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RESEARCH ARTICLE

Insights from gene effects on agronomic, oleic acid and oil content using generation mean analysis in sunflower (*Helianthus annuus* L.)

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Abstract

Plant hybridization produces hybrids with desirable traits such as high oil content, oleic acid and yield, enhancing the significance of crops. Understanding genetic dominance is essential for studying gene action in breeding programs. Using four parental lines, this study assessed gene action, genetic advance with heritability and heterosis for oleic acid, oil content, agronomic and yield traits in sunflowers. The IR6 × HO-5-29 ($P_1 \times P_2$) cross I population demonstrated superior performance, while the CMSB825B × COSF6B ($P_3 \times P_4$) cross II population also performed well based on mean performance. Generation mean analysis revealed that additive and dominance gene actions influenced trait inheritance, with dominance effects being more pronounced. Additive × additive interactions played a key role in traits like days to flowering and maturity, palmitic acid content and oleic acid content in cross I and head diameter in cross II. Additive × dominance interactions significantly influenced head diameter, 100-seed weight and oleic acid content in cross I and plant height in cross II. Dominance × dominance interactions strongly influenced seed and oil yield per plant, oil content and linoleic acid content in cross I and seed and oil yield per plant and volume weight in cross II. Duplicate gene action was observed for head diameter and 100-seed weight, whereas complementary gene action was observed for seed and oil yield per plant in both crosses. These findings offer valuable insights for plant breeders and farmers, supporting the development of sunflower varieties and hybrids with enhanced oleic content, oil content and yield.

Keywords

additive interactions; gene actions; GMA; oil content; oleic acid content

Introduction

Sunflower (*Helianthus annuus L.*) is an essential source of vegetable oil globally. In India, the largest producer of oilseeds, the oilseed sector holds a significant position in agriculture, ranking second only to food grains in terms of area and value. India is the fifth-largest vegetable oil producer globally, after the USA, China, Brazil and Argentina. However, India produces a relatively small amount of sunflower seeds. In 2023-2024, it ranked 14th globally, producing 112000 metric tons, only 0.2% of the world's total (1). The leading sunflower seed producers are Russia (31%), Ukraine (28%) and the European Union (18%). In India, sunflowers are primarily grown in Karnataka, Haryana and Odisha, with smaller amounts in states like Telangana, Bihar and Tamil Nadu (2).

Sunflower is native to southwestern North America and domesticated in central North America. It belongs to the Asteraceae family. It is a cross-pollinated crop with chromosomes (2n = 34), known for its high yield potential and adaptability to diverse environments (3,4). Sunflowers used in food and non-food industries with high oleic acid cultivars like Pervenets, developed to meet market demands (5-7). Sunflower seeds contain 35-45% oil, primarily oleic acid content (OAC) (20-25%) and linoleic acid (55-70%), with composition influenced by genetics and environment (7). Traditional genotypes are classified by oleic acid content as high oleic (75-91%), mid-oleic (42-72%) and low oleic (14-39%). Pervenets were developed using 0.5% DMS solution on VNIMK 8931 seeds, which resulted in 80-90% oleic acid (5).

High-oleic sunflower oil offers numerous benefits for consumption and food processing due to its excessive oxidative firmness, resistance to inflated temperatures and lack of trans fat. It has reduced rancidity, a longer shelf life and lower processing costs. Additionally, it positively impacts factor VII coagulant activity and blood lipids (8). These advantages drive high demand and efforts to develop high-oleic sunflower lines/ hybrids and understand the mechanisms behind improved OAC (9). OAC inheritance in sunflowers is influenced by genetic background and environment. The partial dominance and dominance inheritance for high OAC were noticed (10-11). Additive gene action, modifiers and multiple genes contribute to this trait (12-14). At least three loci and a strong maternal effect influence the high-oleic trait. Further testing across various crosses and conditions is recommended (15).

Genetic improvement relies on selecting progenies with varying genetic values. Additive and dominant effects, known as gene actions , are estimated through Generation Mean Analysis (GMA), which aids breeders in developing new varieties (16-17). The six-parameter GMA model involves six populations (P_1, P_2, F_1, B_1, B_2 and F_2) to study gene actions and linkages. GMA is a valuable tool for understanding the genetic basis of qualitative and quantitative traits in crops like sunflowers. It analyzes variations within and between generations derived from crosses between different parental lines, estimating genetic correlations based on quantitative genetics and Mendelian inheritance (18). GMA is used to refine polygenic traits such as grain yield and its impact on other characteristics (18-19). Geneticists and plant breeders utilize GMA to understand the inheritance of essential attributes (20). Improving grain yield requires understanding the inheritance of agronomic traits that influence yield (18). GMA effectively estimates genetic influences on polygenic traits (18,21 -22). This study aims to determine gene action in the inheritance of oil content, oleic acid, grain yield and selected agronomic characteristics.

Materials and Methods

Location and climatic conditions

The research was conducted at the Department of Oilseeds, Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore. The study location is 426.72 meters above mean sea level, with geographic coordinates of 11 °N latitude and 77 °E longitude. The experimental farm has sandy loam soil and the region has a tropical climate between 24 °C and 34 °C.

Crossing and F_1 generation development

This study used four sunflower parents to produce two populations: IR6 × HO-5-29 (P_1 × P_2) cross I and CMS825B × COSF6B (P_3 × P_4) cross II. F_1 hybrids were produced during the 2022 *Rabi* season. Parents P_1 and P_4 exhibited high oil content (39 -42%), while P_2 and P_3 had lower oil content (25-32%).

Development of B_1, B_2 and F_2 generations

In the 2023 *Kharif* season, four parents and two F1 hybrids crosses were sown in an experimental field. The F_1 generation was backcrossed with its respective parents to produce the first and second backcross (F_1 × P_1 and F_1 × P_2) generations. Concurrently, F_2 seeds are produced from the selfing of F_1 plants.

Field evaluation of P_1, P_2, B_1, B_2, F_1 and F_2 generations

The experiments followed a randomized complete block design (RCBD) with three replications. Seeds from the six populations, including P_1, P_2, F_1, B_1, B_2 and F_2, were sown during the *Rabi* season 2023. Planting was carried out intra and inter-row spacing of 30 × 45 cm. Standard agricultural practices were followed per recommended guidelines to ensure healthy crop cultivation. Each cross's six populations were grown in three replications: P_1, P_2 and F_1in 1 row, B_1 and B_2in 2 rows and F_2in 6 rows were allotted for each replication. Thirty plants from P_1, P_2 and F_1, 50 plants from B_1 and B_2 and 200 plants from the segregating F_2 population were selected for data recording.

Observations recorded

Nine traits were recorded from each genotype: days to first flowering (DF), days to maturity (DM), plant height (PH) (cm), head diameter (HD) (cm), hundred seed weight (HSW) (g), volume weight per 100 ml (VW) (g), oil content (OC) (%), seed yield per plant (SYP) (g) and oil yield per plant (OYP). In cross II, nine traits were analyzed. In comparison, cross I included four additional traits: oleic acid content (OAC) (%), linoleic acid content (LAC) (%), palmitic acid content (PAC) (%) and stearic acid content (SAC) (%) as the parents, HO-5-29 (P_2) possessed high OAC (80-85%) and low oil content (OC) (25-32%) and IR6 (P_1) had moderate OAC (40-45%) and high OC (39-42%). Thirteen traits are divided into agronomic, yield and oil traits. Agronomic traits include days to first flowering and maturity, plant height and head diameter. Yield traits include 100-seed weight, volume weight and seed and oil yield per plant. Oil traits consist of oil content and fatty acids (oleic, linoleic, stearic and palmitic acids).

Estimation of oil content and fatty acids using NIR spectrometer

Each sample's oil content and fatty acids (OAC, LAC, PAC and SAC) were estimated using a NIR spectrometer (Manufacturer: ZEUTEC, Germany; Model: SPA 1.0) concerning an established standard graph. Calibration requires a fine powder, obtained by grinding 5-6 grams of sunflower seeds from each sample using a mixer grinder for 1 to 2 minutes. The OC and fatty acids of the seeds are expressed as percentages (23).

Statistical analysis

Scaling tests (A, B, C and D) were performed for each trait to evaluate the additive dominance model and detect non-allelic gene interactions, following the approach with the different generations of both crosses (24). Significance was assessed *via* a t -test, with results considered significant if they deviated from zero within their standard errors as given in Equation 1-4 (25).

$$A=\overline{2BCP_1}-\bar{P}_1-\bar{F}_1=0 \quad \text{(Eqn. 1)}$$

$$B=\overline{2BCP_2}-\bar{P}_2-\bar{F}_1=0 \quad \text{(Eqn. 2)}$$

$$C=\overline{4F_2}-\overline{2F_1}-\bar{P}_1-\bar{P}_2=0 \quad \text{(Eqn. 3)}$$

$$D=\overline{2F_2}-\overline{BCP_1}-\overline{BCP_2}=0 \quad \text{(Eqn. 4)}$$

Here, $\bar{P}_1$, $\bar{P}_2$, $\bar{F}_1$, $\overline{BCP_1}$, $\overline{BCP_2}$ and $\overline{F_2}$represent the means of different generations. The variances were calculated from the variances of these respective generations.

Standard errors (SEs) were computed as the square roots of variances and a t-test was used to detect deviations from zero by comparing t-values with 5% and 1% significance levels. Genetic effects were estimated via a six-parameter model, calculating the mean (*m*), additive (*d*), dominance (*h*) and non-allelic interactions (*i, j, l*) as given in Equation 5-10 (26)

$$m=\bar{F}_2 \quad \text{(Eqn. 5)}$$

$$d=\overline{BCP1}_1-\overline{BCP1}_2 \quad \text{(Eqn. 6)}$$

$$h=\bar{F}_1-4\bar{F}_2-\left(\tfrac{1}{2}\right)\bar{P}_1-\left(\tfrac{1}{2}\right)\bar{P}_2+2\,\overline{BCP1}_1+2\,\overline{BCP1}_2 \quad \text{(Eqn. 7)}$$

$$i=2\overline{BCP1}_1+2\,\overline{BCP1}_2-4\,\bar{F}_2 \quad \text{(Eqn. 8)}$$

$$j=\overline{BCP1}_1-(1/2)\bar{P}_1-2\,\overline{BCP1}_2+(1/2)\,\bar{P}_2 \quad \text{(Eqn. 9)}$$

$$l=\bar{P}_1+\bar{P}_2+2\,\bar{F}_1+4\bar{F}_2-4\,\overline{BCP1}_1-4\,\overline{BCP1}_2 \quad \text{(Eqn. 10)}$$

where, $\bar{P}_1$, $\bar{P}_2$, $\bar{F}_1$, $\overline{BCP}_1$, $\overline{BCP}_2$ and $\overline{F}_2$ are the means of the respective generations. Statistical analyses were performed via MS Excel and the TNAUSTAT package (27). Heterosis, degree of dominance and inbreeding depression were assessed; better and mid-parent heterosis (BPH and MPH) were calculated according to the standard method (28). Residual heterosis over the mid-parent value (RHM) was calculated (29). The degree of dominance (DD), Inbreeding depression (ID), heritability (broad-sense) and genetic advance (GA), percentage GA over the percent of the mean (GAM) was determined as per equation 11-18 (30-33).

$$\text{MPH}\ (\%)=\frac{\bar{F}_1-\overline{MP}}{\overline{MP}}\times 100 \quad \text{(Eqn. 11)}$$

$$\text{BPH}\ (\%)=\frac{\bar{F}_1-\overline{BP}}{\overline{BP}}\times 100 \quad \text{(Eqn. 12)}$$

$$\text{RHM}\ (\%)=\frac{\bar{F}_2-\overline{MP}}{\overline{MP}}\times 100 \quad \text{(Eqn. 13)}$$

$$\text{ID}\ (\%)=\frac{\bar{F}_1-\bar{F}_2}{\bar{F}_1}\times 100 \quad \text{(Eqn. 14)}$$

$$DD=\sqrt{H/D} \quad \text{(Eqn. 15)}$$

$$H=\frac{VF_2-(VP_1+VP_2+VF_1)/3}{VF_2}\times 100 \quad \text{(Eqn. 16)}$$

$$GA=\frac{VF_2-(VE)}{SQRT(VF_2)}\times K \quad \text{(Eqn. 17)}$$

$$GAM=\frac{GA}{\text{Mean of } F_2}\times 100 \quad \text{(Eqn. 18)}$$

Results and Discussion

Variations of traits across generations within the population

Genetic analysis of quantitative traits, mainly through generation mean analysis (GMA), enables precise partitioning of genetic variance and helps optimize breeding programs by understanding the relationship between yield and its components (17). Non-allelic interactions, or epistasis, play a significant role in genetic variance, influencing breeding strategies for crop improvement (22, 34). Improving any trait requires knowledge of the gene action involved in its expression. Various biometrical methods, such as line × tester, diallel, partial diallel, GMA and triple test cross (TTC), are used to estimate gene action. Among these, only GMA and TTC assess non-allelic interactions. While TTC identifies the presence or absence of epistasis, it does not measure its components.

In contrast, GMA evaluates both the presence of epistasis and the magnitude of its components (35). This study investigates genetic dominance in sunflower populations, focusing on yield traits, oil content and oleic acid content. It evaluates gene action, heritability, genetic advances and heterosis, providing insights for breeding high-yield sunflowers with enhanced oil and oleic acid content. To estimate epistatic effects from two crosses, generation mean analysis was conducted using Hayman's six-parameter model (26). This comprehensive approach aims to improve the understanding of genetic factors influencing sunflower traits, facilitating the development of superior cultivars.

Our findings revealed wide variation in means among the six populations from the two studied crosses (P_1, P_2, F_1, B_1, B_2 and F_2) across most traits (Table 1). In cross I (IR6 × HO-5-29), traits such as PH, HD, SYP, HSW, VW, OC, OYP and OAC and in cross II (CMS 825B × COSF 6B), traits including HD, SYP, HSW, VW, OC and OYP, showed F_1 dominance over the parents, suggesting that overdominance may significantly influence these traits. Additionally, transgressive segregation in successive generations conveyed complementary genes and epistatic effects, enhancing these traits. Conversely, traits like DF, DM, LAC, PAC and SAC in cross I and PH, DF and DM in cross II exhibited less dominance. They were sometimes intermediate between the parents, indicating partial control by the cross itself.

Scaling test and gene action

Gene action is crucial in plant breeding, enabling breeders to evaluate parental potential, optimize hybrids and utilize additive effects and heterosis to enhance yield and resilience (17, 22). The scaling test supports the additive-dominance model. All traits except plant height are significant in cross I, while all characteristics are significant in cross II (CMS 825B × COSF 6B). For the essential characteristics, a six-parameter model, accounting for additive, dominance and interaction effects, was used to identify the best-fit models (Table 2). This analysis highlighted significant non-allelic interactions and estimated various genetic components. In cross II, plant height is significant across all four scales.

In contrast, none of the scales for plant height in cross I are significant, necessitating a three-parameter model for this trait. The dominance effect exceeds the additive effect, with no evidence of epistatic effects. The significance of a gene effect indicates its role in trait inheritance. When multiple gene effects are significant for a trait, the magnitude of each effect determines its primary influence on the inheritance of that trait (21, 36-38). The mean effects were highly significant across all traits presented in Table 2. For additive and dominance genetic

Table 1. Mean performance and standard error of yield-contributing traits in six populations of sunflower in two crosses

Characters	Cross	P_1	P_2	F_1	F_2	B_1	B_2
Plant height (cm)	I	127.10 ± 1.28	85.67 ±0.98	156.43 ± 1.11	130.74 ± 1.67	139.22 ± 1.59	122.22 ± 2.47
	II	160.60 ± 0.58	118.20 ± 0.80	140.77 ± 0.76	131.22 ± 1.60	147.82 ± 0.98	123.20 ± 1.24
Head diameter (cm)	I	8.72 ± 0.14	12.47 ± 0.26	14.93 ± 0.20	12.88 ± 0.19	12.96 ± 0.25	13.80 ± 0.18
	II	11.10 ± 0.19	13.00 ± 0.15	14.50 ± 0.21	13.22 ± 0.13	13.58 ± 0.16	14.22 ± 0.17
Seed yield per plant (g)	I	18.37 ± 0.54	33.5 ± 0.97	48.37 ± 1.61	37.27 ± 1.05	27.83 ± 1.30	39.70 ± 1.67
	II	26.22 ± 0.46	31.76 ± 0.47	37.20 ± 0.83	31.63 ± 0.81	27.13 ± 0.49	33.39 ± 0.77
Volume weight per 100 ml (g)	I	35.62 ± 0.57	35.41 ± 0.67	42.22 ± 0.37	41.50 ± 0.24	40.97 ± 0.22	42.06 ± 0.26
	II	40.96 ± 0.27	41.30 ± 0.42	47.60 ± 0.27	41.89 ± 0.18	41.02 ± 0.33	42.85 ± 0.41
Hundred seed weight (g)	I	2.86 ± 0.10	4.80 ± 0.10	5.44 ± 0.11	5.04 ± 0.09	5.11 ± 0.10	5.28 ± 0.09
	II	6.18 ± 0.08	5.23 ± 0.14	6.00 ± 0.13	6.37 ± 0.05	6.20 ± 0.09	6.56 ± 0.08
Days to first flowering	I	66.60 ± 0.40	64.07 ± 0.31	65.90 ± 0.29	62.95 ± 0.30	65.32 ± 0.32	63.02 ± 0.45
	II	61.07 ± 0.56	55.07 ± 0.40	60.73 ± 0.73	59.55 ± 0.28	56.94 ± 0.38	60.80 ± 0.43
Days to maturity	I	99.60 ± 0.40	97.07 ± 0.31	98.90 ± 0.29	95.95 ± 0.30	98.32 ± 0.32	96.02 ± 0.45
	II	89.07 ± 0.56	83.07 ± 0.40	88.73 ± 0.73	87.55 ± 0.28	84.94 ± 0.38	88.80 ± 0.43
Oil content (%)	I	40.77 ± 0.27	30.43 ± 0.34	41.53 ± 0.25	37.15 ± 0.39	37.10 ± 0.40	35.32 ± 0.44
	II	28.23 ± 0.42	41.27 ± 0.31	41.93 ± 0.39	36.15 ± 0.48	34.82 ± 0.66	39.88 ± 0.48
Oil yield per plant (g)	I	7.48 ± 0.56	10.23 ± 0.94	20.1 ± 1.60	10.26 ± 1.03	14.12 ± 1.32	13.84 ± 1.48
	II	7.39 ± 0.15	13.11 ± 0.23	15.63 ± 0.42	11.43 ± 0.34	9.44 ± 0.24	13.32 ± 0.36
Oleic acid content(%)	I	42.50 ± 0.30	85.55 ± 0.46	86.80 ± 0.46	67.10 ± 1.22	72.79 ± 0.98	77.04 ± 0.78
Linoleic acid content (%)	I	52.53 ± 0.45	11.20 ± 0.45	9.75 ± 0.45	27.79 ± 1.17	23.16 ± 0.95	19.05 ± 0.76
Palmitic acid content (%)	I	0.60 ± 0.05	0.50 ± 0.03	0.57 ± 0.03	0.36 ± 0.01	0.54 ± 0.04	0.45 ± 0.02
Stearic acid content (%)	I	4.72 ± 0.30	2.82 ± 0.23	2.95 ± 0.23	4.50 ± 0.10	3.90 ± 0.22	3.70 ± 0.18

Cross I: $P_1 \times P_2$, IR6 × HO-5-29, Cross II: $P_3 \times P_4$, CMSB825B × COSF6B.

Table 2. Estimates of scaling test and genetic components of generation mean for the two sunflower crosses

Characters	Cross	Scaling test				Genetic components of generation mean					
		A	B	C	D	*m*	*d*	*h*	*i*	*j*	*l*
Plant height (cm)	I	-5.09	2.34	-2.67	0.04	106.46**	20.72**	47.14**	-	-	-
	II	-5.73 **	-12.57 **	-35.47 **	-8.59 **	131.22 **	24.62 **	18.55 **	17.18 *	3.42 *	1.11
Head diameter (cm)	I	2.27**	0.20	0.45	-1.01*	12.88**	-0.84**	6.36**	2.02*	1.03**	-4.49**
	II	1.56 **	0.94 *	-0.24	-1.37 **	13.22 **	-0.64 **	5.19 **	2.74 **	0.31	-5.24 **
Seed yield per plant (g)	I	-11.07**	-2.50	0.43	7.00*	37.27**	-11.87**	8.41	-14.00*	-4.29*	27.58**
	II	-9.17 **	-2.17 *	-5.87	2.73	31.63**	-6.27 **	2.75	-5.47	-3.50 **	16.81 **
Volume weight per 100 ml (g)	I	4.11**	6.50**	10.53**	-0.04	41.50**	-1.09**	6.78**	0.08	-1.19*	-10.69**
	II	-6.53**	-3.20**	-9.89**	-0.08	41.89**	-1.83**	6.64**	0.16	-1.66 **	9.57**
Hundred seed weight (g)	I	1.91**	0.31	1.62**	-0.30	5.04**	-0.17	2.21**	0.61	0.80**	-2.83**
	II	0.22	1.88**	2.07**	-0.02	6.37**	-0.36**	0.33	0.03	-0.83**	-2.13**
Days to first flowering	I	-1.86**	-3.93**	-10.69**	-2.45**	62.95**	2.30**	5.47**	4.90**	1.03	0.89
	II	-7.92**	5.80**	0.60	1.36	59.55**	-3.86**	-0.05	-2.72	-6.86**	4.84
Days to maturity	I	-1.86*	-3.93**	-10.69**	-2.45**	95.95**	2.30**	5.47**	4.90**	1.03	0.89
	II	-7.92**	5.80**	0.60	1.36	87.55**	-3.86**	-0.05	-2.72	-6.86**	4.84
Oil content (%)	I	-8.10**	-1.33	-5.69**	1.87	37.15**	1.78**	2.19	-3.74	-3.39**	13.17**
	II	-0.53	-3.44**	-8.77**	-2.40	36.15**	-5.06**	11.98**	4.80	1.46	-0.83
Oil yield per plant (g)	I	-11.22**	-4.57	-3.38	6.21*	35.79**	-10.44**	9.99	-12.41*	-3.33	28.20**
	II	-4.16**	-2.12*	-6.06**	0.10	11.43**	-3.88**	5.17**	-0.21	-1.02*	6.48**
Oleic acid content (%)	I	16.27**	-18.27**	-33.25**	-15.62**	67.10**	-4.25**	54.02**	31.25**	17.27**	-29.25**
Linoleic acid content (%)	I	-15.96**	17.16**	27.95**	13.37**	27.79**	4.11**	-48.86**	-26.75**	-16.56**	25.55**
Palmitic acid content (%)	I	-0.09	-0.18**	-0.81**	-0.27**	0.36**	0.09*	0.56**	0.54**	0.04	-0.27
Stearic acid content (%)	I	0.15	1.65**	4.57**	1.39**	4.50**	0.20	-3.60**	-2.78**	-0.75*	0.99

Cross I: $P_1 \times P_2$, IR6 × HO-5-29, Cross II: $P_3 \times P_4$, CMSB825B × COSF6B; A, B, C and D are scales, *m*: mean; *d*:additive; *h*:dominance, *i*: additive x additive, *j*: additive x dominant and *l*:dominant x dominant, one asterisk (*) and two asterisks (**) indicates significant at 5% and 1% probability levels, respectively.

effects, all traits, except plant height in cross II (CMS 825B × COSF 6B) and linoleic acid content in cross I (IR6 × HO-5-29), showed h > d, indicating that dominance genetic effects play a major role, with heterozygotes having a significant advantage or exhibiting a distinct phenotype compared to homozygotes. In contrast, for plant height in cross II (CMS 825B × COSF 6B) and linoleic acid content in cross I, h < d, suggesting that these traits are primarily influenced by additive genetic effects, where the contribution of individual alleles is more impactful than allele interactions. The estimates for the additive component (*d*) were highly significant and positive for PH, DF, DM, OC and LAC in cross I (IR6 × HO-5-29), as well as for plant height in cross II, indicating a substantial additive genetic contribution to these traits. Selection based on additive genetic variance can be effective. Conversely, the traits HD, SYP, VW, OYP and OAC in cross I, along with HD, SYP, VW, DF, DM, OC and OYP in cross II (CMS 825B × COSF 6B), were highly significant but negative, indicating a substantial negative additive genetic effect. Selection against these traits (or for their reduction) will be effective, as each favourable allele contributes negatively. The traits hundred seed weight and palmitic acid content were not significant in cross I, indicating that additive genetic effects are not contributing significantly to these traits.

The estimates for the dominance component (*h*) were non-significant for traits such as SYP, OC and OYP in cross I (IR6 × HO-5-29) and SYP, HSW, DF and DM in cross II, indicating that dominance is not a significant contributor to these traits. Positively highly significant values were observed for PH, HD, VW, HSW, DF, DM, OAC and PAC in cross I and for PH, HD, VW and OYP in cross II (CMS 825B × COSF 6B), indicating a substantial positive dominance effect, where heterozygotes exhibit superior performance compared to the average of the homozygotes. Negatively highly significant values were shown for LAC and SAC in cross I, indicating a substantial negative dominance effect, where heterozygotes perform worse than the average of the homozygotes. Highlighted the prominence of additive and dominance variance, with non-additive components being more significant (12). It was found that dominant genes significantly affected the seed set (39). The additive effects were the most significant in the cross, with partial dominance and no epistasis, while additive and dominant effects in some crosses and significant epistatic effects in others (40–41).

Non-allelic interactions

Epistasis studies help breeders to understand gene interactions influencing complex traits, enhancing selection strategies and hybrid performance. This knowledge optimizes breeding programs by targeting specific gene combinations for desirable traits (36-37). The estimates for the additive × additive component *(i)* showed highly significant positive values for DF, DM, OAC and PAC in cross I (IR6 × HO-5-29) and for head diameter in cross II (CMS 825B × COSF 6B), indicating substantial positive interactions between additive effects, where combinations of alleles from different loci enhance the trait (Table 2). Conversely, the SYP and OYP traits showed significant negative values in cross I, indicating substantial negative interactions between additive effects, where combinations of alleles from different loci reduce the trait. The additive × dominance component (*j*) estimates were highly significant and positive for HD, HSW and OAC in cross I (IR6 × HO-5-29), indicating a substantial positive interaction between additive and dominance effects. This suggests that dominant alleles enhance the additive effect of other loci. Conversely, OC and LAC in cross I and SYP, VW, HSW, DF and DM in cross II (CMS 825B × COSF 6B) showed highly significant negative values, indicating a substantial negative interaction between additive and dominance effects, where dominant alleles reduce the additive effect of other loci. The estimates for the dominance × dominance component (*l*) exhibited highly significant positive values for SYP, OC, OYP and LAC in cross I (IR6 × HO-5-29) and for SYP, VW and OYP in cross II, indicating a substantial positive interaction between dominance effects. This suggests that combinations of dominant alleles from different loci enhance the trait. Significant parameters indicate important genetic effects in trait inheritance, which breeders should consider in their selection strategies. Non-significant parameters suggest that the corresponding genetic effects are less influential and may be less relevant in breeding programs (16,21,37-38). Significant additive × dominant gene (*j*) epistasis was found in three combinations, along with (*i*) and (*l*) interactions in several crosses (39). Significant additive × dominance effects were reported, with dominance being influential (40). The varying importance of epistatic gene effects was observed over two years, highlighting significant *i* and *l* effects in specific crosses that emphasized the role of dominant genes in seed set inheritance (41-42).

Duplicate gene action was observed in cross I (IR6 × HO-5-29) for traits such as head diameter, volume weight, 100-seed weight and fatty acid content (oleic, linoleic, stearic and palmitic acids). Cross II (CMS 825B × COSF 6B) was noted for head diameter, 100-seed weight, days to flowering and maturity and oil content. Breeders should first use bi-parental mating to improve these traits, followed by recurrent selection in subsequent generations. Duplicate gene action involves dominance effects where heterozygotes express the dominant phenotype, with each gene acting independently. Dominant × dominant epistasis leads to duplicate epistasis, producing intermediate trait values between additive and dominance effects (37). Complementary gene action was found in cross I for seed and oil yield per plant, days to flowering and maturity and oil content and in cross II for plant height, volume weight and seed and oil yield per plant. Selection for these traits is more effective in later generations, as complementary gene action occurs when dominant alleles from different loci combine to enhance a trait. Understanding these gene effects is essential for improving desirable crop traits. Results are cross-specific and may not apply universally to all parent plants. Both additive and non-additive effects can be used in selection, including dominance x dominance and complementary interactions. Breeding strategies such as reciprocal recurrent selection or bi-parental mating are effective when both effects are present. Additionally, recurrent selection through one or two cycles of crossing selected plants can help accumulate beneficial genes, improving traits like seed yield.

Heterosis and degree of dominance

Hybridization is an effective method for enhancing plant traits and contributing to global food security. Genetic dominance in hybrids or plant populations is essential for determining gene effects and developing improved varieties. Heterosis, the superior performance of hybrids over their parents, boosts crop productivity by combining positive traits from both parents (36-37). Dominance heterosis allows dominant alleles to outperform recessive ones, enabling inbred lines to match F_1hybrids by removing deleterious alleles while pooling favourable ones (16,38).

Our findings include mid and better-parent heterosis (MPH and BPH), residual heterosis over mid-parent (RHM), inbreeding depression and degree of dominance for both crosses (Table 3). For mid-parent heterosis (MPH), all traits except DF, DM, LAC, PAC and SAC are highly significant in cross I (IR6 × HO-5-29). All traits except plant height (PH) are highly significant in cross II. The highest MPH values in both crosses are observed in seed and oil yield, while the lowest values are found in linoleic and steric acid content in cross I (IR6 × HO-5-29) and in Plant height and days to maturity in cross II (CMS 825B × COSF 6B). For better parent heterosis (BPH), cross I shows significant traits such as PH, HD, SYP, HSW, OC, OYP and OAC, while cross II (CMS 825B × COSF 6B) demonstrates highly significant traits including PH, HD, SYP, VW, HSW and OYP. Volume weight, linoleic acid in Cross I and oil content in cross II are significant. The highest BPH values in cross I are observed in OAC and OYP, while in cross II, they are in OYP and SYP. High residual heterosis (RHM) values are observed in SYP and OYP for cross I (IR6 × HO-5-29) and in HSW and OYP for cross II. Highly significant traits in cross I include PH, DM, VW, SYP, HSW, OC, OYP and OAC, while cross

Table 3. Assessment of heterosis, inbreeding depression and degree of dominance of two crosses of sunflower

Characters	Cross	Heterosis				DD
		MPH	BPH	RHM	ID	
Plant height (cm)	I	47.05**	23.08**	22.90**	16.42	-0.69
	II	0.98	-12.35**	-5.87**	6.79	-0.95
Head diameter (cm)	I	40.97**	19.79**	21.54**	13.78	-0.87
	II	20.33**	11.54**	9.67**	8.86	-0.90
Seed yield per plant (g)	I	86.35**	44.23**	43.59**	22.95	-0.58
	II	28.34**	17.16**	9.11**	14.98	-0.96
Volume weight per 100 ml (g)	I	18.87**	18.53*	16.85**	1.70	-1.32
	II	15.74**	15.28**	1.86**	12.00	-3.03
Hundred seed weight (g)	I	41.93**	13.27**	31.54**	7.32	-0.91
	II	5.23**	-2.83	11.68**	-6.13	-1.18
Days to first flowering	I	0.87	-1.05	-3.66	4.48	-0.75
	II	4.59**	-0.55	2.55**	1.95	-1.12
Days to maturity	I	0.58	-0.70	-2.43	2.99	-0.75
	II	3.10**	-0.37	1.72*	1.33	-1.12
Oil content (%)	I	16.67**	1.88**	4.34**	10.57	-0.85
	II	20.67**	1.62*	4.03**	13.79	-0.75
Oil yield per plant (g)	I	88.09**	46.99**	40.72**	25.19	-0.68
	II	52.48	19.23**	11.46**	26.90	-0.94
Oleic acid content (%)	I	35.57**	104.21**	4.80**	22.69	-0.93
Linoleic acid content (%)	I	-69.41	-81.45*	-12.77*	-185.16	-0.93
Palmitic acid content (%)	I	3.67	-4.86	-34.74	37.05	-1.34
Stearic acid content (%)	I	-21.79	-37.55	19.47	-52.76	-1.11

Cross I: $P_1 \times P_2$, IR6 × HO-5-29, Cross II: $P_3 \times P_4$, CMSB825B × COSF6B; MPH: mid-parent heterosis, BPH: better parent heterosis, RHM: residual over mid-parent heterosis, ID: inbreeding depression and DD: degree of dominance.

II includes PH, DM, SYP, VW, HSW, DF, OC and OYP. LAC is significant in cross I and DM in Cross II. DF, DM, PAC and SAC are non-significant in cross I. Substantial and high values of MPH and BPH indicate that the hybrid outperforms its parents, reflecting strong hybrid vigour. In contrast, non-significant and low values suggest weaker hybrid vigour, with performance closely aligned to that of the parents (16,36,38).

In breeding programs, understanding the degree of dominance is essential for predicting hybrid performance and enhancing traits such as yield and yield contributing traits. In cross I (IR6 × HO-5-29), traits like VW, PAC and SAC exhibited a degree of dominance greater than unity (±1.0), while in cross II (CMS 825B × COSF 6B), traits such as VW, HSW, DF and DM showed similar patterns. This suggests that overdominance significantly influences the inheritance of these traits. For the remaining characteristics in both crosses, the degree of dominance ranged from zero to ±1.0, indicating partial to complete dominance effects in their inheritance. Inbreeding depression (ID) refers to declining vigour, fertility and overall performance from breeding closely related plants. Understanding this phenomenon is crucial for maintaining crop performance. Most traits in both crosses show low ID, except for LAC and SAC in cross I, which exhibit high ID. Low ID suggests that the breeding population retains good performance despite some inbreeding. Managing inbreeding depression is vital for sustaining crop performance. Breeders can mitigate its negative effects and enhance crop resilience and productivity through hybrid breeding and careful selection. F_1 and F_2 means for the cross were intermediate between parental means, with F_1 values closely aligning with mid-parent values (40). Variable F_1 yields were observed over the years, with consecutive increases in the first and second years, highlighting significant heterosis (41).

Heritability and genetic advance

Heritability, genetic advance and genetic advance as a percentage of the mean are key for predicting selection response. High values indicate strong genetic influence and potential for significant trait improvement, guiding breeders in making informed breeding decisions and understanding expected outcomes (43-44). High broad-sense heritability was observed for PH, HD, SYP, HSW, DF, DM, OC, OYP, OAC, LAC and SAC in cross I (IR6 × HO-5-29) and for PH, SYP, OC and OYP in cross II (Table 4). Correspondingly, high estimates of GA and GAM were found for these traits, suggesting that these traits are directly inherited, controlled by a few key genes, or significantly influenced by additive gene effects, indicating that assortment will be more effective due to strong genetic influence and minimal environmental impact. Conversely, cross II distinguished low broad-sense heritability for VW, HSW, DF and DM. Low genetic estimates for GA and GAM were observed in VW and DM in cross I and VW, HSW, DF and DM in cross II, indicating these traits are more inclined by the environment, making selection less effective. Researchers reported high heritability and significant genetic advances for OYP and PH (43). The researchers observed the high heritability across all traits and significant genetic advances for DF, PH and OC (44-45). There is high heritability for DM, moderate heritability for DF and OC and notable genetic advances for SYP and DM (46). High-oleic sunflower oil is valued for its heart-health benefits, rich monounsaturated fatty acids and greater stability during processing (5,9,47). Sunflower breeding focuses on developing high-oleic hybrids to improve seed and oil yields. The higher oleic acid content increases the oil's shelf life and oxidative stability, benefiting pharmaceutical, cosmetic, industrial and edible applications. Heterosis plays a crucial role in optimizing genotypes for enhanced fatty acid.

Table 4. Estimates of variability analysis in the two crosses of sunflower

Characters	Cross	H^2 bs	GA	GAM
Plant height (cm)	I	93.10	45.26	34.62
	II	97.00	45.24	34.48
Head diameter (cm)	I	82.60	4.56	35.40
	II	68.70	2.55	19.26
Seed yield per plant (g)	I	82.90	25.48	68.36
	II	91.60	21.66	68.47
Volume weight per 100 ml (g)	I	19.00	1.30	3.14
	II	52.10	2.75	6.56
Hundred seed weight (g)	I	79.60	2.00	39.61
	II	19.10	0.29	4.52
Days to first flowering	I	81.00	7.03	11.17
	II	34.90	2.83	4.76
Days to maturity	I	81.00	7.03	7.33
	II	34.90	2.83	3.24
Oil content (%)	I	91.70	10.50	28.28
	II	90.60	12.54	34.68
Oil yield per plant (g)	I	82.20	24.60	68.74
	II	89.00	8.76	76.66
Oleic acid content (%)	I	98.30	35.05	52.23
Linoleic acid content (%)	I	97.80	33.25	91.65
Palmitic acid content (%)	I	13.30	0.05	13.13
Stearic acid content (%)	I	93.10	45.26	34.62

Cross I, $P_1 \times P_2$, IR6 × HO-5-29, cross II, $P_3 \times P_4$, CMSB825B × COSF6B; H^2bs %: broad sense heritability, GA: Genetic advance; GAM: Genetic advance as a percent of the mean.

Conclusion

This study shows the importance of additive and dominance gene actions in sunflower traits like oil content, seed yield and oleic acid content, using two crosses: IR6 × HO-5-29 (cross I) and CMS 825B × COSF 6B (cross II). Cross I performed better overall, with strong dominance effects, making it a good candidate for hybrid breeding. While duplicate gene action created challenges in improving traits like head diameter and 100-seed weight, complementary gene action for seed and oil yield highlighted the benefits of selecting in later generations. High heritability and genetic advancement confirm that choosing the proper traits can be effective and the observed hybrid vigour (heterosis) shows the value of hybridization in overcoming weaknesses. Further genetic and genomic studies are needed to understand specific gene interactions, especially with more inbred lines. These findings provide valuable insights for sunflower breeders and farmers in developing high-yielding, high-oil varieties and hybrids.

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Authors' contributions

Conceptualization and coordination of the research work were carried out by SL, KT and SR. Resources were provided by KT, SR, HS and SM. Methodology was developed by KT, SR, HS, SM and AB. Data collection, formal analysis, and original draft preparation were carried out by SL. Writing, editing and review were handled by SL, GV and AE. Supervision was provided by KT, SR, HS, SM and AB. All authors have reviewed and approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest : The authors state that they have no conflicts of interest regarding the publication.

Ethical approval : This article does not involve any studies conducted by the authors with human participants or animals.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors used the QuillBot tool to enhance language and readability and carefully reviewed the content afterwards.

Data availability

The datasets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

References

1. USDA. Production - Sunflowerseed [intenet]. United States Department of Agriculture; 2024 [cited 2024 Sept 18]. Available from: https://fas.usda.gov/data/production/commodity/2224000
2. UPAg. Unified Portal for Agricultural Statistics [internet]. New Delhi: Department of Agriculture and Farmer's Welfare. 2024 [cited 2024 Sept 18]. Available from: https://upag.gov.in/
3. Sampath L, Sasikala R, Kalaimagal T, Santhiya V, Antony B. Genetic diversity analysis in sunflower (*Helianthus annuus* L.) germplasms. J Oilseeds Res; 2023,38(3):244-50. https://doi.org/10.56739/jor.v40iSpecialissue.145374
4. Lavudya S, Thiyagarajan K, Ramasamy S, Sankarasubramanian H, Muniyandi S, Bellie A, Kumar S, Dhanapal S. Assessing population structure and morpho-molecular characterization of sunflower (*Helianthus annuus* L.) for elite germplasm identification. Peer J. 2024;12:e18205.https://doi.org/10.7717/peerj.18205
5. Soldatov KI. Chemical mutagenesis in sunflower breeding. In: Proc. 7th Int. Sunflower Conf., Krasnodar, USSR ;1976 Jun 27 Vlaardingen, the Netherlands: Int. Sunflower Assoc; 1976 [cited 2024 Sep 18]. p. 352-7). Available from: https://www.scirp.org
6. Cvejić S, Miladinović D, Jocić S. Mutation breeding for changed oil

quality in sunflower. In: Tomlekova NB, Kozgar NI, Wani MR, Editors. Mutagenesis: exploring genetic diversity of crops. Leiden, The Netherlands: Wageningen Academic 2014. p. 77-96. https://doi.org/10.3920/9789086867967_006

7. Premnath A, Narayana M, Ramakrishnan C, Kuppusamy S, Chockalingam V. Mapping quantitative trait loci controlling oil content, oleic acid and linoleic acid content in sunflower (*Helianthus annuus* L.). Mol Breed. 2016;36:1-7. https://doi.org/10.1007/s11032-016-0527-2
8. Vannozzi GP. The perspectives of use of high oleic sunflower for oleochemistry and energy raws/perspectivas en la utilización de girasol de alto contenido oleico en la industria de procesamiento y como materia prima para la producción de energía/perspectives de l'utilisation du tournesol à haute teneur oléique dans l'industrie de transformation et comme base de production d'énergie. Helia. 2006;29(44):1-24. https://doi.org/10.2298/hel0644001v
9. Regitano A, Miguel AM, Mourad AL, Henriques EA, Alves RM. Environmental effect on sunflower oil quality. Crop Breed Appl Biotechnol. 2016;16(3):197-204. https://doi.org/10.1590/1984-70332016v16n3a30
10. Fick GN. Inheritance of high oleic acid in the seed oil of sunflower. In: Proceedings of Sunflower Research Workshop Bismarck, USA:Workshop. Natl. Sunflower Assooc., 1984 [cited 2024 18 Sept]. p. 1-8.
11. Urie AL. Inheritance of very high oleic acid content in sunflower. In: Proc. 6th Sunflower Res Bismarck, USA:Workshop. Natl. Sunflower Assooc., 1984 [cited 2024 18 Sept]. p. 9-10.
12. Joksimović J, Atlagić J, Marinković R, Jovanović D. Genetic control of oleic and linoleic acid contents in sunflower/control genético del contenido de aceite oleico y linólico en girasol/contrôle génétique des contenus d'acide oléique et linoléique chez le tournesol. Helia. 2006;29(44):33-40. https://doi.org/10.2298/hel0644033j
13. Lacombe S, Kaan F, Griveau Y, Bervillé A. The pervenets high oleic mutation: methodological studies/mutación altamente oleica pervenets: investigaciones metodológicas/mutation d'acides oléiques gras pervenets: recherches méthodologiques. Helia. 2004;27(40):41-54. https://doi.org/10.2298/hel0440041l
14. Berville A. Oil composition variations. In: Jinguo Hu, Gerald S, Kole C, editors. Genetics, genomics and breeding of sunflower. Boca Raton: Routledge; 2010. p. 253-77. https://doi.org/10.1201/b10192
15. Ferfuia C, Vannozzi GP. Maternal effect on seed fatty acid composition in a reciprocal cross of high oleic sunflower (*Helianthus annuus* L.). Euphytica. 2015;205:325-36. https://doi.org/10.1007/s10681-015-1378-3
16. Ganapati RK, Rasul MG, Sarker U, Singha A, Faruquee M. Gene action of yield and yield contributing traits of submergence tolerant rice (*Oryza sativa* L.) in Bangladesh. Bull Nat Res Centre. 2020;44:1-7. https://doi.org/10.1186/s42269-019-0261-0
17. Patel DK, Patel A, Patel CJ, Jat AL. Generation Mean Analysis for Seed Yield and Wilt Resistance in Castor (*Ricinus communis* L.). Ind J Agric Res. 2024;58(2). https://doi.org/10.18805/IJARe.A-5685
18. Sandhu R, Singh B, Delvadiya IR, Pandey MK, Rai SK, Attri M. Genetic analysis of grain yield and its contributing traits in four bread wheat (*Triticum aestivum* L.) crosses using six parameter model. Elect J Pl Breed. 2023;14(1):154-9. https://doi.org/10.37992/2023.1401.032
19. Chandra D, Islam MA, Barma NC. Variability and interrelationship of nine quantitative characters in F5 bulks of five wheat crosses. Pak J Biol Sci. 2004;7(6):1040-5. https://doi.org/10.3923/pjbs.2004.1040.1045
20. Khaled M. Estimation of genetic variance for yield and yield components in two bread wheat (*Triticum aestivum* L.) crosses. J Plant Prod. 2007;32(10):8043-53. https://doi.org/10.21608/jpp.2007.220889
21. Singh CM, Singh AK, Mishra SB, Pandey A. Generation mean analysis to estimate the genetic parameters for yield improvement and inheritance of seed colour and lusture in mungbean [*Vigna radiata* (L.) Wilczek]. Legume Res. 2016;39(4):494-501. https://doi.org/10.18805/lr.v0iOF.10762
22. Pathak S, Pant U, Yadav VN, Mishra A. Analysis of genetic architecture through generation mean analysis for yield and yield contributing traits in crosses of Indian Mustard (*Brassica juncea*). J Adv Biol Biotech. 2024;27(8):462-70. https://doi.org/10.9734/jabb/2024/v27i81158
23. Anuradha B, Manivannan N, Sasikala R, Harish S, Senthivelu M. Genetic variability and association studies in BC 3 F 1 population of sunflower (*Helianthus annuus* L.). Electronic Journal of Plant Breeding. 2023;14(3):923-7. https://doi.org/10.37992/2023.1403.104
24. Mather K, Jinks JL, Mather K, Jinks JL. Components of means: additive and dominance effects. In: Kenneth M, John LJ, editors. Biometrical genetics: The study of continuous variation. Boston, MA:Springer; 1971.p.65-82. https://doi.org/10.1007/978-1-4899-3404-8_4
25. Singh RK, Chaudhary BD. Biometrical methods in quantitative genetic analysis. Lucknow: Kalyani Publisher; 1981
26. Hayman BI. The separation of epistatic from additive and dominance variation in generation means. Heredity;1958:371-90
27. Manivannan N. TNAUSTAT-Statistical package [internet]. Coimbatore: TNAU; 2018 [cited 2024 Sept 18] Available from: https: //sites.google.com/site/tnaustat
28. Fonseca S, Patterson FL. Hybrid vigor in a seven-parent diallel cross in common winter wheat (*Triticum aestivum* L.). Crop Sci. 1968;8(1):85-8. https://doi.org/10.2135/cropsci1968.0011183X000800010025x
29. Rao, N. Statistics for Agricultural Sciences. New Delhi: Oxford and IBH Publishing; 1980.
30. Robinson HF, Comstock RE, Harvey PH. Estimates of heritability and the degree of dominance in corn. Agron J; 1949:353-9.
31. Kempthorne O. An introduction to genetic statistics. New York: John Wiley and Sons, Inc.; 1957.
32. Warner JN. A method for estimating heritability. Agron J. 1952;44:427-30.
33. Johnson HW, Robinson HF, Comstock RE. Estimates of genetic and environmental variability in soybeans. Agron J. 1955;314-8.
34. Gaoh BS, Gangashetty PI, Mohammed R, Dzidzienyo DK, Tongoona P. Generation mean analysis of pearl millet [*Pennisetum glaucum* (L.) R. Br.] grain iron and zinc contents and agronomic traits in West Africa. J Cereal Sci. 2020;96:103066. https://doi.org/10.1016/j.jcs.2020.103066
35. Yadav S, Singh SP, Singhal T, Anju-Mahendru S, Bhargavi HA, Aavula N, Goswami S, Satyavathi CT. Genetic elucidations of grain iron, zinc and agronomic traits by generation mean analysis in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. J Cereal Sci. 2023;113:103751 https://doi.org/10.1016/j.jcs.2023.103751
36. Labroo MR, Studer AJ, Rutkoski JE. Heterosis and hybrid crop breeding: a multidisciplinary review. Front Gene. 2021;12:643761. https://doi.org/10.3389/fgene.2021.643761
37. Hassan HM, Hadifa AA, El-Leithy SA, Batool M, Sherif A, Al-Ashkar I, Ueda A, Rahman MA, Hossain MA, Elsabagh A. Variable level of genetic dominance controls important agronomic traits in rice populations under water deficit condition. PeerJ. 2023;11:e14833. https://doi.org/10.7717/peerj.14833
38. Pujar M, Govindaraj M, Gangaprasad S, Kanatti A, Gowda TH, Dushyantha Kumar BM, Satish KM. Generation mean analysis reveals the predominant gene effects for grain iron and zinc contents in pearl millet. Front Pl Sci. 2022;12:693680. https://doi.org/10.3389/fpls.2021.693680
39. Jocić S, Škorić D. Inheritance of some yield components in sunflower.). In: Proceedings, 16th International Sunflower Conference; 2004 29 Aug-2 Sept; 2004, Fargo, North Dakota, USA. Paris: International Sunflower Association. 2004 [cited 2024 18

Sept]. p. 503-10 Available from: https://www.isasunflower.org/

40. Cukadar-Olmedo B, Miller JF. Inheritance of the stay-green trait in sunflower. Crop Sci. 1997;37(1):150. https://doi.org/10.2135/cropsci1997.0011183X003700010026x

41. Marinković R, Vasić D, Joksimović J, Jovanović D, Atlagić J. Gene actions for seed yield in sunflower (*Helianthus annuus*). In: Proceedings, 16th International Sunflower Conference; 2004 29 Aug -2 Sept; 2004, Fargo, North Dakota, USA. Paris: International Sunflower Association. 2004 [cited 2024 18 Sept]. p. 511-6 Available from: https://www.isasunflower.org/

42. Gangappa E, Channakrishnaiah KM, Thakur S, Ramesh S. Genetic architecture of yield and its attributes in sunflower (*Helianthus annuus* L.). Helia. 1997,85-93.

43. Lagiso TM, Singh BC, Weyessa B. Evaluation of sunflower (*Helianthus annuus* L.) genotypes for quantitative traits and character association of seed yield and yield components at Oromia region, Ethiopia. Euphytica. 2021;217(2):27. https://doi.org/10.1007/s10681-020-02743-2

44. Delen Y, Palali-Delen S, Xu G, Neji M, Yang J, Dweikat I. Dissecting the genetic architecture of morphological traits in sunflower (*Helianthus annuus* L.). Genes. 2024;15(7). https://doi.org/10.3390/genes15070950

45. Vivek M, Sasikala R, Thangaraj K, Harish S, Sudha M. Exploring the genetic variability and association for yield and its integrant traits in sunflower (*Helianthus annuus* L.). Elec J Pl Breed. 2023;14(3):1090-6. https://doi.org/10.37992/2023.1403.123

46. Dudhe MY, Mulpuri S, Meena HP, Ajjanavara RR, Kodeboyina VS, Adala VR. Genetic variability, diversity and identification of trait-specific accessions from the conserved sunflower germplasm for exploitation in the breeding programme. Agric Res. 2020;9:9-22. https://doi.org/10.1007/s40003-019-00406-w

47. Izquierdo N, Aguirrezábal L, Andrade F, Pereyra V. Night temperature affects fatty acid composition in sunflower oil depending on the hybrid and the phenological stage. Field Crops Res. 2002;77(2-3):115-26. https://doi.org/10.1016/S0378-4290(02)00060-6