al. (2012), Mirzahashemi et al. (2014), Waghmode et al. (2021). Significant additive × dominance (j) epistatic gene effect was found for the characters days to 50% flowering, plant height, number of primary branch per plant, days to maturity, number of seeds per capitulum and seed yield at 1% significance level and rosette period at 5% significance level. Similar findings obtained by Narkhede and Patil, (1987), Kumar et al. (2012), Mirzahashemi et al. (2014), Waghmode et al. (2021). Dominance × dominance type of gene interaction was significant for rosette period, plant height, number of primary branch per plant, number of capitulum per plant, length of bracts on capitulum, days to maturity, 100 seed weight, seed yield per plant and oil content. Here, epistasis is absent for number of seeds per capitulum. Similar result obtained by Ragab (1991), Mirzahasemi et al., (2013), Mirzahashemi et al. (2014), Waghmode et al. (2021). Duplicate type of gene interaction was obtained for the

characters rosette period, number of primary branch/plant, number of capitulum/plant, length of bracts on capitulum, days to maturity, seed yield and oil content which is in agreement with Kumar et al. (2012); Mirzahashemi et al. (2014); Waghmode et al. (2020) while complementary gene interaction was obtained for the characters days to 50% flowering and plant height which is in agreement with [Prasad et al., 1993; Mirzahashemi et al., 2014]. The estimates of scaling test and genetic components are given in table-8.

Table-8 : Estimates of Scaling test and joint test for yield and its components in cross EC 755664xGMU-1217

Parameters	Characters										
	Rosette period	Days to 50% flowering	Plant height	No. of primary branch/pt.	Number of capitulum/pt.	Length of bracts on capitulum	Days to maturity	No. of seeds /capitulum	100 seed weight	Seed yield	Oil cor (%)
A	-16.56 ± 0.75**	6.46 ± 0.68**	15.58 ± 2.62**	-4.167 ± 1.135**	-5.5 ± 2.659**	-0.70 ± 0.14	-21.47 ± 0.64 **	4.76 ± 2.11**	0.30 ± 0.12	43.90 ± 2.65**	2.1 0.7
B	-21.05 ± 0.49**	-2.92 ± 0.72*	47.83 ± 3.6**	3 ± 1.479	-10.256 ± 2.693**	0.94 ± 0.28	-24.88 ± 0.33**	-1.76 ± 2.2	-1.63 ± 0.13	24.97 ± 8.45**	-0.5 1.3
C	-15.74 ± 0.53**	7.15 ± 0.33**	35.68 ± 3.06**	27.553 ± 1.241**	50.52 ± 4.188**	4.63 ± 0.20**	-19.80 ± 0.68**	1.53 ± 3.83	0.95 ± 0.06	167.99 ± 3.84**	-15 ± 1
D	-10.93 ± 0.41**	-1.80 ± 0.49	13.87 ± 2.34**	-14.36 ± 0.873**	-33.138 ± 2.067**	-2.19 ± 0.16*	-13.28 ± 0.41**	0.73 ± 2.13	-1.14 ± 0.09	-49.55 ± 4.38**	8.6 0.6
χ^2	2246.81**	538.21**	270.42**	639.86**	269.89**	850.19**	6184.41**	6.11*	446.09**	1982.01**	372
m	40.58 ± 0.04 **	99.65 ± 0.05**	93.71 ± 0.56**	5.487 ± 0.176**	18.32 ± 0.792**	2.33 ± 0.03*	149.86 ± 0.13**	32.53 ± 0.84 **	3.90 ± 0.00**	24.27 ± 0.59**	35. 0.1
d	0.55 ± 0.40	-1.11 ± 0.48	11.55 ± 2.04 **	1.333 ± 0.799	1.556 ± 1.328	0.93 ± 0.14	-0.55 ± 0.31	2.33 ± 1.31	-0.62 ± 0.08	-8.55 ± 4.21*	2.1 0.6
h	15.84 ± 0.86**	11.65 ± 0.99**	-1.67 ± 4.79	35.103 ± 1.82**	78.909 ± 4.355**	5.28 ± 0.33**	19.14 ± 0.85**	3.83 ± 4.36	1.65 ± 0.18	171.96 ± 8.89**	-16 ± 1.
i	21.87 ± 0.82**	3.60 ± 0.98*	-27.74 ± 4.68**	28.72 ± 1.746**	66.276 ± 4.134**	4.39 ± 0.32**	26.56 ± 0.83**	-1.46 ± 4.27	2.29 ± 0.18*	99.11 ± 8.76**	-17 ± 1.
j	-4.48 ± 0.87*	-9.38 ± 0.98**	32.24 ± 4.35**	7.167 ± 1.83**	-4.756 ± 3.754	1.65 ± 0.32	-3.41 ± 0.70 **	-6.53 ± 2.90**	-1.93 ± 0.18	-18.93 ± 8.77**	-2.6 1.4
l	-59.49 ± 1.68**	-0.06 ± 1.96	91.16 ± 8.74**	-29.887 ± 3.43**	-82.031 ± 6.763**	-4.15 ± 0.61**	-72.92 ± 1.43**	4.46 ± 6.49	-3.62 ± 0.36**	-30.23 ± 17.28*	18. 2.7
Types of epistatic interaction	Duplicate	-	-	Duplicate	Duplicate	Duplicate	Duplicate	-	-	Duplicate	Duplicate
** significance at 1% table value, * significance at 5% table value											

Discussion:

Significant deviation from zero was found for all the six crosses for one or more scaling test and for joint scaling test also, the chi square calculated value was found to be significantly deviated for all the crosses for trait rosette period. Obtaining significant deviation in the scaling test and joint scaling test depicts that the additive-dominant model is inadequate and thus for the inheritance of this trait, there is the presence of non-allelic interactions. The mean value 'm' was found to be positive and significant in all the crosses. The gene effect 'd' was found to be positive and significant indicating the midpoint to be more nearer to the female parent. The value of 'h' also found to be significant and positive while 'l' gene effect was negative and significant. So, overall for the trait rosette period, duplicate type of epistasis was found to present in all the six crosses. And for the components of gene effect, the dominance × dominance type of epistasis was found to be more overpowering to other epistasis type which allows breeders to choose the right type of breeding method based on type of pollination. Further improvement of the trait rosette period can be done through heterosis breeding. The scaling test value found to be significantly deviated from zero which explained the inadequacy of additive-dominance model and indicates the presence of epistasis for the trait days to 50% flowering. Thus as a whole for the character days to 50% flowering either duplicate or complementary gene action is present depending on the type of crosses. Also the more contributing interaction in some cross was found to be dominant × dominant while in some crosses, it was found to be additive × additive type of gene action. Scaling test and joint scaling test was found to be significant for all the crosses studied for plant height. For the cross EC 755673 X GMU 6891, highest mean value was obtained for F₁ plants having plant height of 140 cm and lowest mean value was obtained for P₂ plants having a plant height of 95 cm. Highest value of scale was obtained for C scale indicating the presence of dominance × dominance epistasis. All the components of gene effects m, d, h, i, j and l possess positive sign. The trait is governed by complementary gene action as the gene effect h and l have both positive sign. Same gene interaction and gene effect was found for the cross EC 755673 X GMU-1217 and GMU 6854 X GMU 1217. The highest mean value for the cross EC 755664 X GMU 2830 for plant height was found to be in F₁ which means F₁ plants possess highest plant height with an average of 121cm while the least mean value was obtained for P₁ and they have a medium plant height of 84cm. Highest scale was found for D scale indicating the presence of additive × additive type of gene action. Highest interaction was found for 'l' i.e the dominance × dominance interaction is dominant for the inheritance of the trait. The trait is governed by duplicate gene action as the value of gene effect 'h' and 'l' have opposite sign. Same gene interaction and gene effect was found for the

cross EC 755673 X GMU 2830. The highest mean value for the cross EC 755664 X GMU 1217 was found in F1 plants having an average plant height of 122cm and the lowest mean value was obtained for BC1 having an average plant height of 80 cm. The highest interaction was observed for the gene effect dominance $\times$ dominance [I] interaction. Neither complementary nor duplicate gene action is present for this cross. Both scaling and joint scaling test was found to be significant for all the crosses for the trait primary branches per plant. Highest interaction was obtained for additive $\times$ additive and dominance $\times$ dominance. Since the dominance effect and dominance $\times$ dominance gene action have contrasting sign, the trait is governed by duplicate gene action. The mean 'm' was found significant different for each of the cross. The gene effect 'd' showed a combination of positive and negative sign and they are not found to be significant in all the crosses. The gene effect 'h', possess all positive sign and they are found to be significant. The highest interaction in all the crosses was found for the 'I' (dominance $\times$ dominance) interaction. All the crosses for this trait present duplicate gene action for the inheritance of this trait. The scaling test A, B and C were found significant in most of the crosses even though in some crosses all the scales were not significant for the trait number of capitulum/plant. From the scaling test, it was observed that majority of epistasis for this cross is governed by additive $\times$ additive gene effect and dominance $\times$ dominance gene effect. The value of 'm' was found to be significantly different for all the crosses. Depending on the crosses, the value of 'd' changes based on which it makes the cross either significant or non-significant. The gene effect 'h' has positive sign and it is contradictory to the sign of 'I', so duplicate gene interaction is present for the inheritance of this character. For bract length, A and B scale were mostly insignificant which suggest the absence of all types of epistasis at once. In most of the crosses, the C and D scale were mostly significant indicating the presence of additive $\times$ additive gene interaction and dominance $\times$ dominance gene interaction. There is significant difference in the value of mean 'm'. The gene effect 'd' was not significant for any of the crosses. The trait was found to be governed by duplicate gene action in almost all the crosses. The scaling test was found significant for all the scales A, B, C and D so presence of all three types of epistasis occurs for trait days to maturity. The mean values 'm' were found to be significantly different for all the crosses except for few crosses where the gene effect 'd' were not significant. Highest interaction of epistasis in all the crosses was found for 'I' (dominance $\times$ dominance). The gene effect 'h' and 'I' have contrasting sign for the trait in all the crosses so for the inheritance of this trait, duplicate gene interaction is present. As a whole for the trait number of seeds/capitulum, none of the crosses have all the scales significant. Some crosses have significance in few scale while some cross have significance in few scale. The components of gene effect 'm' was found to be highly significant and are found to be significantly different for all the crosses. For some of the crosses, the trait is governed by duplicate type of epistasis. For 100 seed weight, few scaling test were significant for crosses. The mean component was found to be significantly different for all the crosses. The component of gene effect 'h' and 'I' have contrasting sign, so duplicate gene interaction is present for the inheritance of this trait. The scaling test A, B, C and D was found to be highly significant for all the crosses for the trait seed yield. The component of gene effect 'm' was found to be positive and significantly different for all the crosses. The gene effect 'd' consist of positive and negative sign for the crosses. The sign of 'h' and 'I' have similar sign in some cross while in some cross they have opposite sign so both D and C type of gene interaction occurs for this trait. The cross EC 755673 X GMU 2830 and EC 755673 X GMU 1217 does not contain neither complementary nor duplicate gene action. The scaling test were found to be highly significant for all the crosses, the joint scaling test was also highly significant for the trait oil content. The mean 'm' was found to be significantly different for all the crosses. Highest contribution for gene interaction in all the crosses was found to be 'I' (dominance $\times$ dominance). Since the gene effect 'h' and 'I' have contrasting sign, duplicate type of gene effect is present for the inheritance of this trait.

Conclusion

Safflower is a neglected oilseed crop. Even though fatty acid fraction content of safflower oil is considered good, due to its limited production, the production and productivity of the crops cannot be increased. Due to limited knowledge regarding the gene action responsible for important traits in safflower, choosing the best breeding method for improvement of the crop is not clear. Through this study, the gene action responsible for different important traits has been discussed so that best breeding method to be applied for faster crop improvement of safflower can be achieved.

The relative expression of main gene effects revealed major contribution of dominance effects associated with dominance $\times$ dominance type of interaction of all characters in majority of crosses. Both additive and dominance gene effects were significant for majority of characters in all crosses. Duplicate type of epistasis played a major role in expression of most of the traits. Complementary type of epistasis was observed for days to 50% flowering, plant height, seed yield. The study provides heterosis breeding and recurrent selection to be suitable breeding program for the improvement of the characters studied. Selection between lines and families would be rewarding if high epistatic variance is present. For those characters having equal magnitude of additive and dominance variance, either population improvement programme or composite variety can be opted for the development of superior lines with desirable genes.

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The author does not have any conflict of interest

Contribution of Authors:

Yengkhom Linthoingambi Devi did the phenotyping and analysis of data; Rajeev Shrivastava checked and edit the manuscript.

Author Contribution

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