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Combining Ability Analysis and Nature of Gene Action for Yield, Oil Content and Associated Quantitative Traits in Linseed (*Linum usitatissimum* L.)

Patil Lalit Anil [a++*], Dhuppe Mohan Vaijnath [b#], Wadikar Padmakar Balasaheb [a†], Pole Shivshankar Panditrao [b‡], Mirkad Shambhonarayan Bhaskar [c^], Surya Prakash Sharma [a++] and Panchal Vijay Waman [a++]

[a] *Department of Genetics and Plant Breeding, College of Agriculture, Latur (VNMKV, Parbhani) Maharashtra, India.*
[b] *Oilseeds Research Station, Latur (VNMKV, Parbhani) Maharashtra, India.*
[c] *Department of Genetics and Plant Breeding, College of Agriculture, Parbhani (VNMKV, Parbhani) Maharashtra, India.*

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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[++] *M.Sc. (Agri.) Scholar;* [#] *Oilseeds Specialist;* [†] *Associate Professor;* [‡] *Junior Breeder;* [^] *Ph.D. Scholar;*
**Corresponding author: E-mail: patillalitanil@gmail.com;*

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Abstract

Aims: The present investigation was undertaken to estimate the general combining ability (GCA), specific combining ability (SCA), and nature of gene action governing seed yield, oil content, and associated quantitative traits in linseed (*Linum usitatissimum* L.), and to identify superior parents and cross combinations for future breeding programmes.
Study Design: Line × Tester mating design.
Place and Duration of Study: The experiment was conducted at the Oilseeds Research Station, Latur, Maharashtra, India, during the rabi *season* of 2025–26.
Methodology: Seven genetically diverse lines were crossed with six testers using the Line × Tester mating design to produce 42 F_1 hybrids. The experimental material, comprising 13 parents, 42 F_1 hybrids, and one standard check, was evaluated in a randomised block design with two replications. Observations were recorded for ten quantitative traits: days to 50% flowering, days to maturity, plant height, number of branches per plant, number of capsules per plant, number of seeds per capsule, harvest index, 1000-seed weight, seed yield per plant, and oil content. Combining ability analysis was conducted following the method proposed by Kempthorne (1957) to estimate GCA and SCA effects and determine the nature of gene action.
Results: Analysis of variance revealed significant differences among the genotypes for all the traits studied, indicating substantial genetic variability. Significant GCA and SCA variances were observed for most traits, demonstrating the involvement of both additive and non-additive gene effects in their inheritance. Among the parents, T-397, RLC-198, RLC-197, JLS-95, and RL-18123 were identified as superior general combiners for different economically important traits. The crosses OL-2013-14-2026 × BLS-2023R-20, NL-421 × BLS-2023R-19, LCK-2431 × JLS-95, and OL-2022-23-5 × BLS-2022R-30 exhibited desirable specific combining ability effects for seed yield and related traits. The results indicated the predominance of additive gene action for certain traits and non-additive gene action for others, suggesting the usefulness of both selection and hybridisation in linseed improvement.
Conclusion: The identified superior general combiners and specific cross combinations constitute valuable genetic resources for developing high-yielding linseed cultivars with improved quality. The findings provide useful information for selecting suitable parents and adopting appropriate breeding strategies for the genetic improvement of linseed.

Keywords: Linseed; line × tester analysis; general combining ability; specific combining ability; gene action; seed yield.

1. Introduction

Linseed (*Linum usitatissimum* L.; 2n = 30), commonly known as flax, is one of the oldest cultivated oilseed crops and is valued for its dual purpose as a source of edible oil and natural fibre. The crop has gained considerable economic importance owing to its nutritional, industrial, and pharmaceutical applications. Linseed seeds contain approximately 35–45% oil, which is rich in α-linolenic acid (an omega-3 fatty acid) recognised for its beneficial effects on cardiovascular health and human nutrition. Besides its nutritional value, linseed oil is widely used in the manufacture of paints, varnishes, printing inks, linoleum, cosmetics, and pharmaceutical products because of its excellent drying properties, whereas flax fibre is extensively utilised in the textile industry because of its superior strength and durability. These diverse applications make linseed an economically important crop worldwide (Green, 1986; Oomah, 2001).

According to the Food and Agriculture Organization of the United Nations (FAO, 2024), India is among the major linseed-producing countries. However, its average productivity remains considerably lower than the attainable genetic potential. The low productivity is primarily attributed to the cultivation of low-yielding cultivars, narrow genetic diversity, susceptibility to biotic and abiotic stresses, and inadequate exploitation of genetically superior parental materials in breeding programmes. Since seed yield is a complex quantitative trait governed by several component characters and strongly influenced by environmental conditions, the development of high-yielding cultivars with improved oil content requires a comprehensive understanding of the genetic architecture controlling these economically important traits (Mahawar et al., 2021; Mohammadi et al., 2010).

Recent assessments of linseed germplasm have also documented substantial variation in flowering, maturity, plant architecture, seed yield, and oil-related traits, thereby supporting the use of genetically diverse parents in crop improvement programmes (Ankit et al., 2024; Deshmukh et al., 2025; Kaur et al., 2024; Yadav et al., 2024).

Combining ability analysis is one of the most effective biometrical approaches for assessing the breeding potential of parental genotypes and identifying superior hybrid combinations. The concepts of general combining ability (GCA) and specific combining ability (SCA), proposed by Sprague and Tatum (1942), facilitate the partitioning of genetic variation into additive and non-additive genetic components. General combining ability reflects the average breeding performance of a parent and is primarily associated with additive gene effects, whereas specific combining ability represents the performance of individual cross combinations and is mainly governed by dominance and epistatic interactions. Estimates of GCA and SCA provide valuable information for parent selection, the identification of promising hybrids, and the formulation of appropriate breeding strategies for crop improvement (Falconer, 1989; Sprague & Tatum, 1942).

Among the available mating designs, the Line × Tester analysis proposed by Kempthorne (1957) is widely employed in self-pollinated crops because it provides reliable estimates of combining ability while requiring a relatively small number of crosses. The method enables breeders to identify superior general combiners and promising hybrid combinations, in addition to providing information on the relative importance of additive and non-additive gene effects. Such information is useful for selecting appropriate breeding methods, including pedigree selection, recurrent selection, and hybridisation, depending on the nature of gene action controlling different traits. Several investigators have successfully utilised Line × Tester analysis in linseed to identify superior parents and promising cross combinations for seed yield and associated traits (Mahto et al., 2019; Shivankar et al., 2021; Singh et al., 2016; Wadikar et al., 2019).

Recent combining-ability evidence further indicates that the relative contributions of additive and non-additive gene effects may differ across traits and parental combinations, reinforcing the need to evaluate specific breeding materials under relevant environments (Bezil et al., 2026).

Although several studies have demonstrated the usefulness of combining ability analysis in linseed, the magnitude and nature of gene action governing quantitative traits often vary with the genetic constitution of the parental lines and the prevailing environmental conditions. Moreover, information on the combining ability of newly developed breeding materials adapted to the agro-climatic conditions of Maharashtra remains limited. Therefore, the continuous evaluation of diverse parental lines is essential for identifying superior combiners and developing high-yielding cultivars with improved oil content. Hence, the present investigation was undertaken to estimate general and specific combining ability, elucidate the nature of gene action governing seed yield, oil content, and associated quantitative traits, and identify superior parents and promising cross combinations in linseed using the Line × Tester mating design.

2. Materials and Methods

The experiment was conducted during the rabi season of 2025–26 at the Oilseeds Research Station, Latur, Vasantrao Naik Marathwada Krishi Vidyapeeth (VNMKV), Parbhani, Maharashtra, India. The experimental site was located at 18°25′9.2″ N latitude and 76°36′53.4″ E longitude, at an elevation of approximately 631 m above mean sea level. The region is characterised by a semi-arid tropical climate and deep black (Vertisol) soils suitable for linseed cultivation. The experimental material comprised 13 parental genotypes, including seven lines (OL-2013-14-2026, OL-2022-23-5, RLC-197, NL-421, T-397, RLC-198, and LCK-2431) and six testers (RL-18123, BLS-2022R-30, KOTA BARANI ALSI-4, JLS-95, BLS-2023R-19, and BLS-2023R-20). Forty-two F_1 hybrids were developed by crossing the seven lines with the six testers using the Line × Tester mating design proposed by Kempthorne (1957). The field evaluation included 13 parents, 42 F_1 hybrids, and one standard check (LSL-93).

Hybridisation was carried out during the preceding crop season by manually emasculating healthy flower buds of the female parents in the evening before anthesis, followed by pollination on the following morning using freshly collected pollen from the respective male parents. The pollinated flowers were tagged and protected until maturity, and the harvested F_1 seeds were used for field evaluation. The experiment was laid out in a randomised block design (RBD) with two replications. Each genotype was grown in a single 3.0 m row, with 30 cm between rows and 10 cm between plants. Recommended agronomic and plant-protection practices were followed to ensure uniform crop growth throughout the experimental period.

Observations were recorded on five randomly selected competitive plants from each genotype in each replication for all quantitative traits, except days to 50% flowering and days to maturity, which were recorded on a plot basis. Data were collected for days to 50% flowering, days to maturity, plant height (cm), number of branches per plant, number of capsules per plant, number of seeds per capsule, harvest index (%), 1000-seed weight (g), seed yield per plant (g), and oil content (%). Oil content was estimated using nuclear magnetic resonance (NMR). The experimental data were subjected to analysis of variance (ANOVA) for a randomised block design following the procedure of Panse and Sukhatme (1985). Combining ability analysis was performed using the Line × Tester method proposed by Kempthorne (1957) to estimate general combining ability (GCA) and specific combining ability (SCA) effects. The variance components and the relative importance of additive and non-additive gene action were estimated, and the statistical analyses were conducted using R software.

3. Results and Discussion

Table 1. Analysis of variance for parents and hybrids for ten quantitative traits in linseed (*Linum usitatissimum* L.)

Sr. No.	Character	Replication (df = 1)	Treatment (df = 55)	Error (df = 55)	S.E. (±)
1	Days to 50 per cent flowering	7.000	22.917**	1.764	0.939
2	Days to maturity	0.893	6.321*	3.547	1.332
3	Plant height (cm)	1.080	174.654**	13.779	2.625
4	Number of branches per plant	0.321	1.850**	0.151	0.275
5	Number of capsules per plant	21.790	150.650**	8.803	2.098
6	Number of seeds per capsule	1.556	2.372**	0.487	0.493
7	Harvest index (%)	4.220	81.656**	5.383	1.641
8	1000-seed weight (g)	0.311	1.650**	0.106	0.230
9	Seed yield per plant (g)	0.173	1.294**	0.061	0.174
10	Oil content (%)	0.112	6.011**	0.981	0.700

The analysis of variance revealed highly significant differences among the parents, hybrids, and the standard check for all the quantitative traits studied, except days to maturity, for which the differences were significant at the 5% probability level (Table 1). The significant treatment mean squares indicated substantial genetic variability in the experimental material for seed yield, oil content, and their associated quantitative traits. Such variability provides considerable scope for identifying superior parental lines and promising hybrid combinations, thereby facilitating effective genetic improvement through appropriate breeding strategies.

Significant variation in plant height, number of branches per plant, number of capsules per plant, number of seeds per capsule, harvest index, 1000-seed weight, seed yield per plant, and oil content demonstrated considerable genetic diversity among the evaluated genotypes. The availability of such variability is a prerequisite for effective combining ability analysis and the selection of desirable parents and hybrids in breeding programmes. Similar observations have been reported for yield and associated traits in linseed, indicating the suitability of diverse genetic material for combining ability studies (Allard, 1960; Bhateria et al., 2006; Rathva et al., 2023; Singh & Tewari, 2016; Singh et al., 2022).

The observed variability among the experimental genotypes justified the subsequent estimation of general combining ability (GCA), specific combining ability (SCA), and the nature of gene action governing the inheritance of the studied traits. The significant differences among the treatments indicated adequate genetic diversity in the breeding material and provided a sound basis for identifying superior combiners and promising cross combinations for improving seed yield, oil content, and other economically important traits in linseed.

The estimates of general combining ability (GCA) effects revealed considerable variation among the parental genotypes for all the quantitative traits studied, indicating the importance of additive gene effects in the inheritance of several characters (Table 2). For days to 50 per cent flowering, significant negative GCA effects were recorded for LCK-2431 among the lines and RL-18123 among the testers, indicating their potential as desirable general combiners for developing early-flowering genotypes. Likewise, LCK-2431 exhibited negative GCA effects for days to maturity, suggesting its usefulness in breeding programmes aimed at developing early-maturing cultivars. Similar observations on the identification of superior general combiners for earliness have been reported by Ahmad et al. (2021) and Bisht and Paul (2019).

For plant height, T-397 exhibited significant negative GCA effects and was identified as the most desirable general combiner for developing relatively shorter plants. Among the yield-contributing traits, JLS-95 and KOTA BARANI ALSI-4 exhibited significant positive GCA effects for the number of capsules per plant, whereas BLS-2023R-20 was identified as a desirable tester for the number of branches per plant and the number of seeds per capsule. Significant positive GCA effects for seed yield per plant were recorded for RLC-198 and T-397 among the lines, whereas RL-18123 and JLS-95 emerged as superior testers for seed yield. These parents may therefore be effectively utilised in breeding programmes aimed at improving productivity. Comparable results have been reported by Bhateria et al. (2006) and Rathva et al. (2023), who also identified superior general combiners for seed yield and its component traits in linseed.

For quality traits, RLC-197 exhibited significant positive GCA effects for oil content among the lines, whereas JLS-95 and BLS-2022R-30 were identified as desirable testers for improving oil content. Similarly, OL-2013-14-2026 showed significant positive GCA effects for 1000-seed weight, indicating its potential as a valuable parent for improving seed size. The identification of these superior general combiners suggests the presence of favourable additive gene effects controlling the respective traits, which can be effectively exploited through selection in subsequent generations. Similar findings have been reported by Bhateria et al. (2006), Bisht and Paul (2019), and Singh et al. (2022).

The estimates of specific combining ability (SCA) effects revealed significant variation among the cross combinations for the quantitative traits studied, indicating the importance of non-additive gene effects in the inheritance of these characters (Table 3). For days to 50 per cent flowering, for which negative SCA effects are desirable in developing early-flowering genotypes, LCK-2431 × BLS-2023R-19, LCK-2431 × BLS-2023R-20, and OL-2013-14-2026 × BLS-2022R-30 exhibited significant negative SCA effects and were identified as promising cross combinations for earliness. Similar results were reported by Kumar et al. (2016) and Kumar et al. (2017), who identified specific cross combinations with desirable SCA effects for early flowering in linseed.

For plant height, significant negative SCA effects were observed in LCK-2431 × BLS-2023R-19, RLC-198 × BLS-2023R-20, and RLC-197 × KOTA BARANI ALSI-4, suggesting their suitability for developing comparatively shorter plant types. Among the yield-contributing traits, NL-421 × KOTA BARANI ALSI-4 and RLC-197 × RL-18123 exhibited desirable SCA effects for the number of capsules per plant, whereas RLC-198 × RL-18123 was identified as a superior cross for the number of branches per plant. Similar observations were reported by Khan et al. (1999) and Wadikar et al. (2019), who also demonstrated the importance of specific combining ability in identifying superior cross combinations for yield-attributing traits in linseed.

For harvest index, T-397 × KOTA BARANI ALSI-4, OL-2022-23-5 × BLS-2023R-19, and RLC-197 × KOTA BARANI ALSI-4 exhibited significant positive SCA effects, whereas RLC-198 × BLS-2023R-20 and OL-2022-23-5 × BLS-2022R-30 were identified as promising cross combinations for improving 1000-seed weight. Similar findings have been reported by Ahmad et al. (2021), who observed that favourable non-additive gene interactions contributed significantly to the improvement of yield-related traits in linseed.

Among all the hybrids, OL-2013-14-2026 × BLS-2023R-20 exhibited the highest significant positive SCA effect for seed yield per plant, followed by NL-421 × BLS-2023R-19, LCK-2431 × JLS-95, OL-2022-23-5 × BLS-2022R-30, and LCK-2431 × BLS-2023R-20. These crosses may therefore be considered the most promising combinations for enhancing seed yield in future breeding programmes. Although positive SCA effects for oil content were observed in several hybrids, OL-2022-23-5 × BLS-2022R-30, NL-421 × RL-18123, and T-397 × BLS-2022R-30 recorded comparatively higher estimates and may serve as useful breeding material for improving oil content. Comparable findings were reported by Bhateria et al. (2006) and Rathva et al. (2023), who also identified superior specific combiners for seed yield and quality traits in linseed.

The superiority of these cross combinations indicates the predominance of favourable non-additive gene interactions governing the expression of economically important traits. Therefore, these hybrids may be effectively utilised for heterosis breeding and for selecting superior segregants in advanced generations to develop high-yielding linseed cultivars with improved quality.

Table 2. General combining ability (GCA) effects of lines and testers for ten quantitative traits in linseed (*Linum usitatissimum* L.)

Parents	DFF	DM	PH	NBP	NCP	NSPC	HI	TSW	SYP	OC
Lines										
OL-2013-14-2026	-0.05	0.02	2.69	-0.82*	-5.03**	-0.38	-0.51	0.51**	-0.05	-0.75
OL-2022-23-5	1.45	1.27	4.97**	0.08	2.17	-0.80*	2.76**	0.12	-0.47**	0.56
RLC-197	1.20	-0.14	1.14	-0.14	2.70	-0.08	1.82	0.12	-0.37**	1.56**
NL-421	0.62	0.44	-1.46	0.11	0.23	0.45	-0.84	0.26	0.27	0.58
T-397	0.45	0.02	-5.65**	0.38	2.27	0.32	-2.94**	-0.09	0.25*	-1.65**
RLC-198	0.54	0.27	-2.00	0.10	-2.53*	0.42	1.22	-0.38**	0.40**	0.53
LCK-2431	-4.21*	-1.89	0.30	0.30	0.20	0.07	-1.50	-0.53**	-0.03	-0.83
Testers										
RL-18123	-2.76**	-0.73	-3.01	-0.10	-3.98**	-0.13	1.59	0.14	0.33**	-1.16**
BLS-2022R-30	1.31*	0.20	4.73**	-0.30	-2.48	0.28	0.95	0.56**	0.07	1.09**
KOTA BARANI ALSI-4	0.38	-1.01	3.03	-0.05	6.65**	-0.05	1.15	-0.14	0.09	-0.50
JLS-95	-1.26*	0.49	1.04	0.07	7.54**	-1.42**	-0.67	0.01	0.39**	1.87**
BLS-2023R-19	1.02	1.35	-2.57	0.03	-2.48	0.27	-1.56	-0.09	-0.33**	-0.87*
BLS-2023R-20	1.31*	-0.30	-3.21*	0.35*	-5.26**	1.05**	-1.46	-0.49**	-0.55**	-0.43

Abbreviations: DFF = Days to 50% flowering; DM = Days to maturity; PH = Plant height (cm); NBP = Number of branches per plant; NCP = Number of capsules per plant; NSPC = Number of seeds per capsule; HI = Harvest index (%); TSW = 1000-seed weight (g); SYP = Seed yield per plant (g); OC = Oil content (%)
**Significant at P ≤ 0.05; **Significant at P ≤ 0.01*

Table 3. Specific combining ability (SCA) effects of 42 crosses for ten quantitative traits in linseed (*Linum usitatissimum* L.)

Crosses	DFF	DM	PH	NBP	NCP	NSPC	HI	TSW	SYP	OC
OL-2013-14-2026 × RL-18123	0.26	-1.52	2.40	-0.86*	-3.82	0.07	6.83**	0.06	-0.06	-0.12
OL-2013-14-2026 × BLS-2022R-30	-3.31*	0.05	-5.35	0.14	2.98	-0.15	5.75*	0.54	-0.21	-1.439
OL-2013-14-2026 × KOTA BARANI ALSI-4	2.62*	1.26	-1.75	-0.32	-3.85	0.18	-4.92*	-0.46	0.18	0.61
OL-2013-14-2026 × JLS-95	-0.74	-2.24	-5.16	-0.04	-0.74	0.25	2.24	-0.01	-0.52*	0.498
OL-2013-14-2026 × BLS-2023R-19	0.98	2.40	9.45*	0.41	2.78	-0.63	-3.63	-0.06	-0.81**	0.438
OL-2013-14-2026 × BLS-2023R-20	0.19	0.05	0.40	0.68	2.66	0.28	-6.27**	-0.06	1.42**	0.013
OL-2022-23-5 × RL-18123	-0.74	-1.27	0.51	-0.46	2.58	-0.82	2.23	0.44	0.15	0.239
OL-2022-23-5 × BLS-2022R-30	0.19	1.80	1.37	0.14	-6.02	0.07	-2.43	0.78*	1.01**	1.06
OL-2022-23-5 × KOTA BARANI ALSI-4	-0.88	-0.99	-0.63	-0.02	3.95	-0.70	-12.61**	0.03	0.00	-0.666
OL-2022-23-5 × JLS-95	-1.24	-0.99	-2.54	-0.24	-5.14	0.67	5.84*	0.22	-0.90**	-0.102
OL-2022-23-5 × BLS-2023R-19	1.48	-0.35	0.37	-0.09	3.98	0.38	8.62**	-1.08**	-0.29	-0.837

Crosses	DFF	DM	PH	NBP	NCP	NSPC	HI	TSW	SYP	OC
OL-2022-23-5 × BLS-2023R-20	1.19	1.80	0.91	0.68	0.66	0.40	-1.65	-0.38	0.04	0.307
RLC-197 × RL-18123	0.01	1.14	0.35	0.65	6.24*	-0.03	-7.10**	-0.26	-0.15	-0.902
RLC-197 × BLS-2022R-30	0.94	-0.29	10.00*	-0.25	-3.36	-0.15	3.38	-0.32	0.71**	-0.376
RLC-197 × KOTA BARANI ALSI-4	-1.63	-0.57	-12.40**	-0.50	-0.99	-0.02	8.23**	-0.52	0.10	0.783
RLC-197 × JLS-95	-0.99	1.43	-7.31	0.08	-3.27	0.15	-8.82**	0.62	-0.20	0.412
RLC-197 × BLS-2023R-19	1.23	-1.43	1.80	0.42	0.64	0.07	0.37	0.02	0.31	0.287
RLC-197 × BLS-2023R-20	0.44	-0.29	7.55	-0.40	0.73	-0.02	3.94	0.47	-0.76**	-0.204
NL-421 × RL-18123	1.10	0.56	-4.85	-0.20	-0.89	0.73	7.65**	-0.29	-0.58*	1.031
NL-421 × BLS-2022R-30	0.02	-0.87	-2.60	0.00	1.31	1.22	-11.05**	-0.36	0.68*	-0.744
NL-421 × KOTA BARANI ALSI-4	-2.05	-0.65	1.70	0.75	7.28*	-0.55	3.62	0.59	0.46	-0.334
NL-421 × JLS-95	-1.90	-0.65	-1.11	-0.07	3.80	-0.58	0.26	-0.01	-0.04	-0.336
NL-421 × BLS-2023R-19	1.81	1.49	-2.30	-0.63	-8.49**	-0.27	-6.90**	0.54	1.08**	-0.286
NL-421 × BLS-2023R-20	1.02	0.13	9.15*	0.15	-3.00	-0.55	6.42**	-0.46	-1.60**	0.669
T-397 × RL-18123	2.26	0.98	2.23	0.74	-2.72	0.77	-4.88*	-0.24	0.44	-0.188
T-397 × BLS-2022R-30	1.19	-0.95	-5.21	-0.36	-0.52	-0.15	-4.96*	0.59	-1.51**	0.982
T-397 × KOTA BARANI ALSI-4	-2.38	-0.24	1.09	-0.42	-2.75	-0.82	9.35**	0.59	0.08	-0.713
T-397 × JLS-95	-1.74	0.26	1.47	0.36	4.56	-0.25	3.47	-0.61	0.38	0.005
T-397 × BLS-2023R-19	0.98	0.40	1.99	0.41	5.48	0.17	-4.34	0.14	0.09	-0.225
T-397 × BLS-2023R-20	-0.31	-0.45	-1.57	-0.72	-4.04	0.28	1.36	-0.46	0.52*	0.139
RLC-198 × RL-18123	-0.32	0.73	-5.32	0.82*	0.08	-0.33	5.18*	0.15	0.29	0.492
RLC-198 × BLS-2022R-30	1.61	-0.20	-2.76	-0.08	0.68	-1.15	6.37**	-0.57	-0.66*	0.307
RLC-198 × KOTA BARANI ALSI-4	-0.46	-0.49	8.64*	0.16	-0.35	0.58	-7.67**	0.08	0.33	0.327
RLC-198 × JLS-95	-1.32	-0.49	7.72	-0.35	2.56	-0.35	-6.96**	-0.62	0.23	-0.875
RLC-198 × BLS-2023R-19	-1.11	-0.35	12.94**	-0.31	-1.32	0.87	5.50*	0.03	0.34	0.125
RLC-198 × BLS-2023R-20	1.61	0.80	-21.22**	-0.24	-1.64	0.38	-2.42	0.93**	-0.53*	-0.376
LCK-2431 × RL-18123	-2.57	-0.61	4.68	-0.68	-1.46	-0.38	-9.92**	0.15	-0.08	-0.551
LCK-2431 × BLS-2022R-30	-0.64	0.46	4.54	0.42	4.94	0.30	2.94	-0.67	-0.02	0.210
LCK-2431 × KOTA BARANI ALSI-4	4.79**	1.68	3.34	0.36	-3.29	1.33	4.01	-0.32	-1.14**	-0.006
LCK-2431 × JLS-95	7.93**	2.68	6.92	0.25	-1.77	0.10	3.99	0.43	1.06**	0.398
LCK-2431 × BLS-2023R-19	-5.36**	-2.18	-24.26**	-0.21	-3.06	-0.58	0.37	0.43	-0.72**	0.498
LCK-2431 × BLS-2023R-20	-4.14**	-2.04	4.78	-0.14	4.63	-0.77	-1.39	-0.02	0.90**	-0.548

Table 4. Estimates of GCA and SCA variance components and the nature of gene action for different quantitative traits in linseed (*Linum usitatissimum* L.)

Character	σ²GCA	σ²SCA	σ²GCA/σ²SCA	Predominant gene action	Suggested breeding approach
Days to 50% flowering	2.16	6.14	0.35	Non-additive	Heterosis breeding / Selection in later generations
Days to maturity	0.53	0.00	-20.74	Additive	Pedigree selection
Plant height (cm)	0.47	65.76	0.01	Non-additive	Heterosis breeding
Number of branches per plant	0.06	0.19	0.33	Non-additive	Heterosis breeding
Number of capsules per plant	17.01	13.25	1.28	Additive	Direct selection
Number of seeds per capsule	0.37	0.16	2.25	Additive	Direct selection
Harvest index (%)	-4.58	46.39	-0.10	Non-additive	Selection in later generations
1000-seed weight (g)	0.08	0.23	0.35	Non-additive	Heterosis breeding
Seed yield per plant (g)	0.03	0.59	0.05	Non-additive	Heterosis breeding
Oil content (%)	1.28	0.00	0.00	Additive	Direct selection

σ²GCA = General combining ability variance; σ²SCA = Specific combining ability variance.

The estimates of general combining ability (σ²GCA) and specific combining ability (σ²SCA) variances revealed the relative importance of additive and non-additive gene effects governing the inheritance of the studied quantitative traits (Table 4). The predominance of non-additive gene action was observed for days to 50 per cent flowering, plant height, number of branches per plant, harvest index, 1000-seed weight, and seed yield per plant, as evidenced by lower σ²GCA/σ²SCA ratios. These results suggest that dominance and epistatic gene effects played a major role in the inheritance of these traits, indicating that the exploitation of heterosis and selection in advanced segregating generations would be effective breeding strategies. Similar findings have been reported by Ahmad et al. (2021), Bhateria et al. (2006), and Falconer (1989), who emphasised the importance of non-additive gene action in improving complex quantitative traits in linseed.

In contrast, additive gene action was predominant for days to maturity, number of capsules per plant, number of seeds per capsule, and oil content, as indicated by relatively higher σ²GCA estimates and σ²GCA/σ²SCA ratios. The predominance of additive genetic effects suggests that these traits can be effectively improved through direct selection and pedigree breeding methods because favourable alleles are more readily transmitted to subsequent generations. Comparable observations have been reported by Bisht and Paul (2019), Mahawar et al. (2021), and Rathva et al. (2023), who also documented the predominance of additive gene action for several yield-contributing and quality traits in linseed.

The results indicate that both additive and non-additive gene effects govern the inheritance of economically important traits in linseed. Therefore, the choice of breeding strategy should be trait-specific. Selection-based breeding approaches would be more effective for traits predominantly governed by additive gene action, whereas heterosis breeding followed by selection in later generations would be appropriate for traits controlled by non-additive gene action. Such an approach would facilitate the development of high-yielding and oil-rich linseed cultivars.

4. Conclusion

The present investigation demonstrated substantial genetic variability among the parental lines, testers, and their F_1 hybrids for seed yield, oil content, and associated quantitative traits in linseed. Combining ability analysis revealed that both additive and non-additive gene effects governed the inheritance of the studied characters. Additive gene action predominated for days to maturity, number of capsules per plant, number of seeds per capsule, and oil content, indicating the suitability of selection-based breeding approaches for improving these traits. In contrast, non-additive gene action predominated for days to 50 per cent flowering, plant height, number of branches per plant, harvest index, 1000-seed weight, and seed yield per plant, suggesting that heterosis breeding and selection in advanced segregating generations would be more effective.

Among the parental genotypes, RLC-198, T-397, and RLC-197 were identified as promising general combiners among the lines, whereas JLS-95 and RL-18123 emerged as desirable testers for improving seed yield and related traits. Among the hybrids, OL-2013-14-2026 × BLS-2023R-20, OL-2022-23-5 × BLS-2022R-30, NL-421 × BLS-2023R-19, and LCK-2431 × JLS-95 were identified as promising cross combinations for different yield-attributing traits. These parental lines and hybrids constitute valuable genetic resources for future linseed improvement programmes. Further multi-location evaluation and validation across environments are recommended before their utilisation in cultivar development.

5. Limitation

The present investigation was conducted at a single location during one cropping season with two replications, which may limit the wider applicability of the findings under diverse agro-climatic conditions. The combining ability estimates were based on a specific set of seven lines and six testers. Therefore, the identified superior combiners and cross combinations may perform differently under varying environmental conditions and genetic backgrounds. Consequently, further validation through multi-location and multi-season evaluations is recommended to assess the stability, adaptability, and consistency of the identified parents and hybrids before their utilisation in large-scale breeding programmes and cultivar development.

Declaration of AI Use

This manuscript was prepared through the collective intellectual contributions of all the authors, including the study design, experimentation, data analysis, interpretation of results and manuscript preparation. The authors acknowledge the use of Grammarly and ChatGPT (OpenAI) solely for language editing, grammar improvement, sentence refinement and reference formatting. These artificial intelligence (AI)-assisted tools were not used to generate, fabricate or manipulate experimental data, results or scientific conclusions, nor were they credited as authors. All AI-assisted content was critically reviewed, verified, revised and approved by the authors, who accept full responsibility for the accuracy, integrity and originality of the manuscript.

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Competing Interests

The authors declare that they have no known competing financial or non-financial interests, personal relationships, or affiliations that could have influenced the work reported in this manuscript.

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