



RESEARCH ARTICLE

# Epistasis and gene effects for phenology, yield and oil content in sesame revealed by joint-scaling and six-parameter analysis

Roshan Parihar<sup>1\*</sup>, Rajeev Shrivastava<sup>2</sup>, Mayuri Sahu<sup>2</sup>, Devchand Salam<sup>3</sup>, Sonali Kar<sup>4</sup>, Rajaram Kanwar<sup>4</sup>,  
Nirmodh Prabha<sup>5</sup> & Kiran Tigga<sup>6</sup>

<sup>1</sup>Section of Genetics and Plant Breeding, Barrister Thakur Chhedilal College of Agriculture & Research Station, Indira Gandhi Krishi Vishwavidyalaya (IGKV), Bilaspur 495 001, Chhattisgarh, India

<sup>2</sup>Department of Genetics and Plant Breeding, College of Agriculture, Indira Gandhi Krishi Vishwavidyalaya (IGKV), Bilaspur 495001, Chhattisgarh, India

<sup>3</sup>Section of Plant Pathology, Zonal Agricultural Research Station, Indira Gandhi Krishi Vishwavidyalaya (IGKV), Jagdalpur 494 005, Chhattisgarh, India

<sup>4</sup>Section of Genetics and Plant Breeding, Zonal Agricultural Research Station, Indira Gandhi Krishi Vishwavidyalaya (IGKV), Jagdalpur 494 005, Chhattisgarh, India

<sup>5</sup>S K College of Agriculture and Research Station, Indira Gandhi Krishi Vishwavidyalaya (IGKV), Kawardha 491 995, Chhattisgarh, India

<sup>6</sup>Section of Genetics and Plant Breeding, Zonal Agricultural Research Station, Indira Gandhi Krishi Vishwavidyalaya (IGKV), Ambikapur 497 001, Chhattisgarh, India

\*Correspondence email - [roshan.parihar@igkv.ac.in](mailto:roshan.parihar@igkv.ac.in)

Received: 16 January 2026; Accepted: 15 March 2026; Available online: Version 1.0: 14 April 2026; Version 2.0: 21 April 2026

**Cite this article:** Roshan P, Rajeev S, Mayuri S, Devchand S, Sonali K, Rajaram K, Nirmodh P, Kiran T. Epistasis and gene effects for phenology, yield and oil content in sesame revealed by joint-scaling and six-parameter analysis. Plant Science Today. 2026; 13(2): 1-7. <https://doi.org/10.14719/pst.13702>

## Abstract

An investigation was undertaken at the Instructional Farm, Barrister Thakur Chhedilal College of Agriculture and Research Station, Bilaspur, Chhattisgarh, India, a constituent college of Indira Gandhi Krishi Vishwavidyalaya, Raipur, Chhattisgarh, India to elucidate the nature of gene action for yield and its component traits in sesame (*Sesamum indicum* L.) through generation mean analysis in five crosses, namely Thilarani × TKG 55, Thilarani × Phule til, Thilarani × PKDS 12, Thilarani × JTS 08 and Thilothamma × JTS 08. The adequacy of the additive-dominance model was tested using A, B, C and D scaling tests. Significant scale effects for most traits indicated the presence of non-allelic gene interactions, demonstrating that simple additive-dominance inheritance was insufficient to explain trait expression. Pronounced epistasis was observed for days to 50 % flowering and days to maturity particularly in Thilarani × TKG 55, Thilarani × PKDS 12 and Thilarani × JTS 08, while seed yield per plant showed strong gene interaction in all crosses except Thilothamma × JTS 08. Generation mean analysis using the six-parameter model ( $m, d, h, i, j, l$ ) revealed that both additive and non-additive gene effects governed the inheritance of the studied characters. Dominance effects were generally higher than additive effects for traits such as number of capsules per plant, biological yield and seed yield, especially in Thilarani × PKDS 12 and Thilarani × JTS 08. Duplicate type epistasis predominated in most crosses, indicating dispersion of favourable alleles, whereas complementary epistasis was observed in specific combinations such as Thilarani × Phule til and Thilothamma × JTS 08. Traits like capsule length, number of seeds per capsule, thousand seed weight and oil content exhibited appreciable additive effects in certain crosses, suggesting the presence of fixable genetic variance. Overall, the study indicates that yield and its components in sesame are governed by complex inheritance involving additive, dominance and epistatic gene effects, necessitating appropriate breeding strategies for the development of superior genotypes.

**Keywords:** epistasis; generation-mean analysis; heterosis; Hayman six-parameter model; joint-scaling test; sesame

## Introduction

Sesame (*Sesamum indicum* L.) is an ancient and globally important oilseed crop valued for its oil, nutritional properties and resilience under marginal conditions. Genetic improvement of sesame depends on understanding the inheritance of key agronomic and quality traits, including phenology, yield components and oil content. Quantitative traits are often controlled by multiple genes with additive and non-additive effects and epistasis can substantially influence trait expression and heterosis. Classical approaches such as generation mean analysis, scaling tests and joint-scaling methods, remain powerful tools for dissecting gene action when experimental generation series ( $P_1, P_2, F_1, F_2, BC_1, BC_2$ ) are available.

Hayman's six-parameter model (1958) (1) partitions generation means into additive ( $d$ ), dominance ( $h$ ) and epistatic ( $i, j, l$ ) components, while Cavalli's (1952) joint-scaling test evaluates the adequacy of additive-dominance models (1, 2). In the present study, parental varieties were selected based on their genetic diversity, contrasting performance for important agronomic and yield traits, adaptability to local agro-climatic conditions and desirable oil content. Using these criteria, five crosses- Thilarani × TKG 55, Thilarani × Phule Til, Thilarani × PKDS 12, Thilarani × JTS 08 and Thilothamma × JTS 08-were developed to generate six experimental generations ( $P_1, P_2, F_1, F_2, BC_1$  and  $BC_2$ ). The novelty of the present investigation lies in the comparative genetic dissection of multiple sesame crosses involving important varieties under the

agro-climatic conditions of central India, with simultaneous estimation of additive, dominance and epistatic effects along with heterosis, inbreeding depression and effective number of factors. Such a comprehensive analysis provides deeper insight into the genetic control of yield and related traits and offers useful information for designing effective breeding strategies in sesame.

## Materials and Methods

### Experimental site and material

The experiment was conducted at the Instructional Farm, Barrister Thakur Chhedilal College of Agriculture and Research Station, Bilaspur, Chhattisgarh, India, a constituent college of Indira Gandhi Krishi Vishwavidyalaya, Raipur, Chhattisgarh, India (265 m above mean sea level; 21°47'–23°08' N latitude and 81°14'–83°15' E longitude). The initial crosses were made during rabi 2019–2020, backcrosses were made during kharif 2020 and experimental trial in 2 replications were laid down in rabi 2020–2021 season. The soil of the experimental site was medium black and the crop was grown under irrigated conditions.

Five sesame (*S. indicum*) cross combinations were developed using diverse parental lines: Thilarani × TKG 55, Thilarani × Phule Til, Thilarani × PKDS 12, Thilarani × JTS 08 and Thilothamma × JTS 08 (Table 1). Initial crosses were made during late rabi 2019–2020 through hand emasculation followed by controlled pollination. During kharif 2020, backcrosses were performed on  $F_1$  plants using both parents, while  $F_1$  plants were also selfed to obtain  $F_2$  seeds.

For each cross, six generations, namely  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$  ( $F_1 \times P_1$ ) and  $BC_2$  ( $F_1 \times P_2$ ), were developed and evaluated. The generations were evaluated in a compact family block design (CFBD) with 2 replications. Each replication consisted of 6 blocks and the generations were randomized within each block. A uniform plot size was maintained, with rows 4 m long, spaced 50 cm apart and plants spaced 20 cm apart. Standard agronomic practices and plant protection measures were followed throughout the crop growth period.

The initial seed material was obtained from the ICAR–Project Coordinating Unit on Sesame and Niger, JNKV Campus, Jabalpur, Madhya Pradesh, through an official request for research purposes. The salient features of the source material are presented in Table 1.

### Plant population and sampling procedure

For each cross, six generations ( $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$  and  $BC_2$ ) were grown pre replication with adequate plant population to ensure reliable estimates of generation means. In each replication,  $P_1$ ,  $P_2$  and  $F_1$  generations were represented by 20 plants each;  $BC_1$  and  $BC_2$  generations by 40 plants each and the  $F_2$  generation by 150 plants to capture maximum segregation. Observations were recorded on individual plants excluding border plants to avoid edge effects. Generation means were calculated based on observations recorded from the sampled plants within each generation and replication.

### Traits and measurements

Recorded observations included days to 50 % flowering, days to maturity, plant height (cm), number of primary and secondary branches per plant, number of capsules per plant, capsule length (cm), number of seeds per capsule, 1000-seed weight (g), biological yield per plant (g), seed yield per plant (g), harvest index (%) and oil content (%; Soxhlet extraction, AOAC 1965) (3).

### Statistical analyses

Analyses were performed in OPSTAT (4). Analysis of variance (ANOVA) for the CFBD design was conducted following the method of Panse and Sukhatme (1969) (5). Simple scaling tests (A–D) were computed as described by Hayman and Mather (1955) (6). Where scaling tests indicated the presence of epistasis, Hayman's six-parameter model ( $m, d, h, i, j, l$ ) was fitted to estimate gene effects. In the absence of epistasis, the three-parameter additive–dominance model (7) and Cavalli's joint-scaling test (1952) were used. Variance components (E, D, H), degree of dominance, potency ratios, effective factor estimates were also calculated (Burton; Castle-Wright) (8).

## Results and Discussion

### Scaling tests, gene interaction and genetic parameters for quantitative traits in sesame

The adequacy of the additive–dominance model for different quantitative traits in sesame was evaluated using A, B, C and D scaling tests. Under the additive–dominance model, the expected values of these scales are zero. Significant deviation of any scale from zero indicates the presence of non-allelic gene interaction (epistasis), suggesting that the additive–dominance model is inadequate for explaining trait inheritance (5, 9). In general, the A

**Table 1.** Characteristics features of sesame parental materials used for studies

| Sl. No. | Variety     | Developing institute                                | Key characteristics                                                                    |
|---------|-------------|-----------------------------------------------------|----------------------------------------------------------------------------------------|
| 1.      | TKG 55      | Jawaharlal Nehru Krishi Vishwa Vidyalaya, Jabalpur  | Average yield: 6.50–7.00 q/ha; oil content: 50–53%; maturity: 82–85 days; white seeds. |
| 2.      | Phule Til   | Mahatma Phule Krishi Vidyapeeth, Rahuri             | Average yield: 6.00–7.00 q/ha; Oil %: 49–51; maturity: 90–95 days; white seed.         |
| 3.      | PKDS 12     | Dr Panjabrao Deshmukh Krishi Vidyapeeth, Akola      | Average yield: 7.00–7.50 q/ha; Oil %: 48–52; maturity: 82–85 days; white seed.         |
| 4.      | JTS 08      | Jawaharlal Nehru Krishi Vishwa Vidyalaya, Jabalpur  | Average yield: 6.50–7.00 q/ha; Oil %: 50–53; maturity: 82–85 days; white seed.         |
| 5.      | Thilarani   | Acharya N. G. Ranga Agricultural University, Guntur | Average yield: 5.50–6.00 q/ha; Oil % : 50–53; maturity: 82–86 days; dark brown seeds.  |
| 6.      | Thilothamma | Tamil Nadu Agricultural University, Coimbatore      | Average yield: 5.50–6.00 q/ha; Oil %: 42–44; maturity: 80–85 days; black brown seeds.  |

The varieties were brought from Project Coordinating Unit, AICRP of Sesame and Niger, Jawaharlal Nehru Krishi Vishwa Vidyalaya Campus, Jabalpur, Madhya Pradesh.

**Table 2.** Scaling test results (A, B, C and D) and estimation of gene interactions for quantitative traits in different sesame crosses

| Crosses                                       | Scale (A) | Scale (B) | Scale (C) | Scale (D) | Gene interaction |
|-----------------------------------------------|-----------|-----------|-----------|-----------|------------------|
| <b>Days to 50 % flowering</b>                 |           |           |           |           |                  |
| Thilarani X TKG 55                            | -37.09**  | -40.17**  | -49.02**  | -14.12**  | Present          |
| Thilarani X Phule til                         | -1.2      | -3.95**   | -103.66** | 49.25**   | Absent           |
| Thilarani X PKDS 12                           | -45.33**  | -49.88**  | -85.32**  | -4.94**   | Present          |
| Thilarani X JTS 08                            | -30.26**  | -27.82**  | -37.85**  | -10.11**  | Present          |
| Thilothamma X JTS 08                          | -44.13**  | -44.06**  | -83.23**  | -2.48     | Absent           |
| <b>Days to maturity</b>                       |           |           |           |           |                  |
| Thilarani X TKG 55                            | -36.39**  | -47.42**  | -51.89**  | -15.96**  | Present          |
| Thilarani X Phule til                         | 5.05**    | 0.05      | -90.66    | 47.88**   | Absent           |
| Thilarani X PKDS 12                           | -31.75**  | -40.65**  | -60.48**  | -5.95**   | Present          |
| Thilarani X JTS 08                            | -39.78**  | -42.62**  | -44.65**  | -18.87**  | Present          |
| Thilothamma X JTS 08                          | -33.83**  | -32.86**  | -91.73**  | 12.52**   | Present          |
| <b>Plant height (cm)</b>                      |           |           |           |           |                  |
| Thilarani X TKG 55                            | 20.77**   | 13.93**   | 10.26     | 12.22**   | Absent           |
| Thilarani X Phule til                         | 20.35**   | 21.3**    | 115.56**  | -36.955** | Present          |
| Thilarani X PKDS 12                           | -16.1*    | 6.55      | 31.979**  | -20.764** | Absent           |
| Thilarani X JTS 08                            | 6.52      | 11.35*    | 45.321**  | -13.726** | Absent           |
| Thilothamma X JTS 08                          | -8.87     | 22.18**   | 11.91     | 0.7       | Absent           |
| <b>Number of primary branches per plant</b>   |           |           |           |           |                  |
| Thilarani X TKG 55                            | 0.91      | -0.41     | 0.46      | 0.02      | Absent           |
| Thilarani X Phule til                         | 2.85**    | -0.1      | 6.35**    | -1.8**    | Absent           |
| Thilarani X PKDS 12                           | 1.433**   | 0.68      | 9.44**    | -3.66**   | Absent           |
| Thilarani X JTS 08                            | 0.89      | 1.84**    | 6.05**    | -1.66**   | Absent           |
| Thilothamma X JTS 08                          | -1.05*    | -0.62     | -0.27     | -0.7      | Absent           |
| <b>Number of secondary branches per plant</b> |           |           |           |           |                  |
| Thilarani X TKG 55                            | 0.53      | -1.3*     | 6.11**    | -3.44**   | Absent           |
| Thilarani X Phule til                         | 1.45**    | 0.65      | 5.49**    | -1.69**   | Absent           |
| Thilarani X PKDS 12                           | 0.76**    | -0.53     | 9.68**    | -4.72**   | Absent           |
| Thilarani X JTS 08                            | 0.74      | 1.07**    | 7.53**    | -2.86**   | Absent           |
| Thilothamma X JTS 08                          | 1.21      | 0.86      | 3.47**    | -0.7      | Absent           |
| <b>Number of capsules per plant</b>           |           |           |           |           |                  |
| Thilarani X TKG 55                            | 30.8**    | 15.62     | 118.18**  | -35.88**  | Absent           |
| Thilarani X Phule til                         | 28.5**    | 78.5**    | 143.57**  | -18.285*  | Present          |
| Thilarani X PKDS 12                           | 35.417**  | 15.717*   | 156.519** | -52.693** | Present          |
| Thilarani X JTS 08                            | 10.78     | -11.9     | 103.8**   | -52.46**  | Absent           |
| Thilothamma X JTS 08                          | 27**      | 6.94      | 152.3**   | -59.18**  | Absent           |
| <b>Capsule length (cm)</b>                    |           |           |           |           |                  |
| Thilarani X TKG 55                            | 0.14      | -0.09     | 0.46**    | -0.20**   | Absent           |
| Thilarani X Phule til                         | 0.11      | -0.15     | 0.50**    | -0.27**   | Absent           |
| Thilarani X PKDS 12                           | 0.14      | -0.14     | 0.82**    | -0.40**   | Absent           |
| Thilarani X JTS 08                            | 0.44**    | 0.32**    | 0.81**    | -0.02     | Absent           |
| Thilothamma X JTS 08                          | -0.01     | -0.23**   | 0.06      | -0.15*    | Absent           |
| <b>Number of seeds per capsule</b>            |           |           |           |           |                  |
| Thilarani X TKG 55                            | 7.4**     | 2.17      | 29.21**   | -9.82**   | Absent           |
| Thilarani X Phule til                         | 4.7       | -3.8      | 10.32*    | -4.71*    | Absent           |
| Thilarani X PKDS 12                           | 8.1**     | 8.2**     | 26.77**   | -5.23*    | Present          |
| Thilarani X JTS 08                            | 10.7**    | 12.28**   | 27.95**   | -2.48     | Absent           |
| Thilothamma X JTS 08                          | 11.19**   | 3.06      | 24.81**   | -5.28**   | Absent           |
| <b>Thousand seed weight (g)</b>               |           |           |           |           |                  |
| Thilarani X TKG 55                            | 0.67**    | 0.31      | 1.04**    | -0.02     | Absent           |
| Thilarani X Phule til                         | 0.21      | 0.55**    | 1.90**    | -0.56**   | Absent           |
| Thilarani X PKDS 12                           | 0.54**    | -0.11     | 2.03**    | -0.80**   | Absent           |
| Thilarani X JTS 08                            | 0.79**    | 0.30*     | 1.86**    | -0.38**   | Present          |
| Thilothamma X JTS 08                          | -0.36*    | -0.31**   | -0.32     | -0.17     | Absent           |
| <b>Biological yield (g/plant)</b>             |           |           |           |           |                  |
| Thilarani X TKG 55                            | 12.74     | -22.97    | 74.89**   | -42.56**  | Absent           |
| Thilarani X Phule til                         | 36.89**   | 64.56**   | 157.18**  | -27.86**  | Present          |
| Thilarani X PKDS 12                           | 56.86**   | 23.29*    | 216.23**  | -68.03**  | Present          |
| Thilarani X JTS 08                            | -8.56     | -49.68**  | 72.33**   | -65.28**  | Absent           |
| Thilothamma X JTS 08                          | 23.04**   | -0.84     | 135.70**  | -56.75**  | Absent           |
| <b>Seed yield (g/plant)</b>                   |           |           |           |           |                  |
| Thilarani X TKG 55                            | 10.29**   | 5.32*     | 31.77**   | -8.07**   | Present          |
| Thilarani X Phule til                         | 8.06**    | 15.89**   | 34.68**   | -5.36**   | Present          |
| Thilarani X PKDS 12                           | 11.82**   | 5.95**    | 44.72**   | -13.47**  | Present          |
| Thilarani X JTS 08                            | 9.23**    | 3.61*     | 33.46**   | -10.30**  | Present          |
| Thilothamma X JTS 08                          | 6.27**    | 0.74      | 30.04**   | -11.51**  | Absent           |
| <b>Harvest index (%)</b>                      |           |           |           |           |                  |
| Thilarani X TKG 55                            | -0.11     | 2.15**    | 1.97      | 0.03      | Absent           |
| Thilarani X Phule til                         | 1.30      | 3.97**    | 5.23**    | 0.02      | Absent           |
| Thilarani X PKDS 12                           | 1.04      | 1.32      | 4.05**    | -0.84     | Absent           |
| Thilarani X JTS 08                            | 7.37**    | 9.71**    | 16.41**   | 0.33      | Absent           |
| Thilothamma X JTS 08                          | 2.03**    | 0.57      | 3.44**    | -0.41     | Absent           |
| <b>Oil content (%)</b>                        |           |           |           |           |                  |
| Thilarani X TKG 55                            | 1.84      | -0.04     | -13.18**  | 7.49**    | Absent           |
| Thilarani X Phule til                         | -14.27**  | -5.09**   | -17.32**  | -1.02*    | Present          |
| Thilarani X PKDS 12                           | 2.46*     | 4.02**    | 6.36**    | 0.05      | Absent           |
| Thilarani X JTS 08                            | 4.30**    | -0.78     | -2.52     | 3.02**    | Absent           |
| Thilothamma X JTS 08                          | -2.56**   | -2.42*    | -5.17**   | 0.09      | Absent           |

**Table 3.** Scaling test results with estimation of gene effects for quantitative traits in different sesame crosses

| Crosses                                       | (m)      | (d)      | (h)      | (i)      | (j)      | (l)       | Epistasis | X <sup>2</sup> (cal) |
|-----------------------------------------------|----------|----------|----------|----------|----------|-----------|-----------|----------------------|
| <b>Days to 50 % flowering</b>                 |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 58.78**  | 0.96     | 32.59**  | 28.24**  | -3.08*   | -105.5**  | D         | 905.63**             |
| Thilarani X Phule til                         | 76.84**  | -3.97**  | -96.66** | -98.51** | -2.75**  | 93.36**   | D         | 1996.08**            |
| Thilarani X PKDS 12                           | 69.26**  | -0.32    | 15.96**  | 9.89**   | -4.55*   | -105.11** | D         | 3748.95**            |
| Thilarani X JTS 08                            | 60.61**  | 0.82     | 26.92**  | 20.22**  | 2.44     | -78.30**  | D         | 908.94**             |
| Thilothamma X JTS 08                          | 68.92**  | 0.76     | 4.53     | 4.96     | 0.07     | -93.15**  | D         | 2712.49**            |
| <b>Days to maturity</b>                       |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 106.86** | 0.96     | 39.94**  | 31.92**  | -11.03** | -115.73** | D         | 1074.72**            |
| Thilarani X Phule til                         | 124.84** | -1.6*    | -82.41** | -95.76** | -5**     | 100.86**  | D         | 1582.02**            |
| Thilarani X PKDS 12                           | 113.32** | -0.05    | 24.41**  | 11.91**  | -8.9**   | -84.31**  | D         | 369.06**             |
| Thilarani X JTS 08                            | 108.61** | 1.58     | 45.84**  | 37.74**  | -2.84    | -120.14** | D         | 1820.53**            |
| Thilothamma X JTS 08                          | 120.92** | 5.76**   | -21.21** | -25.04** | 0.97     | -41.65**  | C         | 2370.41**            |
| <b>Plant height (cm)</b>                      |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 116.46** | 3.98*    | 14.01    | -24.44** | -6.84    | 59.14**   | C         | 32.35**              |
| Thilarani X Phule til                         | 97.56**  | -6.82**  | 100.41** | 73.91**  | 0.95     | -32.26*   | D         | 163.14**             |
| Thilarani X PKDS 12                           | 106.94   | 14.55**  | 63.45**  | 41.52**  | 22.65*   | -51.07**  | D         | 22.73**              |
| Thilarani X JTS 08                            | 103.65** | 8.04*    | 56.87**  | 27.45**  | 4.83     | -9.58     | D         | 27.57**              |
| Thilothamma X JTS 08                          | 118.01** | 18.2**   | 26.12**  | -1.4     | 31.05**  | 14.71     | C         | 22.13**              |
| <b>Number of primary branches per plant</b>   |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 4.46*    | -1.06*   | 2.51     | -0.04    | -1.32    | 0.54      | C         | 2.56                 |
| Thilarani X Phule til                         | 4.1**    | -2.35**  | 6.82**   | 3.6**    | -2.95**  | -0.85     | D         | 42.46**              |
| Thilarani X PKDS 12                           | 0.8**    | -1.22**  | 11.74**  | 9.45**   | -1.3     | -9.21**   | D         | 129.69**             |
| Thilarani X JTS 08                            | 2.8**    | 0.1      | 4.79**   | 3.32**   | 0.95     | -0.59     | D         | 85.22**              |
| Thilothamma X JTS 08                          | 3.93**   | -0.36    | 2.37*    | 1.4      | 0.43     | -3.07     | D         | 4.31                 |
| <b>Number of secondary branches per plant</b> |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 1.41**   | -1.34**  | 8.90**   | 6.88**   | -1.83**  | -7.65**   | D         | 59.56**              |
| Thilarani X Phule til                         | 1.99**   | -1.17**  | 5.16**   | 3.39**   | -0.8     | -1.29     | D         | 37.24**              |
| Thilarani X PKDS 12                           | 0.8**    | -1.22**  | 11.74**  | 9.45**   | -1.3     | -9.21**   | D         | 167.27**             |
| Thilarani X JTS 08                            | 0.82**   | -0.36    | 6.70**   | 5.72**   | 0.33     | -3.91**   | D         | 118.91**             |
| Thilothamma X JTS 08                          | 1.42**   | -0.3     | 3.32**   | 1.4      | -0.35    | 0.67      | C         | 11.46**              |
| <b>Number of capsules per plant</b>           |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 61.18**  | -19.44** | 100.51** | 71.76**  | -15.18   | -25.34    | D         | 76.25**              |
| Thilarani X Phule til                         | 64.42**  | 6.82     | 76.14**  | 36.57*   | 50**     | 70.43*    | C         | 78.33**              |
| Thilarani X PKDS 12                           | 58.12**  | -22.9**  | 144.80** | 105.38** | -19.7*   | -54.25**  | D         | 11.16                |
| Thilarani X JTS 08                            | 59.1**   | -15.54** | 137.62** | 104.92** | -22.68*  | -106.04** | D         | 123.30**             |
| Thilothamma X JTS 08                          | 57.5*    | -23.38** | 144.91** | 118.36** | -20.06** | -84.42**  | D         | 299.91**             |
| <b>Capsule length (cm)</b>                    |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 2.92**   | -0.19**  | 0.57**   | 0.41**   | -0.23*   | -0.36     | D         | 15.69**              |
| Thilarani X Phule til                         | 2.87**   | -0.18**  | 0.62**   | 0.54**   | -0.26    | -0.57     | D         | 15.48**              |
| Thilarani X PKDS 12                           | 2.91**   | -0.24**  | 0.97**   | 0.81**   | -0.28**  | -0.81**   | D         | 63.08**              |
| Thilarani X JTS 08                            | 2.90**   | -0.09    | 0.37*    | 0.04     | -0.12    | 0.72**    | C         | 50.45**              |
| Thilothamma X JTS 08                          | 2.96**   | -0.11*   | 0.57**   | 0.30*    | -0.21    | -0.55*    | D         | 8.92*                |
| <b>Number of seeds per capsule</b>            |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 44.46**  | -4.54**  | 26.11**  | 19.64**  | -5.23    | -10.07    | D         | 48.97**              |
| Thilarani X Phule til                         | 47.67**  | -6.15**  | 14.52**  | 9.42*    | -8.5*    | -8.52*    | D         | 12.58**              |
| Thilarani X PKDS 12                           | 46.45**  | -3.35    | 17.37**  | 10.47**  | 0.1      | 5.82      | C         | 53.34**              |
| Thilarani X JTS 08                            | 47.13**  | -2.76*   | 14.52**  | 4.97     | 1.58     | 18.00**   | C         | 102.26**             |
| Thilothamma X JTS 08                          | 45.16**  | -4.64**  | 12.83**  | 10.56**  | -8.13**  | 3.69      | C         | 66.44**              |
| <b>Thousand seed weight (g)</b>               |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 3.26**   | -0.29**  | 0.24     | 0.05     | -0.35    | 0.93*     | C         | 24.5**               |
| Thilarani X Phule til                         | 3.17**   | -0.11*   | 1.10**   | 1.13**   | 0.33     | -0.36*    | D         | 48.53**              |
| Thilarani X PKDS 12                           | 3.24**   | -0.60**  | 1.91**   | 1.60**   | -0.65**  | -1.17**   | D         | 109.11**             |
| Thilarani X JTS 08                            | 3.20**   | -0.38**  | 1.07**   | 0.76**   | -0.49**  | 0.32      | C         | 78.92**              |
| Thilothamma X JTS 08                          | 3.19**   | -0.22**  | 1.01**   | 0.35     | 0.04     | -1.03**   | D         | 12.50**              |
| <b>Biological yield (g/plant)</b>             |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 47.60**  | -29.92** | 94.42**  | 85.12**  | -35.72** | -95.35**  | D         | 33.38**              |
| Thilarani X Phule til                         | 53.74**  | -11.55*  | 93.78**  | 55.72**  | 27.67    | 45.73     | C         | 40.97**              |
| Thilarani X PKDS 12                           | 46.76**  | -38.19** | 197.36** | 136.07** | -33.57*  | -55.92    | D         | 244.20**             |
| Thilarani X JTS 08                            | 42.39**  | -26.39** | 182.59** | 130.57** | -41.12** | -188.81** | D         | 77.04**              |
| Thilothamma X JTS 08                          | 42.21**  | -27.24** | 145.66** | 113.50** | -23.88** | -91.30**  | D         | 247.13**             |
| <b>Seed yield (g/plant)</b>                   |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 9.04**   | -5.41**  | 24.26**  | 16.15**  | -4.97*   | -0.53     | D         | 102.03**             |
| Thilarani X Phule til                         | 10.51**  | -0.91*   | 20.02**  | 10.72**  | 7.82**   | 13.23     | C         | 50**                 |
| Thilarani X PKDS 12                           | 8.85**   | -7.33**  | 38.33**  | 26.95**  | -5.86*   | -9.17     | D         | 312.05**             |
| Thilarani X JTS 08                            | 9.07**   | -4.82**  | 31.35**  | 20.61**  | -5.62*   | -7.76     | D         | 235.55**             |
| Thilothamma X JTS 08                          | 8.18**   | -5.71**  | 30.93**  | 23.02**  | -5.53**  | -15.99**  | D         | 370.42**             |
| <b>Harvest index (%)</b>                      |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 19.24**  | 0.48     | -2.29*   | -0.07    | 2.27**   | 2.12      | D         | 12.07**              |
| Thilarani X Phule til                         | 19.31**  | 1.78**   | 1.70     | -0.04*   | 2.66*    | 5.32*     | C         | 35.15**              |
| Thilarani X PKDS 12                           | 19.09**  | 0.08     | 1.00     | 1.68     | 0.27     | 0.68      | C         | 14.70**              |
| Thilarani X JTS 08                            | 19.37**  | 0.16     | 5.27**   | -0.67    | 2.33*    | 17.76**   | C         | 255.34**             |
| Thilothamma X JTS 08                          | 19.67**  | -0.61    | 2.56*    | 0.83     | -1.46    | 1.76      | C         | 13.15**              |
| <b>Oil content (%)</b>                        |          |          |          |          |          |           |           |                      |
| Thilarani X TKG 55                            | 41.21**  | -4.42**  | -11.57** | -14.98** | -1.89    | 16.78**   | D         | 89.98**              |
| Thilarani X Phule til                         | 9.00**   | 1.25     | -1.20*   | 2.04     | 9.17**   | -21.41**  | C         | 163.39**             |
| Thilarani X PKDS 12                           | 40.81**  | -5.13**  | 7.40**   | -0.11    | 1.56     | 6.60**    | C         | 34.06**              |
| Thilarani X JTS 08                            | 39.73**  | -6.64**  | 0.59     | -6.04**  | -5.09**  | 9.56**    | C         | 54.72**              |
| Thilothamma X JTS 08                          | 39.36**  | -0.54    | -2.62    | -0.19    | 0.14     | -4.78     | C         | 35.75**              |

D: Duplicate epistasis; C: Complementary epistasis; m: mean value; d: additive component; h: dominant component; i: axa component; j: axd component; l: dxd component; X<sup>2</sup>- Chi square\*; \*\* Significant at 5 and 1 %.

**Table 4.** Joint scaling test results with allied genetic parameters for quantitative characters in different crosses of sesame

| Crosses                                       | <i>m</i> | <i>d</i> | <i>h</i> | Dom. Deg | X <sup>2</sup> (Cal.) | Potence<br>Ration h1 in<br>F1 | Potence<br>Ration h2 in<br>F2 | NOEG<br>Bartor's<br>Formula | NOEG Castle-<br>Wright's<br>Formula |
|-----------------------------------------------|----------|----------|----------|----------|-----------------------|-------------------------------|-------------------------------|-----------------------------|-------------------------------------|
| <b>Days to 50 % flowering</b>                 |          |          |          |          |                       |                               |                               |                             |                                     |
| Thilarani X TKG 55                            | 44.85**  | -2.45    | 28.44**  | --       | 905.63**              | 1.74                          | 11.54                         | -0.51                       | -0.50                               |
| Thilarani X Phule til                         | 50.97**  | 2.73**   | 3.35**   | 1.10     | 1996.08**             | -0.71                         | -20.64                        | 0.52                        | 0.11                                |
| Thilarani X PKDS 12                           | 46.43**  | -2.29**  | 19.01**  | --       | 3748.95**             | 3.11                          | 24.98                         | 0.26                        | 0.16                                |
| Thilarani X JTS 08                            | 48.44**  | 0.43**   | 9.93**   | 4.79     | 908.94**              | -16.75                        | -64.07                        | 0.20                        | 0.00                                |
| Thilothamma X JTS 08                          | 50.29**  | -0.88**  | 9.85**   | --       | 2712.49**             | -0.58                         | 56.81                         | 0.05                        | 0.01                                |
| <b>Days to maturity</b>                       |          |          |          |          |                       |                               |                               |                             |                                     |
| Thilarani X TKG 55                            | 91.22**  | -6.10    | 32.48**  | --       | 1074.72**             | 1.23                          | 5.24                          | -3.31                       | -2.57                               |
| Thilarani X Phule til                         | 96.13**  | -0.90**  | 14.34**  | --       | 1582.02**             | 14.83                         | 65.2                          | 1.12                        | 0.01                                |
| Thilarani X PKDS 12                           | 92.47**  | -4.36**  | 39.70**  | --       | 369.06**              | 2.84                          | 9.71                          | -0.45                       | -0.33                               |
| Thilarani X JTS 08                            | 94.68**  | -2.45**  | 12.13**  | --       | 1820.53**             | 2.7                           | 10.14                         | 0.08                        | 0.06                                |
| Thilothamma X JTS 08                          | 97.69**  | -4.38**  | 13.50**  | --       | 2370.41**             | 0.72                          | 9.42                          | 1.24                        | 0.68                                |
| <b>Plant height (cm)</b>                      |          |          |          |          |                       |                               |                               |                             |                                     |
| Thilarani X TKG 55                            | 98.63**  | -7.06    | 29.40**  | --       | 32.35**               | 5.19                          | 4.50                          | 0.57                        | 0.09                                |
| Thilarani X Phule til                         | 108.57** | 9.11**   | 14.33**  | 1.25     | 163.14**              | -3.63                         | 4.28                          | 2.15                        | 0.12                                |
| Thilarani X PKDS 12                           | 103.35** | -3.94**  | 19.03**  | --       | 22.73**               | 6.79                          | 1.84                          | 0.34                        | 0.02                                |
| Thilarani X JTS 08                            | 97.63**  | -5.53**  | 26.06**  | --       | 27.57**               | 5.23                          | 1.20                          | 0.29                        | 0.04                                |
| Thilothamma X JTS 08                          | 107.65** | -5.90**  | 24.31**  | --       | 22.13**               | 10.29                         | 8.06                          | 1.23                        | 0.03                                |
| <b>Number of Primary branches per plant</b>   |          |          |          |          |                       |                               |                               |                             |                                     |
| Thilarani X TKG 55                            | 3.29**   | 0.45**   | 2.34**   | 2.26     | 2.56                  | -6.37                         | -5.8                          | 1.70                        | 0.04                                |
| Thilarani X Phule til                         | 4.16**   | 1.26**   | 1.51**   | 1.09     | 42.46**               | -3.68                         | -0.05                         | 6.21                        | 0.36                                |
| Thilarani X PKDS 12                           | 2.95**   | 0.35*    | 1.65**   | 2.15     | 129.69**              | -3.09                         | 2.01                          | -6.44                       | -0.46                               |
| Thilarani X JTS 08                            | 3.21**   | 0.34**   | 0.74**   | 1.47     | 85.22**               | -3.93                         | 4.13                          | 1.03                        | 0.05                                |
| Thilothamma X JTS 08                          | 3.48**   | 0.57**   | 1.07**   | 1.36     | 4.31                  | -1.69                         | -1.93                         | 0.41                        | 0.05                                |
| <b>Number of secondary branches per plant</b> |          |          |          |          |                       |                               |                               |                             |                                     |
| Thilarani X TKG 55                            | 1.84**   | 0.49**   | 1.44**   | 1.71     | 59.56**               | -4.76                         | 2.42                          | 5.41                        | 0.22                                |
| Thilarani X Phule til                         | 2.07**   | 0.88**   | 1.17**   | 1.15     | 37.24**               | -2.29                         | 1.25                          | 7.45                        | 0.73                                |
| Thilarani X PKDS 12                           | 1.73**   | 0.38**   | 1.06**   | 1.66     | 167.27**              | -3.98                         | 4.43                          | -5.08                       | -0.26                               |
| Thilarani X JTS 08                            | 1.71**   | 0.57**   | 0.70**   | 1.10     | 118.91**              | -1.85                         | 5.32                          | 0.62                        | 0.07                                |
| Thilothamma X JTS 08                          | 1.16**   | 0.15     | 1.56**   | 3.23     | 11.46**               | -15.4                         | -1.52                         | 0.31                        | 0.00                                |
| <b>Number of capsules per plant</b>           |          |          |          |          |                       |                               |                               |                             |                                     |
| Thilarani X TKG 55                            | 74.66**  | 11.79**  | 12.66**  | 1.03     | 76.25**               | -2.42                         | 2.56                          | 1.13                        | 0.10                                |
| Thilarani X Phule til                         | 73.84**  | 12.11**  | 7.88     | 0.80     | 78.33**               | -2.17                         | 1.77                          | 17.09                       | 1.75                                |
| Thilarani X PKDS 12                           | 1.20**   | -0.11    | -0.52    | 2.18     | 11.16                 | -3.02                         | 2.97                          | 2.02                        | 0.14                                |
| Thilarani X JTS 08                            | 67.02**  | 4.48**   | 27.49**  | 2.47     | 123.30**              | -7.78                         | 4.57                          | 0.72                        | 0.01                                |
| Thilothamma X JTS 08                          | 75.73**  | 14.95**  | 23.53**  | 1.25     | 299.91**              | -1.98                         | 3.71                          | 2.49                        | 0.27                                |
| <b>Capsule length cm</b>                      |          |          |          |          |                       |                               |                               |                             |                                     |
| Thilarani X TKG 55                            | 2.92**   | 0.12**   | 0.17**   | 1.17     | 15.69**               | -2.09                         | 0.89                          | 0.37                        | 0.04                                |
| Thilarani X Phule til                         | 2.93**   | 0.07**   | 0.02     | 0.61     | 15.48**               | -1.6                          | 3.46                          | 9.76                        | 1.30                                |
| Thilarani X PKDS 12                           | 2.98**   | 0.16**   | 0.13**   | 0.91     | 63.08**               | -1.58                         | 2.51                          | 1.72                        | 0.23                                |
| Thilarani X JTS 08                            | 2.83**   | 0.08**   | 0.31**   | 1.88     | 50.45**               | -9.42                         | 2.24                          | 0.71                        | 0.01                                |
| Thilothamma X JTS 08                          | 2.86**   | 0.04     | 0.27**   | 2.34     | 8.92*                 | -26.99                        | -23.8                         | 0.38                        | 0.00                                |
| <b>Number of seeds per capsule</b>            |          |          |          |          |                       |                               |                               |                             |                                     |
| Thilarani X TKG 55                            | 47.43**  | 1.84**   | 4.47**   | 1.55     | 48.97**               | -3.36                         | 4.22                          | 0.46                        | 0.03                                |
| Thilarani X Phule til                         | 47.89**  | 2.70**   | 2.7      | 1.01     | 12.58**               | -2.68                         | 0.03                          | -3.86                       | -0.32                               |
| Thilarani X PKDS 12                           | 48.73**  | 3.07**   | 1.92     | 0.79     | 53.34**               | -2.02                         | 1.90                          | 3.03                        | 0.33                                |
| Thilarani X JTS 08                            | 46.39**  | 2.97**   | 9.94**   | 1.82     | 102.26**              | -2.69                         | 1.24                          | 1.35                        | 0.11                                |
| Thilothamma X JTS 08                          | 47.71**  | 1.27*    | 2.50*    | 1.40     | 66.44**               | -3.95                         | 17.61                         | 0.07                        | 0.00                                |
| <b>Thousand seed weight</b>                   |          |          |          |          |                       |                               |                               |                             |                                     |
| Thilarani X TKG 55                            | 3.37**   | 0.14**   | -0.08*   | --       | 24.5**                | -1.64                         | 3.07                          | 1.21                        | 0.15                                |
| Thilarani X Phule til                         | 3.52**   | 0.20**   | -0.26*   | --       | 48.53**               | 0.10                          | 3.40                          | 6.86                        | 2.46                                |
| Thilarani X PKDS 12                           | 3.49**   | 0.33**   | 0.17*    | 0.71     | 109.11**              | -1.10                         | 2.60                          | 1.41                        | 0.24                                |
| Thilarani X JTS 08                            | 3.40**   | 0.22**   | -0.001   | --       | 78.92**               | -2.13                         | 4.43                          | 1.26                        | 0.13                                |
| Thilothamma X JTS 08                          | 2.89**   | 0.19**   | 0.59**   | 1.74     | 12.50**               | -2.69                         | -3.35                         | 3.04                        | 0.25                                |

| Biological yield per plant (g) |         |         |         |      |          |       |       |        |       |
|--------------------------------|---------|---------|---------|------|----------|-------|-------|--------|-------|
| Thilarani X TKG 55             | 61.68** | 12.76** | -3.90** | --   | 33.38**  | -0.77 | 2.33  | -0.93  | -0.19 |
| Thilarani X Phule til          | 69.73** | 21.58** | -6.30   | --   | 40.97**  | -1.49 | 1.59  | -1.91  | -0.26 |
| Thilarani X PKDS 12            | 63.24** | 16.99** | 18.08** | 1.03 | 244.20** | -2.86 | 2.18  | 293.76 | 22.90 |
| Thilarani X JTS 08             | 34.10** | 6.79**  | 50.28** | 2.72 | 77.04**  | -8.92 | -2.71 | 1.11   | 0.01  |
| Thilothamma X JTS 08           | 49.48** | 20.26** | 27.78** | 1.17 | 247.13** | -2.10 | 2.33  | 6.48   | 0.68  |
| Seed yield per plant (g)       |         |         |         |      |          |       |       |        |       |
| Thilarani X TKG 55             | 12.34** | 2.78**  | 0.92    | 0.57 | 102.03** | -2.77 | 2.65  | 6.80   | 0.55  |
| Thilarani X Phule til          | 13.94** | 4.29**  | -1.49   | --   | 50**     | -1.92 | 1.66  | -2.15  | -0.24 |
| Thilarani X PKDS 12            | 12.29** | 3.08**  | 4.08**  | 1.15 | 312.05** | -2.58 | 2.49  | 20.76  | 1.80  |
| Thilarani X JTS 08             | 11.02** | 2.44**  | 6.43**  | 1.62 | 235.55** | -5.34 | 2.98  | 3.07   | 0.11  |
| Thilothamma X JTS 08           | 9.06**  | 4.27**  | 7.64**  | 1.33 | 370.42** | -2.68 | 2.41  | 8.41   | 0.70  |
| Harvest index (%)              |         |         |         |      |          |       |       |        |       |
| Thilarani X TKG 55             | 20.66** | 0.38**  | -2.53   | --   | 12.07**  | 3.41  | 4.93  | 0.23   | 0.11  |
| Thilarani X Phule til          | 19.25** | -0.83** | 0.63    | --   | 35.15**  | 3.88  | -1.93 | 0.11   | 0.04  |
| Thilarani X PKDS 12            | 20.13** | -0.09   | -1.27** | 3.74 | 14.70**  | 13.63 | 54.22 | -1.32  | -0.01 |
| Thilarani X JTS 08             | 18.68** | 0.96**  | 2.90**  | 1.73 | 255.34** | -5.92 | 2.23  | 290.07 | 8.95  |
| Thilothamma X JTS 08           | 19.34** | 0.04    | 1.52**  | 5.96 | 13.15**  | 13.95 | 0     | 0.19   | 0.00  |
| Oil content (%)                |         |         |         |      |          |       |       |        |       |
| Thilarani X TKG 55             | 35.36** | 4.62**  | 4.69**  | 1.00 | 89.98**  | -0.98 | -2.87 | -6.75  | -1.24 |
| Thilarani X Phule til          | 40.05** | 0.51    | -4.72** | --   | 163.39** | 0.97  | -1.62 | 6.18   | 4.05  |
| Thilarani X PKDS 12            | 36.79** | 6.49**  | 9.03**  | 1.17 | 34.06**  | -1.27 | -0.73 | 49.24  | 7.75  |
| Thilarani X JTS 08             | 34.36** | 6.70**  | 8.59**  | 1.13 | 54.72**  | -1.61 | -1.92 | -7.83  | -1.03 |
| Thilothamma X JTS 08           | 40.32** | 1.08**  | -3.22** | --   | 35.75**  | 3.96  | -0.27 | 0.21   | 0.07  |

Dom. Degree: Degree of dominance; NOEG: Number of effective genes;  $X^2$  (Cal.): *Chi square value* \*,\*\* Significant at 5 and 1 %.

and B scales detect additive  $\times$  dominance interactions, the C scale reflects dominance  $\times$  dominance interactions and the D scale indicate additive  $\times$  additive interactions (5, 9) (Table 2). When any of the scaling tests were significant, the six-parameter model ( $m, d, h, i, j$  and  $l$ ) was used to estimate gene effects (Table 3), while joint scaling analysis provided associated parameters such as degree of dominance, potence ratio and effective number of genes (Table 4) (1, 2).

Across most traits and crosses, significant scaling tests and  $X^2$  values indicated that the additive-dominance model was inadequate and that epistatic interactions play an important role in the genetic control of yield and related traits in sesame (9–11). However, for certain traits where scaling tests were non-significant, inheritance was adequately explained by additive and dominance gene effects, indicating that the additive-dominance model sufficiently described the genetic architecture of those traits (10, 11).

### Comparative interpretation of gene action across crosses

A comparative assessment of gene effects across the five crosses revealed consistent patterns in the inheritance of several trait groups. Phenological traits, particularly days to 50 % flowering and days to maturity, were predominantly influenced by dominance and duplicate epistatic interactions in most crosses. Crosses involving Thilarani (Thilarani  $\times$  TKG 55, Thilarani  $\times$  PKDS 12 and Thilarani  $\times$  JTS 08) frequently exhibited significant scaling tests and higher dominance effects, indicating that non-additive gene action plays a major role in determining crop duration (9–11). The prevalence of duplicate epistasis for these traits suggests dispersion of favourable alleles between parents, which may reduce the efficiency of early generation selection and favours selection in later segregating generations or exploitation of heterosis (10).

In contrast, certain yield component traits, such as capsule length, number of seeds per capsule and thousand seed weight, showed comparatively stronger additive gene effects with fewer cases of significant epistasis across crosses (9, 10, 12). These traits therefore appear to be governed largely by fixable genetic variance, making them more amenable to improvement through direct selection in segregating populations (9).

For complex yield-related traits, including number of capsules per plant, biological yield and seed yield per plant, dominance and duplicate epistatic interactions were commonly observed across several crosses (10,11). This pattern indicates polygenic inheritance with substantial non-additive gene action, which limits the effectiveness of early generation selection. Consequently, these traits may be more effectively improved through breeding approaches that exploit non-additive effects, such as heterosis breeding, recurrent selection or selection in advanced generations (13,14).

Overall, the comparative analysis across crosses suggests that different breeding strategies may be required for different trait groups. Traits governed mainly by additive effects can be improved through conventional selection methods, whereas traits showing strong dominance and epistatic interactions may benefit from breeding strategies designed to exploit non-additive genetic variation (10, 11).

### Conclusion

The present investigation revealed that the inheritance of most quantitative traits in sesame is governed by complex genetic mechanisms involving both additive and non-additive gene effects. Significant scaling tests results and  $X^2$  values indicated the presence of non-allelic gene interactions for several traits, suggesting that the additive-dominance model alone is inadequate to explain their inheritance. Duplicate epistasis was more frequently observed than complementary epistasis across the studied crosses, indicating a dispersion of favourable alleles among the parental lines. Yield and its major components, including seed yield per plant, biological yield and number of capsules per plant, were predominantly controlled by dominance and epistatic gene effects, indicating the importance of non-additive gene action in their expression. In contrast, traits such as thousand seed weight, capsule length and oil content exhibited relatively stronger additive effects, suggesting their suitability for improvement through direct selection. From a breeding perspective, these findings indicate that traits governed

largely by additive effects can be improved through selection in segregating generations, whereas complex yield traits showing strong dominance and epistasis may be better exploited through heterosis breeding, recurrent selection or selection in advanced generations. Overall, the study highlights the importance of adopting trait-specific breeding strategies for the development of high-yielding sesame varieties.

## Acknowledgements

The authors gratefully acknowledge the staff of the Instructional Farm, Barrister Thakur Chhedilal College of Agriculture and Research Station, Bilaspur, for their field assistance during the experimentation. The authors also gratefully acknowledge the Project Coordinating Unit (Sesame and Niger), JNKVV Campus, Jabalpur, Madhya Pradesh, for kindly supplying the varietal seed materials used in this research work.

## Authors' contributions

RP conceptualised the study, conducted the experiments and performed data analysis. DS, SK, RK and KT assisted in field experimentation and trait data collection. MS and NP contributed to statistical interpretation and manuscript review. RS provided technical guidance and supervised the research. RP drafted the manuscript with input from all co-authors. All authors read and approved the final manuscript.

## Compliance with ethical standards

**Conflict of interest:** Authors do not have any conflict of interests to declare.

**Ethical issues:** None

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