Heliyon 10 (2024) e40555

Contents lists available at ScienceDirect

Heliyon

journal homepage: www.cell.com/heliyon

Research article

Breeding *Brassica juncea* hybrids with higher seed weight and oil content: Defining criteria for selection of parents

Mohit Sharma [a], Prashant Vasisth [a], Gokulan Dhanasekaran [a], Mohan Lal Meena [a], Omkar Maharudra Limbalkar [a,b], Bhaskar Chandra Sahoo [a], Neeraj Kumar [c], Joghee Nanjundan [d], Rajendra Singh [a], Ram Avtar [c], Anshul Watts [e], Naveen Singh [a,*]

[a] *Division of Genetics, Indian Council of Agricultural Research (ICAR)-Indian Agricultural Research Institute, New Delhi, India*
[b] *ICAR-Indian Institute of Agricultural Biotechnology, Ranchi, Jharkhand, India*
[c] *Department of Genetics and Plant Breeding, CCS Haryana Agricultural University, Hisar, Haryana, India*
[d] *ICAR-Indian Agricultural Research Institute, Regional Station, Wellington, India*
[e] *ICAR-National Institute for Plant Biotechnology, New Delhi, India*

ARTICLE INFO

Keywords:
Brassica juncea
Hybrid
1000-Seed weight
Oil content
Combining ability
Reciprocal differences
GGE biplot analysis
Multi-trait genotype-ideotype distance index

ABSTRACT

Most of the released high-yielding hybrids of *Brassica juncea* have a low 1000-seed weight (TSW) with no increment in the percent oil content (OC), and, therefore, these hybrids have poor acceptance among the farmers in India. It is, thus, imperative to understand the genetic basis of these traits and deploy them in commercial hybrid breeding programs. The present study utilized a set of 15 diverse *B. juncea* genotypes with TSW and OC ranging from 1.32 to 8.26 g and 31.93–43.39 %, respectively, to generate 210 hybrids following a full diallel mating scheme. These hybrids along with their parents, were evaluated in three different environments. Inheritance of TSW suggests the predominance of additive gene action, whereas non-additive gene action was observed to regulate OC. Further, TSW and OC were reported to be influenced by maternal and non-maternal effects, respectively. Parents with bold seeds viz., NPJ 253, RH 761 and EC 223389 were identified as good general combiners for both the traits. Hybrid generated from the cross NPJ 253 x NPJ 161, with both parents having high seed weights, exhibited the highest mean values (8.43 g) and heterobeltiosis (17.2 %) for TSW. Whereas, hybrid between parents NPJ 253 and IC 426372, possessing high and low seed weights, respectively, observed the highest mean value (44.95 %) and heterobeltiosis (14.89 %) for OC. Keeping both TSW and OC together, hybrids viz., NPJ 253 x EC 223389 (H1), NPJ 253 x NPJ 161 (H2) and NPJ 253 x Pusa Tarak (H4) were identified as promising using the Multi-trait Genotype-Ideotype Distance Index. Lines with higher TSW and better combining ability for OC shall be converted to male and/or female lines for generating commercial hybrids. The scheme for deploying higher seed weight and improved oil content in *B. juncea* hybrids is discussed.

1. Introduction

The rapeseed-mustard group of crops comprise of economically important cultivated species viz., *B. rapa*, *B. nigra*, *B. oleracea*,

---

[*] Corresponding author.
E-mail address: ns1.genet@gmail.com (N. Singh).

https://doi.org/10.1016/j.heliyon.2024.e40555
Received 27 June 2024; Received in revised form 7 November 2024; Accepted 18 November 2024

B. juncea, *B. napus* and *B. carinata*. Globally, this group of crops ranked second in oilseed production after soybean with a 14.50 % share [1]. India is the third-largest producer of these crops, followed by Canada and China, with a total production of 11.30 million metric tons from a 8.85 million-hectare area, contributing nearly 27 % to India's overall oilseed production [1]. Indian mustard [*Brassica juncea* (L.) Czern and Coss*;* AABB; 2n = 36], an amphidiploid species originated from spontaneous interspecific hybridization between *B. rapa* (AA; 2n = 20) and *B. nigra* (BB; 2n = 16). It covers around 90 % of the area cultivated under rapeseed-mustard group of crops in India [2–4]. Even though it is a key crop for the edible oil industry in this country, a significant quantity of edible oils are imported to meet domestic demands caused by population growth and changing lifestyles [4,5]. Therefore, there is an urgent need to improve the seed and oil yield of Indian mustard to attain self-sufficiency in edible oils in the country.

Being a quantitative trait, seed yield is influenced directly or indirectly by various contributing factors such as seed weight, primary branches per plant, secondary branches per plant, length of siliqua, seeds per siliqua, total biomass, oil content, etc. [6]. It is largely influenced by environmental factors and has low heritability [7,8], thus, affecting genetic gain achieved through directed selection in segregating generations. Thousand Seed Weight (TSW), also related to oil and protein content, is one of the key determinants of productivity and the principal breeding objective in rapeseed-mustard crops [9]. Oil Content (OC), on the other hand, determines the marketable and economic value of the harvested produce.

With the realization of sufficient yield heterosis and availability of efficient hybrid seed production systems, such as Cytoplasmic Genetic Male Sterility, hybrids are commercially deployed for improving yield and oil yield in mustard [8,10–20]. Despite the availability of high yielding hybrids, the area under their cultivation is limited due to the lower TSW and no additional increment in the OC as compared to contemporary pureline varieties. The commercial Indian mustard hybrid DMH-1 has also demonstrated a higher seed yield, albeit with a low seed weight (<4g) [21,22], but could not command farmers' and market preferences. In general, cultivars with a higher TSW and OC determine the market price and, thus, farmer preference. Furthermore, varieties with higher seed weight ensures better plant stand on sowing than the ones with lower seed weight [23–25]. Hence, the improved productivity and market preference of Indian mustard can be achieved by selectively accumulating favourable alleles/genes/QTLs underlying TSW and OC, while maintaining level of heterosis expressed in the hybrids by their male and female parents.

Assessments of general combining ability (GCA) offer insights into the breeding value and additive component of genetic variance, whereas, specific combining ability (SCA) is confined to non-additive effects and variance [26]. Mustard breeders mainly explained seed yield heterosis with a little emphasis on the traits determining market and farmer preference. In most of the previous studies, combining ability and the heterosis for TSW and OC were worked out along with other yield-contributing traits following different mating designs [8,27,28]; however, this could not precisely guide the preference of parents leading to the development of bold seeded hybrids with higher OC and the struggle of breeders is still going on. Interestingly, TSW is regulated by coordinated control of diploid zygotic embryo, triploid endosperm, and maternal integuments [29,30], highlighting the importance of dissecting maternal effects. Half diallel and L x T designs restrict the dissection of maternal effects, whereas full diallel has proven to be highly effective in the estimation of maternal effects utilising reciprocal crosses [31–33]. Thus, a research gap persists in comprehending the genetic regulation of TSW and OC in *B. juncea*.

Further, the intricate nature of TSW and OC arises from the varied responses of genotypes to environmental fluctuations, during the developmental stages of the plant. Consequently, evaluating genotypes across diverse environments to assess genotype x environment (GxE) interaction is crucial for identifying climate-resilient superior genotypes. Numerous statistical approaches are available for assessing hybrid performance and their interaction with the environments, including genotype main effect plus genotype by environment (GGE) biplot analysis [34,35]. Yan and Hunt [36] formulated a biplot approach to visualize diallel analysis. This tool proves very effective in mega-environment analysis, revealing a "which-won-where" pattern and recommending the superior performer in specific environments [37,38].

Although inheritance of TSW has been reported in several *Brassica* species, but only with limited genetic variability. Among the Brassicas, *B. juncea* harbours the maximum phenotypic variation for TSW that varies from ~2.0 to 7.0 g [39]. The present study was planned with much wider genetic variability for TSW, ranging from about 1.32 to 8.26 g, at the Indian Council of Agricultural Research-Indian Agricultural Research Institute, New Delhi, to (i) understand the inheritance of TSW and OC with the widest range of variability; (ii) delineate the selected parents into distinct phenotypic classes and identify good combiners; (iii) elucidate the inter-relationship between TSW and OC in the set of parents and hybrids and; (iv) define a criterion for selection of parents for developing hybrids with acceptable levels of TSW and OC. Enhancing our comprehension of these objectives will empower us to create superior hybrids with higher TSW and OC for harnessing yield heterosis in *B. juncea*.

2. Material and methods

2.1. Plant material

A set of 152 genotypes was seeded in four distinct environments created by manipulating the time of sowing and locations. Sowing was done under timely and late-sown conditions during the 2021-22 crop season at the Indian Council of Agricultural Research-Indian Agricultural Research Institute (ICAR-IARI), New Delhi (latitude–28.641726°N, longitude–77.154518°E and altitude–228 m) and Chaudhary Charan Singh Haryana Agricultural University (CCSHAU), Hisar (latitude–29.149240°N, longitude–75.722580°E and altitude-216 m). ICAR-IARI is situated in the Trans-Gangetic Plain Zone and experiences semi-arid climatic conditions, with soils ranging from light alluvial (*Entisol*) to sandy loam with pH 7.7 [40]. CCSHAU, on the other hand, is situated within the Indo-Gangetic alluvial plain and characterized by arid climate conditions. The soils in this region vary from sandy loam to sandy clay loam in texture and are slightly to moderately alkaline (pH 7.4 to 8.2) in reaction and non-saline in nature [41]. The maximum and minimum temperatures, relative humidity (%), and rainfall (mm) were recorded during different crop growth seasons (2021-22 and 2022-23) at meteorological observatories located near the experimental sites at both locations and are presented in Fig. 2a and b.

For the presented investigation, a total of 15 diverse *B. juncea* genotypes, including cultivars, stable breeding lines, and germplasm of exotic and native origin, spanning a broad range and continuous variation for TSW, were selected. With a range of 1.32–8.26g, this set of genotypes covers the largest range of TSW ever documented in Brassicas (Table 1; Fig. 1). Four genotypes with higher (>5 g), six with medium (3.5–5 g), and five with lower (<3.5 g) seed weights constitute the set. Further, a sufficient and continuous variation for OC in this set of genotypes was intentionally included, which ranged from 31.93 to 43.39 % (Table 1).

2.2. *Generation of hybrids*

In the 2021–22 crop season, 15 diverse parents differing in TSW and OC were crossed in all possible combinations following full diallel mating design at the experimental area of the Division of Genetics, ICAR-IARI, New Delhi. This process aimed to generate a total of 210 F_1 hybrids by attempting 105 direct and 105 reciprocal crosses.

2.3. *Evaluation of F_1 seeds*

Hybrid (F_1) seed from 210 crosses was generated in the 2021-22 crop season. The TSW of these hybrids and parents were recorded to test the contribution of the male and female parents in the development of seed weight.

2.4. *Evaluation of hybrids and parents*

A set of 210 hybrids along with their 15 parents was evaluated in the 2022–23 crop season in three different environments, viz., timely sown (E1) and late sown (E2) conditions at CCSHAU, Hisar, and timely sown conditions at ICAR-IARI, New Delhi (E3). The experiment was conducted in a Randomized Complete Block Design (RCBD) with three replications. Each entry is raised in a single row of 5 m length, with row-to-row and plant-to-plant spacing of 45 and 15 cm, respectively. Two irrigations each of 50 mm depth were applied in plots at 45 and 90 days after sowing (DAS). A fertilization with 60 kg N, 40 Kg P_2O_5, 40 Kg K_2O and 40 kg S/ha was given. The N was applied in two doses, half as basal application and remaining half at first irrigation. All other nutrients were applied as basal

Table 1
Thousand seed weight and oil content of 15 *B. juncea* genotypes evaluated during 2021-22 crop season.

S. N.	Genotype	Pedigree/Source	1000 seed weight (g)[a]		Representing Class of parents for 1000 Seed weight	Oil Content (%)[a]	
			Mean ± SE	Range		Mean ± SE	Range
1	NPJ 253	KMR-12-1/NPJ 156	7.29 ± 0.40	8.26–6.34	High	39.73 ± 1.57	42.49–35.42
2	NPJ 161	DHR-991 x Pusa Jagannath	7.19 ± 0.23	7.86–6.90	High	38.96 ± 1.16	41.53–35.98
3	RH 761	JMR 9738/RH 30	6.08 ± 0.35	7.07–5.48	High	40.10 ± 1.27	43.39–37.23
4	Pusa Tarak	Agra Local/Poorbi Raya	5.34 ± 0.17	5.64–4.92	High	38.25 ± 0.38	38.99–37.43
5	EC 223389	Exotic collection	4.93 ± 0.26	5.65–4.55	Medium	39.38 ± 0.95	41.73–37.28
6	Pusa Agrani	Early mutant of *B. juncea*/Synthetic amphidiploid (*B. compestris* var. toria/ *B. nigra*)	4.15 ± 0.06	4.24–4.02	Medium	36.40 ± 0.77	37.80–34.47
7	Pusa Mustard 30 (PM 30)	Bio 902/ZEM 1	4.08 ± 0.34	4.73–3.15	Medium	35.20 ± 0.87	37.25–33.09
8	Pusa Mustard 21 (PM 21)	Pusa Bold/ZEM 2	4.04 ± 0.50	5.30–2.86	Medium	34.17 ± 1.00	36.77–31.93
9	Pusa Mahak	Pusa Bold/Glossy Mutant	3.66 ± 0.43	4.34–2.49	Medium	37.92 ± 0.95	39.60–35.34
10	Kranti	Selection from Varuna	3.66 ± 0.22	4.26–3.20	Medium	38.07 ± 1.06	40.77–35.60
11	PDZM 31	LES-1-27/NUDHYJ 3	3.33 ± 0.24	3.63–2.60	Low	41.35 ± 0.48	42.08–40.11
12	Heera	ZYR 4/BJ 1058	2.60 ± 0.35	3.52–1.85	Low	37.98 ± 1.82	43.28–35.30
13	Glossy mutant	Non-waxy mutant with white flowers	2.21 ± 0.09	2.34–1.97	Low	41.72 ± 0.43	42.62–40.57
14	IC 597949	Indigenous collection	1.65 ± 0.05	1.72–1.55	Low	37.59 ± 1.22	39.75–34.63
15	IC 426372	Indigenous collection	1.52 ± 0.10	1.73–1.32	Low	37.47 ± 0.62	38.47–35.69

[a] Data recorded under timely sown irrigated conditions during 2021-22 season in three environments.

NPJ 253 (7.29 ± 0.40g) **NPJ 161 (7.19 ± 0.23g)** **RH 761 (6.08 ± 0.35g)** **EC 223389 (4.93 ± 0.26g)**

Pusa Mustard 21 (4.04 ± 0.50g) **PDZM 31 (3.33 ± 0.24g)** **Glossy Mutant (2.21 ± 0.09g)** **IC 426372 (1.52 ± 0.10g)**

Fig. 1. Variation for 1000 seed weight in the parents.

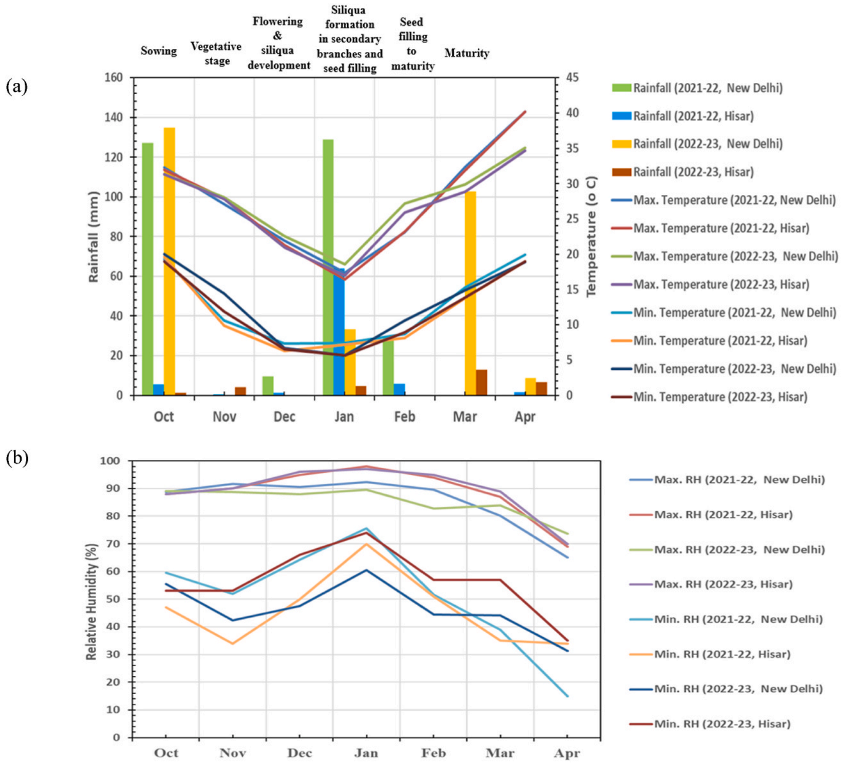

Fig. 2. The maximum, minimum temperatures and rainfall (a); relative humidity (b) recorded from the experimental site (New Delhi and Hisar) during crop growth season (*rabi* 2021-22 and 2022-23).

dose before the last cultivation. Recommended agronomic practices and plant protection measures were followed to raise a healthy crop. Observations on TSW (g) and OC (%) were recorded in all three replications across all environments. The mean phenotypic values for the studied traits were computed from three replications in all the environments and further employed for statistical analysis.

2.5. Genetic and statistical analysis

The mean phenotypic values for the studied traits were used for the analysis of variance using the Statistical Tool for Agricultural Research Version 2.0.1 [42]. Combined best linear unbiased predictors (BLUPs) across the environments were utilized to assess the mean performance of hybrids and parents using multi-environment trial analysis with R software (META-R) [43]. Regression analysis was conducted using R software [44] on the mean performance of parents and hybrids across the environments to determine the relationship between the traits under study. Further, data recorded on 210 F_1's (including reciprocals) and their 15 parents was used to estimate the general combining ability (GCA) of parents and the specific combining ability (SCA) of crosses using the fixed effect model (Model I) of Griffing's Method I [45]. The statistical model for Griffing's Method I (fixed effect model) is as follows:

$$Y_{ijk} = \mu + r_k + g_i + g_j + m_i + s_{ij} + r_{ij} + e_{ijk}$$

Where, Y_{ijk} is the observed mean value of i × jth genotype over k; μ is the general mean; r_k is the replicate effect; g_i is the GCA effect of parent ith; g_j is the GCA effect of parent jth; m_i is the maternal effect of ith parent; s_{ij} is the SCA effect of a cross between ith and jth parent; r_{ij} is the reciprocal effect arising from a reciprocal cross between ith and jth parent and; e_{ijk} is the residual error associated with ijk^{th} individual observations.

The narrow-sense heritability was calculated as per the formula proposed by Mather and Jinks [46]. The analysis of variance, degree of dominance and combining ability were estimated using Plant Breeding Tools Version 1.4 [47], and maternal effects were estimated by Analysis of Genetic Designs with R (AGD-R) Version 5.0 [48] following Griffing's method [45]. The degree of dominance was calculated from dominance and additive variances by applying the formula proposed by Comstock and Robinson [49]. Heterobeltiosis (BPH) was calculated using the standard equation: BPH (%) = (F_1-BP)/BP × 100, where F_1 is the mean value of a hybrid and BP is the value of its superior parent [50]. A novel multi-trait genotype-ideotype distance index (MGIDI) [51] was used to rank the hybrids based on trait values recorded on both TSW and OC, as per the following equation:

$$\mathrm{MGIDI} = \sqrt{\left[\sum\nolimits_{j=1}^{f} (rij - rj)^2\right]}$$

Where, *rij* is the score of the *i*th genotype in the *j*th factor (*i* = *1, 2, …, g; j* = *1, 2, …, f*), being *g* and *f* the number of genotypes and factors, respectively, and *rj* is the *j*th score of the ideotype. The G × E interaction was estimated by R software using Genotype by Environment Analysis tool (GEA-R) [52]. A total of 40 hybrids with MGIDI index <3.0 were selected for visualizing Genotype and Genotype x Environment (GGE) interactions. The biplots were generated involving the 'GGE Model' and the 'gge' function of 'GGE-Biplots' and 'metan' packages of the R software [51,53,54].

3. Results

3.1. Analysis of variance

The analysis of variance revealed significant differences ($p < 0.001$) among hybrids evaluated for the TSW and OC traits in all three environments (Table 2). Overall, GCA, SCA and reciprocal effects significantly contributed to the variability among the parents and hybrids for the traits under study in all three environments. From the pooled analysis of variance, a significant mean sum of squares due to crosses was observed. Thus, indicating the presence of a substantial amount of genetic variation among parents and hybrids for both traits studied. Significant interactions of the crosses, GCA and SCA with the environments for TSW and OC were observed from the pooled analysis of variance (Table 3). The significance of both maternal and non-maternal effects indicated their role in the regulation of TSW, whereas, non-maternal effect predominantly determines the OC (Table 3). Furthermore, the environmental effects were also found to be significant for both traits under study.

Table 2

Analysis of variance for hybrids generated for seed weight and oil content under three different environments.

Trait	Environment	Source of Variation						Mean	CV (%)
		Replication	Crosses	GCA	SCA	Reciprocal	Error		
		Mean Sum of Square							
1000 Seed Weight (g)	Hisar, timely sown (E1)	0.10	4.53[a]	21.08[a]	0.24[a]	0.17[a]	0.04	4.18	8.44
	Hisar, late sown (E2)	0.08	3.53[a]	16.43[a]	0.18[a]	0.14[a]	0.03	3.84	7.61
	New Delhi, timely sown (E3)	0.19	4.89[a]	22.23[a]	0.29[a]	0.22[a]	0.04	4.07	8.01
Oil Content (%)	Hisar, timely sown (E1)	1.06	12.39[a]	28.26[a]	3.03[a]	2.01[a]	0.50	39.63	3.10
	Hisar, late sown (E2)	0.07	11.49[a]	26.51[a]	2.58[a]	2.06[a]	0.48	41.76	2.87
	New Delhi, timely sown (E3)	4.05	14.21[a]	34.88[a]	2.51[a]	2.95[a]	0.55	37.38	3.43
Df		**2**	**224**	**14**	**105**	**105**	**448**		

[a] Significant at p = 0.001; CV= Coefficient of variation; GCA = General Combining Ability; and SCA= Specific Combining Ability.

3.2. Evaluation of hybrid seeds for TSW

The data on TSW recorded on hybrid (F_1) seeds from 210 crosses indicated that the trait is largely influenced by the genotype of their respective female parents (Fig. 3). The mean of the female parental class with different TSW and their derived hybrids followed a similar trend, and observed trait values close to the female parental class with no deviation. Thus, this study was further extended to the harvest of F_1 plants.

3.3. Mean performance of parents and their hybrids

The enormous genetic variability was observed in the parental lines for TSW and OC, ranged from 1.55 to 7.69 g and 32.16–44.58 %, respectively (Table 4). The highest TSW was observed for parents NPJ 253 (7.23 g), while IC 426372 (1.60 g) exhibited the lowest values for this trait across all the environments. Likewise, parents RH 761, NPJ 253, Heera, PDZM 31 and Glossy mutant exhibited higher OC (>40 %) across the environments (Table 4). The mean TSW of hybrids generated among the parents with higher TSW was found to be significantly better than hybrids developed by involving parents with high and medium and high and low values for this trait in all three independent environments and values pooled across the environments (Table 4, Fig. 4, Supplementary Fig. 1). Similarly, the mean performance of hybrids generated by crossing among parents with a medium TSW was found to be significantly better than the ones generated between medium and low, and low and low seed weights of parents across all the environments. None of the hybrids developed from mating between parents with high and low (except PDZM 31 × NPJ 253 in E3) and medium and low (except EC 223389 × PDZM 31 in E2 and E3) could result in hybrids with more than 5 g of average TSW pooled across the environments (Table 4). Moreover, hybrids generated from parents with lower seed weights could not complement to achieve more than 3.5 g of TSW. Parents with higher TSW, on the other hand, resulted in hybrids with a range of 5.1–8.43 g in E1, 4.70–6.93 g in E2, and 5.72–8.11 g in E3 environments. Among all, a hybrid generated by mating between NPJ 253 and NPJ 161 (high × high) exhibited the highest TSW (8.43 g in E1; 6.93 g in E2; 8.11 g in E3) and outperformed their parents across the environments (Supplementary Fig. 2). Although two hybrids generated from parents with medium TSW, viz., EC 223389 × PM 30 (E1 and E3) and PM 30 × PM 21 (E2), outperformed both their respective parents, none of the hybrids from parents with high and medium and high and small were found superior to their respective better parents (Supplementary Fig. 2).

Hybrids produced from parents with high and high and high and low values for TSW were observed to have a higher mean OC than hybrids generated from parents with high and medium, medium and medium, medium and low, and low and low values for seed weight in all the environments (Table 4). The hybrids developed among parents with higher TSW observed OC ranging from 37.49 to 43.10 % in E1, 40.34–43.28 % in E2, and 35.52–40.34 % in E3 environments, whereas hybrids from parents with high and low seed weight observed OC ranging from 37.88 to 44.34, 40.55 to 45.90, and 35.40 to 41.89 in E1, E2, and E3 environments, respectively (Table 4). The highest OC was recovered from the hybrid generated between NPJ 253 and IC 426372 (44.43 %; high × low) in E1 and PDZM 31 and Heera (low × low) in E2 (46.68 %) and E3 (43.70 %) environments (Table 4).

3.4. Relationship between TSW and OC

The linear regression analysis performed between the TSW and OC values of the parents, pooled over the environments, revealed a non-significant relationship between them ($p > 0.5$; Fig. 5a). Similarly, a non-significant relationship was also observed between these two traits in the set of 210 hybrids (Fig. 5b). The coefficient of determination value (R^2) between these two traits was 0.025 and 0.0007 for the parents and their hybrids, respectively, indicating that OC accounts for only 2.5 % of the variance in TSW among the parents

Table 3

Pooled analysis of variance among parents and hybrids evaluated for seed weight and percent oil content across the environments.

Source of Variation	Degree of freedom	Mean Sum of Square	
		1000 Seed Weight	Oil Content
Environment	2	19.98**	3242.66**
Rep (Environment)	6	0.13	1.73
Crosses	224	12.31**	24.60**
Crosses x Environment	448	0.32**	6.74**
GCA	14	176.46**	217.53**
SCA	105	1.62**	14.22**
REC	105	1.12**	9.26*
MAT	14	2.94**	30.58
NONM	91	0.84**	5.98*
GCA x Environment	28	1.38**	25.71**
SCA x Environment	210	0.26**	5.06**
REC x Environment	210	0.24**	5.90**
MAT x Environment	28	0.36**	17.70**
NONM x Environment	182	0.22**	4.09**
Residuals	1344	0.11	1.53

GCA = General Combining Ability Effects; SCA= Specific Combining Ability Effect; REC = reciprocal effects; MAT = maternal effect; NONM = non-maternal effects; **Significant at $p = 0.001$, and *significant at $p = 0.05$.

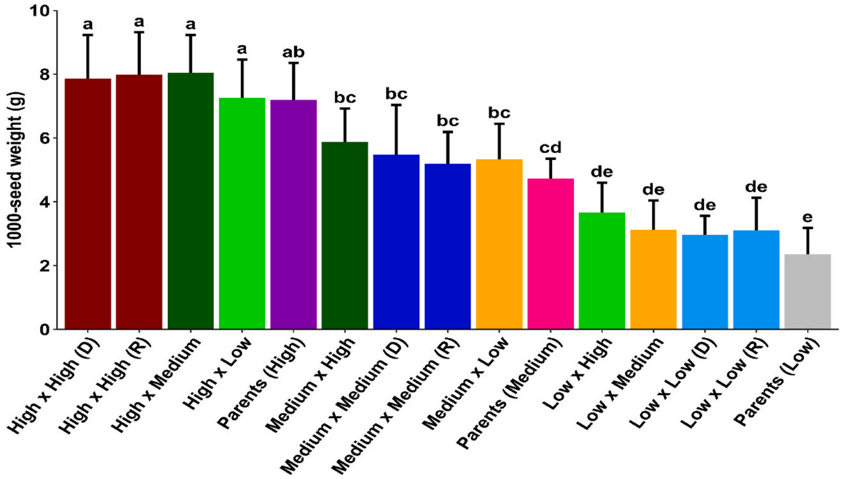

Fig. 3. Mean 1000-seed weight of parental classes and their F_1 seeds generated among and between different parental classes.

and almost 0 % among the hybrids (Fig. 5).

3.5. Combining ability and gene action

Parents and hybrids were observed to have highly significant ($p < 0.001$) GCA and SCA effects, in direct as well as reciprocal crosses, for TSW and OC (Table 2). The variance due to the general combining ability (σ^2_{gca}) was found to be higher than the specific combining ability (σ^2_{sca}) for TSW in all the environments (Table 5), and the GCA/SCA variance ratio for this trait exceeded unity. The average degree of dominance for this trait was observed to be less than one, suggesting strong evidence for the predominance of additive gene action. Further, high narrow-sense heritability (0.85) validates the substantial role of additive components in the inheritance of seed weight. Conversely, the ratio of GCA/SCA variance for OC was found to be less than unity, and the average degree of dominance was more than or close to unity in all the environments (Table 5). Moderate values of narrow sense heritability to the tune of 0.36, 0.39 and 0.48 were observed for OC in E1, E2 and E3 environments, respectively. This implies the significant role of non-additive gene action in governing this trait.

3.6. General combining ability and maternal effect

Most of the parents expressed significant GCA effects for TSW and OC in all three environments (Table 6). Significant and highly positive GCA effects were observed for the parents representing the high and medium values for TSW, including PM 30, Pusa Tarak, RH 761, NPJ 253, NPJ 161, EC 223389, Pusa Agrani, and PM 21, in all environments. Likewise, negative and significant GCA effects were observed in all the environments for parents, viz., Heera, IC 426372, IC 597949, PDZM 31 and Glossy mutant, all representing the low TSW group. The highest GCA effects for TSW were observed in NPJ 253 (E1 = 1.39, E2 = 1.1, and E3 = 1.55). For OC, NPJ 253, RH 761, EC 223389 and Heera exhibited positive and significant GCA effects across all the environments. However, PDZM 31 and Glossy mutant were identified as good general combiners for OC only in E2 and E3 environments. The results suggest that NPJ 253, RH 761 and EC 223389 demonstrated highly significant general combining ability for both TSW and OC under all the test environments (Table 6).

GCA effects of parents were further partitioned into maternal effects. Three parents, viz., Pusa Mustard 30, Pusa Mahak and EC 223389, exhibited significant and positive maternal effects for TSW across the environments. NPJ 253 exhibited significant maternal effects in E1 and E2, while IC 597949 and Glossy mutant displayed significant effects in E2 and E3 environments, respectively. Thus, it manifests the predominance of the maternal effect on TSW. In contrast, the Glossy mutant exhibited a significant maternal effect on OC in all environments. Whereas, EC 223389 and Heera in E3 and IC 597949 and PDZM 31 in both E2 and E3 exhibited a significant positive maternal effect on OC (Table 6). The interaction between the maternal effect and environment was found to influence both the traits studied (Tables 3 and 6).

3.7. Specific combining ability and reciprocal effect

The SCA effects of direct and reciprocal crosses for TSW and OC in each environment are presented in Supplementary Tables 1–6. In the E1 environment, significant SCA effects of TSW were observed for 55 hybrids, including a total of 26 direct and 29 reciprocal cross hybrids. Likewise, in the E2 and E3 environments, a total of 63 (26 direct and 37 reciprocal crosses) and 76 (32 direct and 44 reciprocal crosses) hybrids, respectively, exhibited significant SCA effects. Among these hybrids, 28 direct and 38 reciprocal cross hybrids were observed to be common in either two or more environments. The higher SCA effects for TSW were observed for the hybrids generated

Table 4

The mean, range, and performance of hybrids and parents for 1000 seed weight and oil content in different environments.

Environment	Trait		Hybrids Generated Between Different Parents Catagorised on the Basis of 1000 Seed Weight (g)						Parental with Different Categories of 1000 Seed Weight (g)		
			High × High	High × Medium	High × Low	Medium × Medium	Medium × Low	Low × Low	High	Medium	Low
E1 (Hisar, timely sown)	**1000 seed weight (g)**	**Mean ± SE**	6.41 ± 0.26	5.40 ± 0.10	3.77 ± 0.08	4.59 ± 0.11	3.44 ± 0.06	2.47 ± 0.08	5.89 ± 0.45	4.23 ± 0.27	2.48 ± 0.35
		Range	5.10–8.43	3.98–6.93	2.85–4.86	3.46–5.98	2.57–4.90	1.78–2.96	5.58–7.19	3.43–5.34	1.62–3.45
		Best performing hybrid/parent	NPJ 253 × NPJ 161	NPJ 253 × EC 223389	NPJ 253 × PDZM 31	EC 223389 × PM 30	EC 223389 × PDZM 31	Heera × PDZM 31	NPJ 253	EC 223389	PDZM 31
	Oil content (%)	**Mean ± SE**	40.20 ± 0.46	39.72 ± 0.28	40.72 ± 0.21	38.82 ± 0.40	39.48 ± 0.25	38.66 ± 0.34	40.23 ± 1.78	37.59 ± 1.30	41.02 ± 1.09
		Range	37.49–43.1	35.42–43.78	37.88–44.34	34.70–42.47	35.60–43.22	35.37–40.99	37.02–44.58	32.16–42.00	37.91–44.39
		Best performing hybrid/parent	NPJ 253 × RH 761	NPJ 253 × PM 21	NPJ 253 × IC 426372	EC 223389 × Pusa Agrani	PM 21 × Heera	PDZM 31 × Glossy mutant	RH 761	EC 223389	Heera
E2 (Hisar, late sown)	**1000 seed weight (g)**	**Mean ± SE**	5.57 ± 0.20	4.86 ± 0.09	3.45 ± 0.08	4.42 ± 0.10	3.15 ± 0.06	2.34 ± 0.08	5.47 ± 0.50	4.09 ± 0.17	2.22 ± 0.27
		Range	4.77–6.93	3.47–6.11	2.65–4.43	3.65–5.63	2.28–5.13	1.70–3.28	4.46–6.80	3.78–4.79	1.62–3.07
		Best performing hybrid/parent	NPJ 253 × NPJ 161	NPJ 253 × EC 223389	NPJ 253 × PDZM 31	PM 30 × PM 21	EC 223389 × PDZM 31	Heera × PDZM 31	NPJ 253	EC 223389	PDZM 31
	Oil content (%	**Mean ± SE**	42.40 ± 0.27	41.60 ± 0.23	43.43 ± 0.19	39.87 ± 0.40	41.86 ± 0.21	42.39 ± 0.34	40.00 ± 0.30	39.35 ± 0.55	40.40 ± 1.01
		Range	40.34–43.28	37.96–44.64	40.55–45.90	35.45–43.01	37.96–44.44	40.76–46.68	39-12-40.43	37.96–40.89	37.94–43.24
		Best performing hybrid/parent	NPJ 253 × Pusa Tarak	EC 223389 × RH 761	Glossy mutant × RH 761	Pusa Mahak × EC 223389	EC 223389 × IC 597949	PDZM 31 × Heera	Pusa Tarak	Pusa Agrani	Heera
E3 (Delhi, timely sown)	**1000 seed weight (g)**	**Mean ± SE**	6.62 ± 0.22	5.19 ± 0.12	3.80 ± 0.10	4.36 ± 0.13	3.26 ± 0.07	2.50 ± 0.08	5.94 ± 0.67	3.94 ± 0.22	2.13 ± 0.29
		Range	5.72–8.11	3.17–7.12	2.71–5.15	3.00–5.75	2.11–5.33	1.95–3.17	4.55–7.69	3.20–4.32	1.55–2.95
		Best performing hybrid/parent	NPJ 253 × NPJ 161	NPJ 253 × EC 223389	PDZM 31 × NPJ 253	EC 223389 × PM 30	EC 223389 × PDZM 31	IC 426372 × PDZM 31	NPJ 253	PM 30	PDZM 31
	Oil content (%)	**Mean ± SE**	38.00 ± 0.39	36.97 ± 0.29	38.64 ± 0.30	35.86 ± 0.48	37.30 ± 0.22	38.09 ± 0.47	38.27 ± 1.47	35.74 ± 0.47	38.23 ± 1.26
		Range	35.52–40.34	31.32–41.33	35.40–41.89	25.68–38.89	32.64–40.79	35.14–43.71	34.10–40.82	33.64–36.85	34.84–41.18
		Best performing hybrid/parent	NPJ 253 × Pusa Tarak	EC 223389 × NPJ 253	Glossy mutant × RH 761	PM 21 × EC 223389	Glossy mutant × EC 223389	PDZM 31 × Heera	RH 761	PM 30	Heera

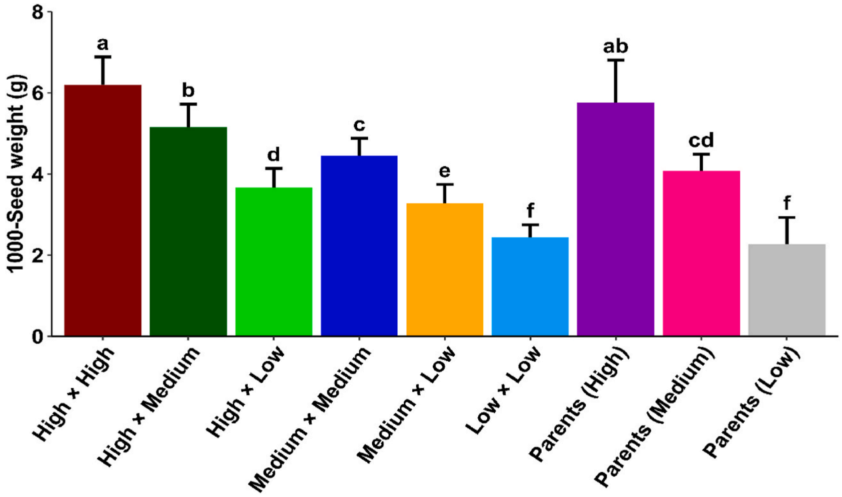

Fig. 4. Mean performance of hybrids and parents for 1000 seed weight estimated by pooled analysis from the harvest of F_1 plants.

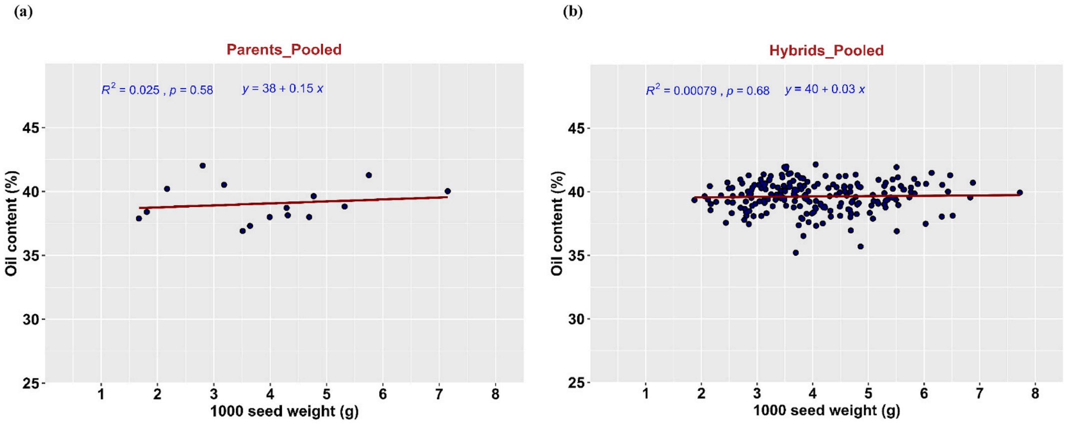

Fig. 5. Linear regression curve between 1000 seed weight and oil content in parents (a) and their hybrids (b).

Table 5

Estimates of the genetic component of variance for seed weight and oil content in parents and their hybrids evaluated under different environments.

Component of variances	Environment	σ^2_{gca}	σ^2 sca	σ^2_{gca}/σ^2 sca	σ^2 rca	σ^2_A	σ^2_D	Average degree of dominance	Narrow sense heritability
1000 seed weight (g)	E1	0.70	0.20	3.46	0.06	2.78	0.43	0.39	0.85
	E2	0.55	0.15	3.67	0.06	2.17	0.32	0.38	0.86
	E3	0.74	0.25	2.92	0.09	2.93	0.54	0.43	0.84
Oil Content (%)	E1	0.93	2.52	0.37	0.75	3.37	5.39	1.26	0.36
	E2	0.87	2.10	0.41	0.79	3.19	4.48	1.19	0.39
	E3	1.14	1.96	0.58	1.20	4.32	4.18	0.98	0.48

E1 = Hisar, timely sown; E2 = Hisar, late sown; and E3 = New Delhi, timely sown; σ^2gca = variance component due to general combining ability; σ^2sca = variance component due to specific combining ability; σ^2_{gca}/σ^2 sca = ratio of variance components due to GCA and SCA; σ^2 rca = variance component due to reciprocal effect; σ^2_A = additive variance; and σ^2_D = dominance variance.

between parents with high mean values, such as NPJ 253 × NPJ 161 and RH 761 × NPJ 253, followed by the hybrids between parents with high and medium values, such as NPJ 161 × EC 223389 and RH 761 × PM 30, evaluated across the environments for this trait. In general, it is observed that most of the hybrids exhibiting significant SCA effects were derived from mating parents with significant positive GCA effects.

Furthermore, a total of 60 hybrids (17 direct and 43 reciprocals) demonstrated significant SCA effects for OC in the E1 environment. Likewise, 54 (23 direct and 31 reciprocals) and 31 hybrids (16 direct and 15 reciprocals) exhibited significant SCA effects in E2 and E3 environments, respectively. Among these, 32 hybrids developed from 12 direct and 20 reciprocal crosses were found to exhibit significant SCA effects in two or more environments. Interestingly, most of these hybrids are generated by parents with either significant

Table 6
General Combining Ability (GCA) and Maternal Effects (MAT) estimated on parents for 1000-seed weight and oil content under different environments.

Trait	1000 seed weight (g)						Oil content (%)					
Environments	E1		E2		E3		E1		E2		E3	
Parents	GCA	MAT	GCA	MAT	GCA	MAT	GCA	MAT	GCA	MAT	GCA	MAT
PM 30	0.37***	0.24***	0.42***	0.27***	0.41***	0.29***	−1.24***	−0.81	−1.98***	−1.16	−1.13***	−0.37
Pusa Tarak	0.30***	−0.18	0.18***	−0.06	0.40***	−0.15	−0.52***	−0.63	0.56***	0.31*	−0.86***	−0.46
RH 761	0.91***	0.01	0.81***	0.02	0.95***	−0.07	1.14***	−0.08	0.56***	−0.23	0.46***	−0.96
NPJ 253	1.39***	0.10**	1.1***	0.08*	1.55***	−0.15	1.66***	0.38**	0.92***	0.12	1.62***	−0.62
NPJ 161	1.02***	−0.01	0.84***	−0.11	1.09***	−0.06	−0.06	0.47***	−0.03	0.08	0.54***	−0.06
Pusa Agrani	0.10**	−0.20	0.13***	−0.08	0.18***	−0.02	0.23	0.18	−0.63***	−0.58	−0.67***	−0.19
PM 21	0.32***	−0.07	0.29***	−0.08	0.38***	−0.07	0.56***	0.23	−0.82***	−0.44	0.08	−0.04
Pusa Mahak	0.06	0.10**	0.22***	0.08*	−0.31***	0.19***	−1.36***	0.25*	−1.64***	−0.58	−1.81***	−0.04
Kranti	−0.14**	0.01	−0.12***	−0.1	−0.39***	0.05	−1.76***	0.08	−0.71***	−0.48	−1.68***	0.54***
EC 223389	0.57***	0.13***	0.58***	0.08**	0.45***	0.15***	1.01***	0.28*	0.96***	0.46***	0.71***	0.05
Heera	−0.88***	−0.02	−0.79***	0.05	−0.84***	−0.04	0.72***	0.28*	0.64***	0.54***	0.48***	−0.01
IC 426372	−1.34***	−0.10	−1.2***	−0.11	−1.2***	−0.14	0.00	−0.28	0.33**	0.34**	−0.42**	−0.16
IC 597949	−1.21***	0.06	−1.05***	0.12***	−1.12***	−0.01	0.03	0.06	0.25*	0.61***	0.04	0.49***
PDZM 31	−0.44***	−0.05	−0.37***	−0.13	−0.35***	−0.1	−0.63***	−0.68	0.75***	0.66***	1.61***	0.81***
Glossy mutant	−1.05***	−0.02	−1.04***	−0.02	−1.18***	0.08*	0.22	0.29*	0.83***	0.36**	1.04***	0.99***

***Significant at p = 0.001; **significant at p = 0.01, *significant at p = 0.05; E1, Hisar (timely sown); E2, Hisar (late sown) and E3, New Delhi (timely sown).

negative GCA or at least one of the parents exhibiting significant negative GCA. The hybrids from reciprocal crosses were observed to express significant maternal effects for TSW, thus, influencing the SCA effects of the reciprocal hybrids (Supplementary Tables 1–6).

3.8. Extent of heterobeltiosis

A broad range for better parent heterosis (heterobeltiosis) was observed for TSW and OC across the environments. Nine hybrids exhibited significant positive heterobeltiosis for TSW in the E1 environment, whereas 10 and 26 hybrids expressed significant heterobeltiosis in the E2 and E3 environments, respectively. Among all the above hybrids, eight expressed significant heterosis in two or more environments (Supplementary Tables 1, 2, and 3). Among the hybrids generated from parents with high seed weight (high x high), the highest heterobeltiosis (17.20 %) was observed for the hybrid NPJ 253 × NPJ 161, which was followed by NPJ 161 × RH 761 (16.19 %) in the E1 environment. A similar trend for heterobeltiosis was observed in the E3 environment. Further, hybrids developed by crossing between parents with medium seed size (medium x medium), such as PM 30 × PM 21 (>24 %) and EC 223389 × PM 30 (>10 %), consistently displayed higher heterobeltiosis across the environments. However, none of the hybrids generated from hybridizing parents with high and low and medium and low values for TSW exhibited better parent heterosis in all three environments, whereas Pusa Mahak × IC 426372, EC 223389 × PDZM 31, IC 597949 × IC 426372 and Glossy mutant × IC 597949 hybrids performed significantly better only in the E3 environment.

A total of 14, 79, and 18 hybrids were found to express significant heterobeltiosis for OC in E1, E2 and E3 environments, respectively. Out of these hybrids, 16 were found to exhibit significant heterobeltiosis, at least in two environments. The hybrids NPJ 161 × IC 426372 (10.32 %), NPJ 253 × IC 426372 (14.89 %) and Pusa Agrani × IC 426372 (7.80 %) expressed significantly better parent heterosis in all three environments (Supplementary Tables 4, 5 and 6). There were more hybrids with substantial heterobeltiosis for OC in the E2 environment than in the other environments, thus establishing the influence of genotype-environment (G × E) interaction.

3.9. Ranking of hybrids based on trait values

A total of 210 hybrids generated in a full diallel design, with 15 parents, were evaluated for TSW and OC in three different environments, and composite ranks were assigned to the hybrids based on *per se* performance for these two important traits. A total of 40 hybrids (H1 to H40) superior for both traits were selected based on the MGIDI index (<3) calculated using the mean values of individual traits pooled over environments (Table 8). The H1 hybrid was identified as the most ideal and stable by this index, followed by H2. The trait values of these 40 hybrids ranged from 2.54 to 8.75 g and 34.42–47.02 % for TSW and OC, respectively.

3.10. Genotype by genotype × environment interactions among test hybrids

Furthermore, to identify the most discriminating and representative environment(s), the same set of hybrids was used for Genotype and Genotype x Environment (GGE) biplot analysis (Table 8). The GGE biplots represented 97.95 % (PC1- 92.72 % and PC2- 5.23 %) and 88.02 % (PC1- 50.91 % and PC2- 37.11 %) of the total variation for TSW and OC, respectively (Supplementary Fig. 3). 'Discrimination vs. Representativeness' view of the GGE biplot reveals that E1 (Hisar) and E3 (New Delhi) environments have a higher vector length and minimum angle to the Average Environment Coordinate (AEC). This signifies that these environments are optimal for the identification of superior hybrids for TSW (Fig. 7a). Similarly, the E2 (Hisar, late sown) environment exhibited a narrow angle with the AEC, highlighting its representativeness among the environments for OC (Fig. 7b).

Hybrids H18 performed better in E1 and E2, whereas H23 and H12 were identified to be better in the E3 environment for TSW (Fig. 6a). For OC, hybrid H30 outperformed all the hybrids in E1, H14 in E2, H32 and H27 in E3 environments (Fig. 6b). The biplot comparing mean vs. stability revealed that hybrid H2 was positioned closest to the AEC, while H1, H3, and H4 exhibited shorter perpendicular distances from the AEC, highlighting the highest stability of these hybrids for TSW (Fig. 8a). Likewise, H14 with the highest OC is positioned closest to AEC, while H5 and H4 hybrids exhibited the shortest vertical distance from AEC signifying their better stability across the environments (Fig. 8b). In the genotype biplot rankings, H2 hybrid occupied the top position, followed by H3, H12, H1, H6, H11 and H4, indicating their superior performance for TSW. Similarly, H5 secured the highest ranking for OC, followed by H14, H34, and H4 hybrids (Supplementary Fig. 4).

4. Discussion

The present study focuses on the seed and oil yield enhancement in the *B. juncea* hybrids to meet edible oil demands. Seed weight and percent oil content not only contribute to the yield but also determine the market acceptability and preference for the released hybrids. Seed and oil yields are directly or indirectly influenced by various contributing factors, including TSW and OC. To find out the ways and means for improving seed and oil productivity in the future hybrids, it is important to identify parents with desirable traits and devise methods to utilize them. The intricate relationship between the contributing factors could not be well understood due to the limited genetic variability available for the trait(s), the insufficient number of hybrids and their reciprocals, insufficient quantity of hand-pollinated hybrid seed, and the lack of multilocation testing and analytical facilities. There are conflicting reports on the association of seed weight/size with OC. These key determinants of productivity are influenced by the varied responses of genotypes to environmental fluctuations at the time of seed development. Therefore, the multilocation evaluation of a large number of hybrids and their reciprocals, derived from parents with sufficient variation, is required for any valid genetic interpretation. Thus, the present study

Table 7

Hybrids possessing high Specific Combining Ability (SCA) effects and heterobeltiosis for 1000 seed weight and oil content across the environments.

Trait	Class(es) of 1000-seed weight of parents used in generating hybrid	Hybrids with highly significant SCA effects and Heterobeltiosis		
		E1 (Hisar, timely sown)	E2 (Hisar, late sown)	E3 (New Delhi, timely sown)
1000 seed weight (g)	high x high	NPJ 253 × NPJ 161 (8.43; 17.2)	–	Pusa Tarak × NPJ 161 (6.18; 15.39), NPJ 161 × Pusa Tarak (6.01; 12.26)
	high x medium	PM 30 × RH 761 (6.78; 21.42)	NPJ 161 × EC 223389 (5.25; 12.62)	PM 30 × Pusa Tarak (6.01; 32.00),Pusa Tarak × Pusa Agrani (5.38, 18.08), Pusa Tarak × PM 21 (5.41; 18.77), NPJ 161 × PM 21 (6.23; 16.41), NPJ 161 × EC 223389 (6.05; 12.99), PM 21 × NPJ 161 (5.96, 11.34)
	high x low	–	–	–
	medium × medium	PM 30 × PM 21 (5.63; 30.66), PM 30 × Kranti (5.19; 34.58), PM 21 × PM 30 (5.29; 22.60)	PM 30 × PM 21(5.63; 30.61), PM 30 × Kranti (5.13; 35.33), PM 21 × PM 30 (5.10; 18.18)	PM 30 × PM 21 (5.38, 24.46), Pusa Agrani × PM 21 (5.19, 20.6), PM 21 × Pusa Agrani (5.01; 16.43), PM 30 × EC 223389 (4.93; 14.12)
	medium × low	NA	NA	Pusa Mahak × IC 426372 (4.13, 29.00), EC 223389 × PDZM 31 (5.33, 26.46)
	low × low	NA	NA	IC 426372 × IC 597949 (1.97, 18.78)
Oil Content (%)	–	PM 30 × IC 426372 (41.30; 8.93) NPJ 253 × IC 426372 (44.33; 6.31) NPJ 161 × IC 426372 (41.81; 10.32) Pusa Agrani × IC 426372 (42.03; 8.74) PM 21 × Pusa Agrani (41.04; 6.18)	PM 21 × NPJ 253 (42.00; 7.36), IC 426372 × NPJ 253 (44.36; 13.39), IC 597949 × NPJ 253 (43.77; 11.88), RH 761 × Pusa Mahak (42.74; 6.03), Pusa Tarak × EC 223389 (44.28; 8.56), Pusa Mahak × EC 223389 (43.01; 5.43), IC 597949 × EC 223389 (43.65; 6.99), NPJ 253 × IC 426372 (44.95; 14.89), Pusa Tarak × IC 597949 (42.68; 5.58), NPJ 253 × IC 597949 (44.28; 13.20), EC 223389 × IC 597949 (44.44; 8.93), IC 426372 × IC 597949 (42.55; 9.16), RH 761 × Glossy mutant (44.69; 5.62), NPJ 161 × PDZM 31 (42.31; 5.34), Kranti × PDZM 31 (42.90; 7.32)	Pusa Agarni × IC 426372 (38.41; 7.80)

*First values in parentheses represent the mean of the respective hybrids, whereas, second represents the percent heterobeltiosis for the trait.

Table 8
Promising hybrids identified on the basis of both seed weight and oil content for GGE biplot analysis using Multi-Trait Genotype-Ideotype Distance Index (MGIDI).

ID	Hybrids	MGIDI index	ID	Hybrids	MGIDI index	ID	Hybrids	MGIDI index
H1	NPJ 253 × EC 223389	1.30	H15	Kranti × NPJ 253	2.31	H29	EC 223389 × Pusa Mustard 21	2.73
H2	NPJ 253 × NPJ 161	1.31	H16	NPJ 161 × Pusa Mustard 21	2.31	H30	NPJ 253 × IC 426372	2.73
H3	NPJ 161 × NPJ 253	1.38	H17	NPJ 253 × PDZM 31	2.33	H31	Pusa Mahak × NPJ 253	2.78
H4	NPJ 253 × Pusa Tarak	1.39	H18	RH 761 × EC 223389	2.35	H32	Glossy mutant × RH 761	2.78
H5	EC 223389 × NPJ 253	1.52	H19	EC 223389 × Pusa Tarak	2.37	H33	EC 223389 × Pusa Agarni	2.84
H6	NPJ 253 × RH 761	1.83	H20	NPJ 253 × Pusa Agarni	2.48	H34	IC 426372 × NPJ 253	2.84
H7	NPJ 253 × Pusa Mustard 21	1.87	H21	EC 223389 × PM 30	2.48	H35	Pusa Mustard 21 × RH 761	2.86
H8	EC 223389 × NPJ 161	1.96	H22	PDZM 31 × NPJ 253	2.50	H36	NPJ 253 × Kranti	2.86
H9	EC 223389 × RH 761	1.98	H23	Pusa Tarak × NPJ 253	2.51	H37	RH 761 × Pusa Mahak	2.95
H10	NPJ 161 × EC 223389	2.06	H24	Pusa Mustard 21 × NPJ 253	2.53	H38	Pusa Mustard 21 × EC 223389	2.99
H11	NPJ 161 × RH 761	2.08	H25	RH 761 × NPJ 161	2.54	H39	Pusa Tarak × NPJ 161	2.99
H12	RH 761 × NPJ 253	2.10	H26	Pusa Tarak × RH 761	2.57	H40	NPJ 161 × Pusa Tarak	2.99
H13	Pusa Agarni × NPJ 253	2.14	H27	PDZM 31 × NPJ 161	2.60			
H14	Glossy mutant × NPJ 253	2.30	H28	PDZM 31 × RH 761	2.72			

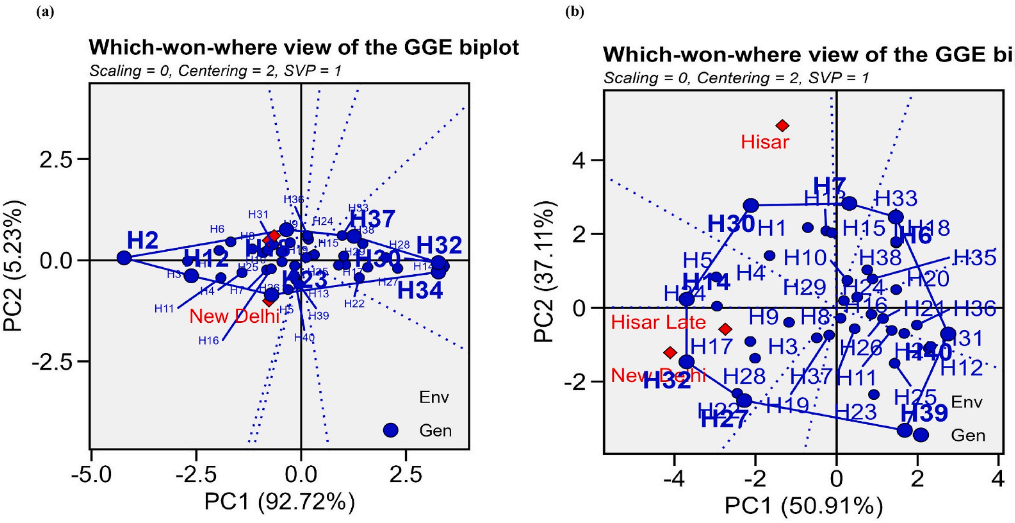

Fig. 6. 'Which-Won-Where' polygon of GGE biplot representing the superior hybrid for (a) 1000-seed weight and (b) oil content (Refer to Table 8 for the hybrid codes).

was planned with a set of 15 parents covering the largest genetic variability for seed weight ever reported, which also includes sufficient variability for OC. These 15 parents were hybridized in all possible combinations following a full diallel mating design. The TSW recorded on F_1 seeds indicated the role of the female parent in the development of seed size. Thus, this set of 210 hybrids was raised along with the parents and evaluated in three different environments to record observations on TSW and OC.

Analysis of variance revealed highly significant differences among parents and hybrids for TSW and OC, illustrating a wide range of variability within the parental lines and hybrids (Table 2). The significance of the mean sum of squares for GCA and SCA in all the environments indicated the relevance of both additive and non-additive variances for both traits. Similar results were also observed in the pooled analysis of variance for hybrids, GCA, SCA and RCA for these traits. Further, the pooled analysis of variance revealed a significant interaction of hybrids, GCA and SCA with the environments for both of these traits, clearly indicating the effect of the environment on the performances of parents and hybrids (Table 3). Earlier studies have also reported similar results [8,28,55–59]. Partitioning of the reciprocal sum of squares revealed the significance of both maternal and non-maternal effects in influencing TSW, whereas a preponderance of significant non-maternal effects was recorded for OC. This suggests that seed weight is influenced by the interplay of nuclear and cytoplasmic factors, or their interactions, while the regulation of OC is primarily under nuclear control.

It was observed that small-seeded parents have a negative impact on the mean TSW of hybrids, whereas a higher TSW was recorded for hybrids generated from parents representing high and medium seed weight classes. These findings imply that the superiority of hybrids may be attributed to the divergence of superior alleles governing the higher seed weight in the parents.

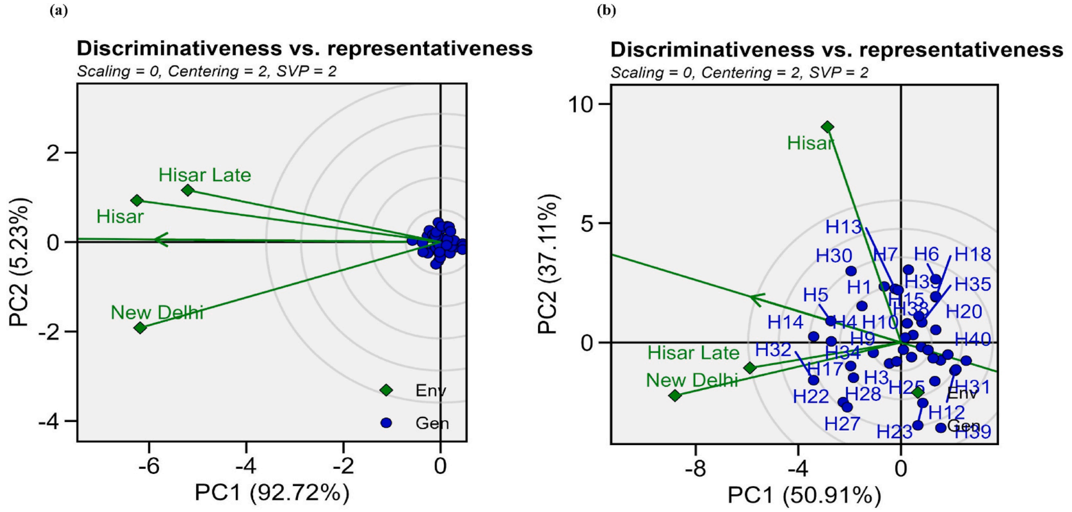

Fig. 7. Discriminative power vs. Representative vision of GGE biplot for (a) seed weight and (b) oil content.

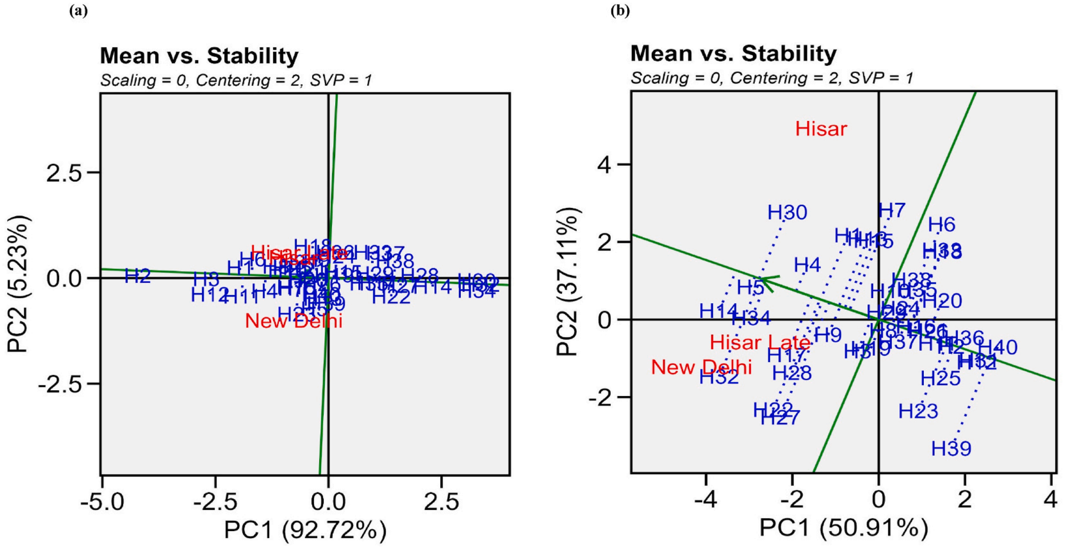

Fig. 8. Mean vs. Stability view of GGE biplot illustrating the similarities among genotypes for (a) seed weight and (b) oil content.

Linear regression analysis, on the other hand, indicated that the relationship between TSW and OC was non-significant in the parents and hybrids pooled across the environments. In addition to this, the expression of heterobeltiosis for TSW and OC is independent of each other in the test hybrids. Although some of the earlier studies have shown a negative association between these two traits [60,61], Limbalkar et al. [62] reported a non-significant relationship between them. The results from the present study provide clear evidence of unrelatedness between TSW and OC in Indian mustard.

4.1. Combining ability variance, heritability and gene action

The analysis of combining ability partitioned the genotypic variability into two components, i.e., GCA (σ^2gca) and SCA (σ^2sca) variances, representing additive and dominance effects, respectively. Combining ability and gene action was frequently used by researchers to select the best breeding procedure for higher genetic gain [8,63,64]. In comparison to σ^2sca higher values were observed for σ^2gca, and the σ^2gca/σ^2sca ratio between them surpassed unity for seed weight (Table 5). This finding provides strong evidence for the preponderance of additive gene action in governing seed weight. The findings are in accordance with the reports of Singh et al. [8] and Priyamedha et al. [61,65] in Indian mustard. Some of the previous studies have also reported the prevalence of non-additive gene action in regulating seed weight in this crop [28,63,66], with a relatively small number of hybrids that were evaluated at a single location. Further, less than one degree of dominance and high narrow sense heritability (84 %) for TSW indicate that this trait can be readily improved through hybridization among the desired genotypes, with higher mean values, followed by selection in the segregating generations and, thus, a high genetic gain can be anticipated [67]. Inter-matting among such derived lines shall help in recovering hybrids with higher TSW.

For OC, the value of SCA variance was higher than GCA variance, and the degree of dominance exceeded unity in all the three environments (Table 5). This implies the role of non-additive gene action in the expression of this trait. Similar findings were also documented by Limbalkar et al. [28], Chand et al. [66], Meena et al. [67] and Akbari et al. [68] in Indian Mustard. Further, the narrow sense heritability was observed to be moderate across the environments, suggesting that the expected genetic gain per cycle of selection and efficacy for selection in segregating generations will be less effective for this trait. However, genetic enhancement and commercial exploitation of OC are possible through the development of hybrids, and selection for this trait involving pedigree or recurrent selections needs to be delayed to advanced filial generations.

4.2. General combining ability effects

The GCA effects can be used to estimate the breeding value of a genotype [69]. The significance of the GCA effect is manifested by additive and additive x additive gene interactions, thus reflecting the heritable portion of genetic variation [26]. In the present study, highly significant and positive GCA effects for TSW were observed in all the environments for the parents, viz., PM 30, Pusa Tarak, RH 761, NPJ 253, NPJ 161, Pusa Agrani, PM 21 and EC 223389, delineated in either high or medium seed weight categories (Table 6). Suggesting that these parents carry favourable alleles responsible for determining higher TSW. The higher GCA effects suggest that the parental mean dominates the general mean, indicating the flow of useful genes from parents to offspring in a higher proportion, in addition to additive gene action [70,71].

Highly significant and positive GCA effects were observed for NPJ 253, RH 761, EC 223389 and Heera for OC in all three environments (Table 6). This implies that these parents are potent combiners for OC. Similar results were reported in some prior studies conducted with a different set of genotypes and following different approaches in *B. juncea* [8,61,63,65]. It was also observed that the parental lines exhibiting high performance were also good general combiners for the respective traits. It can be inferred that selecting potential parents for breeding programs aimed at improving TSW and OC, crucial for seed and oil yield enhancement in Indian mustard, may be judged from their *per se* performance. These findings are in consonance with the studies conducted by Ram et al. [72] and Owusu et al. [73]. The present study also suggests that parents, viz., NPJ 253, RH 761, and EC 223389, exhibit higher *per se* performance and express high GCA for both traits across the environments make them suitable candidates for any breeding program directed towards seed and oil yield enhancement.

4.3. Specific combining ability effect and heterobeltiosis

In the present study, significant SCA effects for TSW and OC were recorded for 66 and 32 hybrids, respectively, in two or more environments (Supplementary Tables 1–6). This implies that these hybrids performed better than the ones predicted to be superior on the basis of the GCA effects of their parents [64]. Significantly higher SCA effects were also reported in previous studies using different sets of *Brassica* genotypes [56,74,75]. The parents with high SCA effects identified in the present study can be used for the development of parental lines for the exploitation of heterosis and generating desirable transgressive segregants for both traits. Interestingly, a significantly higher SCA effect and heterobeltiosis (>15 %) for TSW were observed for the hybrids generated among and between parents with high and medium (high × high, high × medium, and medium × medium) seed weights. Hybrids generated by mating between parents with high and low, medium and low, and low and low seed weights exhibited lower values (Table 7). This implies that the additive effects in parents with higher TSW are responsible for the expression of high SCA effects and heterobeltiosis. Further, hybrids generated from mating between parents with significantly positive GCA effects exhibited a higher SCA effect and heterobeltiosis for seed weight. This could be attributed to the additive x additive gene action, where complementation of favourable alleles in the hybrids led to the expression of high heterosis [71,76]. Contrary to this, hybrids generated between parents with significant and/or non-significant GCA effects for OC could also exhibit higher SCA effects and heterobeltiosis for this trait. Thus, it demonstrates that complementation of underlying genes or loci is responsible for the expression of such SCA effects and heterobeltiosis in derived hybrids [28]. Further, hybrids generated by involving parents with high × low and low x low GCA effects also resulted in better heterosis. Thus, indicating that the loci governing high trait values may express under homozygous and/or heterozygous conditions [77,78]. Furthermore, genes responsible for low trait value may result in high OC in a heterozygous state, primarily due to complementation or overdominance [28,79]. Consequently, this finding suggests the role of non-additive gene action in the inheritance of OC. Therefore, genetic gain could only be achieved through hybridization, followed by selection in advanced filial generations.

4.4. Reciprocal and maternal effects

Reciprocal differences were analyzed to distinguish maternal and non-maternal effects. For both traits under study, reciprocal differences in the hybrids are evident from the significance of its sum of squares (Tables 2 and 3). These differences exist in nature due to the unequal contributions of male and female gametes to the zygote [80,81]. The present study establishes the significance of maternal and non-maternal effects for TSW and OC, respectively, across the environments (Table 3). Reciprocal crosses in several other species have also revealed the prevalence of a strong maternal effect on the seed weight of hybrids [30,33,82,83]. Further, the differences in SCA effects observed for direct and reciprocal crosses might be due to interactions between nuclear and cytoplasmic genes. Yao et al. [84] and Fan et al. [32] reported the reciprocal differences for seed weight in the hybrids and concluded that reciprocal effects influence GCA (*via* maternal) and SCA (*via* non-maternal) effects and their respective variances. Hence, it is concluded from this study that to breed for a higher TSW, at least the female parent must have a higher trait value.

4.5. Genotype × environment interaction

The significance of crosses x environment, GCA x environment, and SCA x environment and the reciprocal effects x environment observed in the pooled analysis of variance in this study indicate that the trait expression in hybrids for TSW and OC is highly influenced by the environment (Table 3), which becomes the basis for investigating the nature and magnitude of genotype-environment interaction (GE) [64]. The top 40 hybrids, identified on the basis of the MGIDI index calculated with the values recorded for both traits, were used for the estimation of G × E interactions and the identification of stable hybrids using the GGE biplot analysis. Several studies have been conducted to identify stable hybrids using the MGIDI index in various crops [85,86]. The genotypes with the lower MGIDI values can be considered ideal genotypes and exhibit desired values for the measured traits [51,87]. Hybrids, viz., NPJ 253 x EC 223389 (H1), NPJ 253 x NPJ 161 (H2) and NPJ 253 x Pusa Tarak (H4), were identified as highly stable on the basis of the MGIDI index in this study (Table 8). A similar approach was used by earlier workers for the identification of stable hybrids [88, 89]. GGE biplots, on the other hand, are an effective graphical approach for the detection of GE interaction and visualize the characteristics of the genotypes studied [35,90,91]. The cumulative contribution of PC1 and PC2 accounts for 97.95 % and 88.02 % of the interaction sum of squares for TSW and OC, respectively, and hence enables effective representation of the variation present in hybrids. Our findings indicate that the E1 and E2 environments demonstrated a stronger discrimination ability for identifying superior hybrids for TSW and OC, respectively. From the which-won-where plot, H2 (NPJ 253 × NPJ 161) and H14 (Glossy mutant × NPJ 253) were identified to be most promising for seed weight and OC, respectively, across the environments. For OC, Glossy mutant × NPJ 253 (H14) was identified as the top performer, while EC 223389 × NPJ 253 (H5) was identified as the most stable across the environments (Fig. 6b). Among the locations, Hisar proved to have better discriminative ability for both traits. A similar approach has been followed for analysing GE interaction in maize [91–93] and rice hybrids [94,95].

The presented study elucidated the inheritance of TSW and OC, reciprocal differences in the hybrids, and influence of G x E in the expression of traits. Despite the unrelated nature of these two traits, the findings will aid in designing breeding programmes to generate and identify desirable parental lines for developing hybrids with higher TSW and OC. The promising parents identified during this study are suitable candidates for conversion to cytoplasmic-genetic male sterility and/or fertility restorer line(s) for commercial exploitation of yield heterosis and breed hybrids with acceptable market preference.

5. Conclusion

The present study was conducted to understand the inheritance of TSW and OC and define a criterion for selecting parents for developing *B. juncea* hybrids with higher TSW and OC. The predominance of additive genetic effects for TSW suggests that the trait can be readily improved through selection, leading to a high genetic gain. However, OC was found to be governed by dominance gene action, and selection for this trait needs to be delayed to advanced filial generations for deriving promising lines. Further, the female parent has a higher influence on the development of TSW, while the OC was not affected by it in the hybrids. Parents, viz., NPJ 253, RH 761, and EC 223389 emerged as excellent general combiners for both traits under study, suggesting the wide adaptability of these parents. Hybrid NPJ 253 × NPJ 161, with both parents having high seed weight, exhibited the highest mean values (8.43 g) and heterobeltiosis (17.2 %) for TSW. Hybrid generated by crossing NPJ 253 and IC 426372 parents, possessing high and low TSW, respectively, observed the highest mean value (44.95 %) and highest heterobeltiosis (14.89 %) for OC. It is therefore important to choose both parents or at least a female parent with bold seeds to recover bold-seeded hybrids. To recover hybrids with high OC, at least one of the parents should have a higher trait value. Complementing selection criteria for both traits shall help develop hybrids with bold seeds and higher oil content. Out of 210 hybrids, NPJ 253 × NPJ 161 (H2) exhibited the highest *per se* performance and stability for TSW. In contrast, EC 223389 × NPJ 253 (H5) was identified as the most stable across the environments for OC using GGE biplot analysis. Overall, the material and insights from the study unveiled new opportunities for researchers to develop and deploy the parental lines for developing high-yielding hybrids and cultivars with bold seeds and higher OC.

CRediT authorship contribution statement

Mohit Sharma: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Prashant Vasisth:** Writing – original draft, Formal analysis, Data curation. **Gokulan Dhanasekaran:** Data curation. **Mohan Lal Meena:** Supervision, Data curation. **Omkar Maharudra Limbalkar:** Writing – review & editing, Formal analysis. **Bhaskar Chandra Sahoo:** Data curation. **Neeraj Kumar:** Visualization, Investigation. **Joghee Nanjundan:** Supervision, Resources. **Rajendra Singh:** Supervision, Resources, Investigation. **Ram Avtar:** Supervision, Resources, Investigation. **Anshul Watts:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Naveen Singh:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Conceptualization.

Data availability statement

All the data are included within the manuscript and the supplementary materials.

Consent for publication

All the authors read the manuscript and agreed with its content for publication.

Funding

The research was funded by ICAR-IARI in-house project and ICAR funded Consortium Research Project on Hybrid Technology (Mustard)

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Naveen Singh reports financial support and administrative support were provided by ICAR - Indian Agricultural Research Institute. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

Mohit Sharma is grateful to the Post-Graduate School, ICAR-Indian Agricultural Research Institute (IARI), New Delhi for granting a Senior Research Fellowship. The authors are thankful to the Division of Genetics, ICAR-IARI, New Delhi for providing facilities for hybridization and evaluation of parental lines and hybrids. The authors are also thankful to the CCS Haryana Agricultural University, Hisar for extending help and resources for the evaluation of plant material.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e40555.

References

[1] Anonymous, Global Agricultural Information Network Circular Series, WAP 5-24, USDA Foreign Agricultural Service, Washington, DC, 2024. Available online: https://www.fas.usda.gov/data/world-agricultural-production. accessed on 17May 2024.

[2] J.S. Chauhan, K.H. Singh, V.V. Singh, S. Kumar, Hundred years of rapeseed-mustard breeding in India: accomplishments and future strategies, Indian J. Agric. Sci. 81 (2011) 1093–1109.

[3] S.K. Sandhu, G. Singh, Genomic-assisted breeding in oilseed Brassicas, in: Biotechnologies of Crop Improvement, vol. 3, Springer, Cham, 2018, pp. 317–348, https://doi.org/10.1007/978-3-319-94746-4_14.

[4] P. Vasisth, N. Singh, O.M. Limbalkar, M. Sharma, G. Dhanasekaran, M.L. Meena, P. Jain, S. Jaiswal, M.A. Iquebal, A. Watts, et al., Introgression of heterotic genomic segments from *Brassica carinata* into *Brassica juncea* for enhancing productivity, Plants 12 (8) (2023) 1677, https://doi.org/10.3390/plants12081677.

[5] R.S. Jat, V.V. Singh, P. Sharma, P.K. Rai, Oilseed Brassica in India: demand, supply, policy perspective and future potential, OCL 26 (2019) 8, https://doi.org/10.1051/ocl/2019005.

[6] R. Saroj, S.L. Soumya, S. Singh, S.M. Sankar, R. Chaudhary, Yashpal, N. Saini, S. Vasudev, D.K. Yadava, Unraveling the relationship between seed yield and yield-related traits in a diversity panel of *Brassica juncea* using multi-traits mixed model, Front. Plant Sci. 12 (2021) 651936, https://doi.org/10.3389/fpls.2021.651936.

[7] V. Rameeh, Combining ability and factor analysis in F2 diallel crosses of rapeseed varieties, Plant Breed. Seed Sci. 62 (2010) 73, https://doi.org/10.2478/v10129-011-0006-1.

[8] N. Singh, D.K. Yadava, V. Sujata, R. Singh, S.C. Giri, B. Dass, B. Siddhartha, K.V. Prabhu, Combining ability and heterobeltiosis for yield and yield contributing traits in high quality oil Indian mustard (*Brassica juncea*) genotypes, Indian J. Agric. Sci. 85 (2015) 498–503, https://doi.org/10.56093/ijas.v85i4.47913.

[9] D. Cai, Y. Xiao, W. Yang, W. Ye, B. Wang, M. Younas, J. Wu, K. Liu, Association mapping of six yield-related traits in rapeseed (*Brassica napus* L.), Theor. Appl. Genet. 127 (2014) 85–96, https://doi.org/10.1007/s00122-013-2203-9.

[10] P.B. Kirti, T. Mohapatra, S. Prakash, V. L Chopra, Development of a stable cytoplasmic male sterile line of *Brassica juncea* from somatic hybrid *Trachystoma balli*+ *Brassica juncea*, Plant Breed. 114 (1995) 434–438, https://doi.org/10.1111/j.1439-0523.1995.tb00826.

[11] S.S. Banga, S.K. Banga, G.S. Sandha, Development and characterization of tournefortii CMS system in *Brassica napus* L, in: Proceedings of the 9th International Rapeseed Congress, vol. 1, Organising Committee, Cambridge, UK, 1995, pp. 55–57.

[12] R.S. Pahwa, S.K. Banga, K.P.S. Gogna, S.S. Banga, Tournefortii male sterile system in *Brassica napus*: identification expression and genetic characterization of male sterile restorers, Plant Breed. 123 (2004) 444–448, https://doi.org/10.1111/j.1439-0523.2004.00960.x.

[13] P. B Kirti, S. Prakash, K. Gaikwad, S. R Bhat, V.D. Kumar, V.L. Chopra, Chloroplast substitution overcomes leaf chlorosis in a *Moricandia arvensis*-based cytoplasmic male sterile *Brassica juncea*, Theor. Appl. Genet. 97 (1998) 1179–1182, https://doi.org/10.1007/s001220051007.

[14] S. Prakash, P. B Kirti, S. R Bhat, K. Gaikwad, V.D. Kumar, V.L. Chopra, A *Moricandia arvensis* based cytoplasmic male sterility and fertility restoration system in *Brassica juncea*, Theor. Appl. Genet. 97 (1998) 488–492, https://doi.org/10.1007/s001220050921.

[15] A. Pathania, S.R. Bhat, V.D. Kumar, Ashutosh, P.B. Kirti, S. Prakash, V.L. Chopra, Cytoplasmic male sterility in alloplasmic *Brassica juncea* carrying *Diplotaxis catholica* cytoplasm: molecular characterization and genetics of fertility restoration, Theor. Appl. Genet. 107 (2003) 455–461, https://doi.org/10.1007/s00122-003-1266-4.

[16] S.S. Banga, J.S. Deol, S.K. Banga, Alloplasmic male-sterile *Brassica juncea* with *Enarthrocarpus lyratus* cytoplasm and the introgression of gene(s) for fertility restoration from cytoplasm donor species, Theor. Appl. Genet. 106 (2003) 1390–1395, https://doi.org/10.1007/s00122-002-1180-1.

[17] H.S. Janeja, S.K. Banga, P.B. Bhasker, S.S. Banga, Alloplasmic male sterile *Brassica napus* with *Enarthrocarpus lyratus* cytoplasm: introgression and molecular mapping of an *E. lyratus* chromosome segment carrying a fertility restoring gene, Genome 46 (2003) 792–797, https://doi.org/10.1139/g03-055.

[18] M. Malik, P. Vyas, N.S. Rangaswamy, K.R. Shivanna, Development of two new cytoplasmic male sterile lines of *Brassica juncea* through wide hybridization, Plant Breed. 118 (1999) 75–78, https://doi.org/10.1046/j.1439-0523.1999.118001075.x.

[19] S.R. Bhat, V. Priya, K.K.A. Dwivedi, S. Prakash, *Diplotaxis erucoides* induced cytoplasmic male sterility in *Brassica juncea* is rescued by the *Moricandia arvensis* restorer: genetic and molecular analyses, Plant Breed. 125 (2006) 150–155, https://doi.org/10.1111/j.1439-0523.2006.01184.x.

[20] S.R. Bhat, P. Kumar, S. Prakash, An improved cytoplasmic male sterile (*Diplotaxis berthautii) Brassica juncea*: identification of restorer and molecular characterization, Euphytica 159 (2008) 145–152, https://doi.org/10.1007/s10681-007-9467-6.

[21] Y.S. Sodhi, A. Chandra, J.K. Verma, N. Arumugam, A. Mukhopadhyay, V. Gupta, D. Pental, A.K. Pradhan, A new cytoplasmic male sterility system for hybrid seed production in Indian oilseed mustard *Brassica juncea*, Theor. Appl. Genet. 114 (1) (2006) 93–99, https://doi.org/10.1007/s00122-006-0413-0.

[22] S. Mathur, K. Paritosh, R. Tandon, D. Pental, A.K. Pradhan, Comparative analysis of seed transcriptome and coexpression analysis reveal candidate genes for enhancing seed size/weight in *Brassica juncea*, Front. Genet. 13 (2022) 814486, https://doi.org/10.3389/fgene.2022.814486.

[23] B.E. Giles, The effects of variation in seed size on growth and reproduction in the wild barley *Hordeum vulgare* ssp. spontaneum, Heredity 64 (2) (1990) 239–250, https://doi.org/10.1038/hdy.1990.29.

[24] S. Ambika, V. Manonmani, G. Somasundaram, Review on effect of seed size on seedling vigour and seed yield, Res. J. Seed Sci. 7 (2) (2014) 31–38, doi: rjss.2014.31.38.

[25] J. Zhang, X. Zhang, X. Liu, Q. Pai, Y. Wang, X. Wu, Molecular network for regulation of seed size in plants, Inter. J. Mol. Sci. 24 (13) (2023) 10666, https://doi.org/10.3390/ijms241310666.

[26] D.S. Falconer, T.F. Mackay, R. Frankham, Introduction to quantitative genetics (4th edn), Trends Genet. 12 (7) (1996) 280.

[27] M. Chaudhary, R. Avtar, V.K. Singh, A. Anu, M. Mahavir, Genetic architecture of yield traits and oil content in Indian mustard (*Brassica juncea*), Indian J. Agric. Sci. 91 (8) (2021) 1185–1189, https://doi.org/10.56093/ijas.v91i8.115871.

[28] O.M. Limbalkar, R. Singh, P. Kumar, J. Nanjundan, C.M. Parihar, P. Vasisth, D.K. Yadava, V. Chinnusamy, N. Singh, Deployment of *Brassica carinata* a. Braun derived *Brassica juncea* (L.) czern. lines for improving heterosis and water use efficiency under water deficit stress conditions, Front. Plant Sci. 12 (2021), https://doi.org/10.3389/fpls.2021.765645.

[29] V. Sundaresan, Control of seed size in plants, Proc. Natl. Acad. Sci. 102 (50) (2005) 17887–17888, https://doi.org/10.1073/pnas.0509021102.

[30] N. Li, D. Song, W. Peng, J. Zhan, J. Shi, X. Wang, G. Liu, H. Wang, Maternal control of seed weight in rapeseed (*Brassica napus* L.): the causal link between the size of pod (mother, source) and seed (offspring, sink), Plant Biotech. J. 17 (4) (2019) 736–749, https://doi.org/10.1111/pbi.13011.

[31] G.M.A. Mahgoub, Partitioning of general and specific combining ability effects for estimating maternal and reciprocal effects, J. Agric. Sci. 3 (2011) 213–221, https://doi.org/10.5539/jas.v3n2p213.

[32] X.M. Fan, Y.D. Zhang, W.H. Yao, Y.Q. Bi, L. Liu, H.M. Chen, M.S. Kang, Reciprocal diallel crosses impact combining ability, variance estimation, and heterotic group classification, Crop Sci. 54 (2014) 89–97, https://doi.org/10.2135/cropsci2013.06.0393.

[33] J. Singh, J.A.C. Michelangeli, S.A. Gezan, H. Lee, C.E. Vallejos, Maternal effects on seed and seedling phenotypes in reciprocal F1 hybrids of the common bean (*Phaseolus vulgaris* L.), Front. Plant Sci. 8 (2017) 42, https://doi.org/10.3389/fpls.2017.00042.

[34] W. Yan, L.A. Hunt, Q. Sheng, Z. Szlavnics, Cultivar evaluation and mega-environment investigation based on the GGE biplot, Crop Sci. 40 (3) (2000) 597–605, https://doi.org/10.2135/cropsci2000.403597x.

[35] W. Yan, M.S. Kang, B. Ma, S. Wood, P.L. Cornelius, GGE biplot vs. AMMI analysis of genotype-by-environment data, Crop Sci. 47 (2007) 643–653, https://doi.org/10.2135/cropsci2006.06.0374.

[36] W. Yan, L.A. Hunt, Biplot analysis of diallel data, Crop Sci. 42 (1) (2002) 21–30, https://doi.org/10.2135/cropsci2002.0021.

[37] W. Yan, M.S. Kang, GGE Biplot Analysis: A Graphical Tool for Breeders, Geneticists, and Agronomists, CRC Press, 2002, https://doi.org/10.1201/9781420040371.

[38] W. Yan, N.A. Tinker, Biplot analysis of multi-environment trial data: principles and applications, Canadian J. Plant Sci. 86 (3) (2006) 623–645, https://doi.org/10.4141/P05-169.

[39] N. Dhaka, K. Rout, S.K. Yadava, Y.S. Sodhi, V. Gupta, D. Pental, A.K. Pradhan, Genetic dissection of seed weight by QTL analysis and detection of allelic variation in Indian and east European gene pool lines of *Brassica juncea*, Theor. Appl. Genet. 130 (2017) 293–307, https://doi.org/10.1007/s00122-016-2811-2.

[40] T.K. Das, R. Bhattacharyya, S. Sudhishri, A.R. Sharma, Y.S. Saharawat, K.K. Bandyopadhyay, S. Sepat, R.S. Bana, P. Aggarwal, R.K. Sharma, A. Bhatia, Conservation agriculture in an irrigated cotton–wheat system of the western Indo-Gangetic Plains: crop and water productivity and economic profitability, Field Crops Res. 158 (2014) 24–33, https://doi.org/10.1016/j.fcr.2013.12.017.

[41] Dinesh, P. Kumar, K.K. Bhardwaj, A. Gill, Anurag, Spatial distribution of nutrients in research farm, department of soil science, CCS HAU hisar, Haryana, Int. J. Plant Soil Sci. 34 (22) (2022) 1546–1554, https://doi.org/10.9734/ijpss/2022/v34i2231531.

[42] IRRI, Statistical tool for agricultural research, Version 2.0.1, in: User's Manual. Biometrics and Breeding Informatics; PBGB, Division, International Rice Research Institute: Los Bãnos, Philippines, 2013.

[43] G. Alvarado, F.M. Rodriguez, A. Pacheco, J. Burgueno, J. Crossa, M. Vargas, P.P. Rodriguez, M.A. Lopez-Cruz, META-R: a software to analyze data from multi-environment plant breeding trials, Crop J. 8 (5) (2020) 745–756, https://doi.org/10.1016/j.cj.2020.03.010.

[44] R Core Team, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, 2023. https://www.R-project.org/.

[45] B. Griffing, Concept of general and specific combining ability in relation to diallel crossing systems, Austral, J. Biol. Sci. 9 (1956) 463–493, https://doi.org/10.1071/BI9560463.

[46] K. Mather, J.L. Jinks, Biometrical Genetics: the Study of Continuous Variation, third ed., Chapman and Hall Publishers, New York, NY, 1982.

[47] PB Tools, version 1.4, Biometrics and Breeding Informatics, PBGB Division, International Rice Research Institute, Los Banos, Laguna, 2014.

[48] F. Rodriguez, G. Alvarado, A. Pacheco, J. Crossa, J. Burgueno, AGD-R (Analysis of genetic designs with R for Windows) version 4.0, International Maize and Wheat Improvement Center (CIMMYT) (2015).

[49] R.E. Comstock, H.F. Robinson, The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance, Biometrics 4 (1948) 254–266, https://doi.org/10.2307/3001412.

[50] F.A. Coffman, Heterosis: specific not general in nature, Sci. 77 (1933) 114–115, https://doi.org/10.1126/science.77.1987.114-c.

[51] T. Olivoto, M. Nardino, MGIDI: toward an effective multivariate selection in biological experiments, Bioinformatics (2020), https://doi.org/10.1093/bioinformatics/btaa981.

[52] A. Pacheco, M. Vargas, G. Alvarado, F. Rodriguez, J. Crossa, J. Burgueno, GEA-R (Genotype X Environment Analysis with R for Windows) Version 4.1, 2015.

[53] T. Olivoto, A.D.C. Lucio, metan: an R package for multi environment trial analysis, Methods Ecol. Evol. 11 (2020) 783–789, https://doi.org/10.1111/2041-210X.13384.

[54] D. Sam, Package 'GGEBiplots'. https://cran.r-project.org/web/packages/GGEBiplots/GGEBiplots.pdf, 2022.

[55] Y.P. Yadav, R. Prakash, R. Singh, R.K. Singh, J.S. Yadava, Genetics of yield and its component characters in Indian mustard, *Brassica juncea* (L.) Czern & Coss under rainfed conditions, J. Oilseeds Res. 22 (2005) 255.

[56] M. Singh, S.H. Satendra, R.K. Dixit, Combining ability of agronomic characters in Indian mustard (*Brassica juncea* (L.) Czern & and Coss), J. Prog. Res. 6 (2006) 69–72.

[57] A. Singh, R. Avtar, D. Singh, O. Sangwan, N.K. Thakral, V.S. Malik, et al., Combining ability analysis for seed yield and component traits in Indian mustard [*Brassica juncea* (L.) Czern & Coss.], Res, Plant Biol. 3 (2013), 26–3.

[58] A.K. Mall, R. Bhajan, Detection of epistasis, additive and dominance variation for some metric traits in Indian mustard under timely and late sown conditions, Prog. Agric. 15 (1) (2015), 99–3.

[59] H.S. Meena, A. Kumar, S. Kulshrestha, B. Ram, V.V. Singh, P.D. Meena, D. Singh, Detection of epistasis, additive and dominance components of variation for seed yield and its attributes in Indian mustard (*Brassica juncea*), Indian J. Agric. Sci. 89 (2) (2019) 261–267, https://doi.org/10.56093/ijas.v89i2.87017.

[60] V.K. Singh, R. Avtar, N.K. Mahavir, R.K. Manjeet, V. Rathore, Assessment of genetic relationship among diverse Indian mustard (*Brassica juncea* L.) genotypes using XLSTAT, Electron, J. Plant Breed. 11 (2) (2020) 674–680.

[61] Z.A. Priyamedha, A. Kumar, H.K. Sharma, V.V. Singh, B. Ram, P.K. Monika, P.K. Rai, Association of genetic distance and combining ability with heterosis in Indian mustard (*Brassica juncea* L.), J. Oilseed Brassica 12 (2) (2021) 67–75.

[62] O.M. Limbalkar, P. Vasisth, R. Singh, M. Rao, G. Singh, L. Singh, D. Gokulan, M. Kumar, M.L. Meena, C.M. Parihar, J. Nanjundan, V. Chinnusamy, K.H. Singh, N. Singh, Infusing genetic variability for productivity and drought tolerance traits from *Brassica carinata* into *Brassica juncea* genotypes, Genet. Resour. Crop Evol. (2024), https://doi.org/10.1007/s10722-024-01922-7.

[63] D.K. Yadava, N. Singh, S. Vasudev, R. Singh, S. Singh, S.C. Giri, V.K. Dwivedi, K.V. Prabhu, Combining ability and heterobeltiosis for yield and yield-contributing traits in Indian mustard (*Brassica juncea*), Indian J. Agri. Sci. 82 (7) (2012) 563–567, https://doi.org/10.56093/ijas.v82i7.21632.

[64] M. Al-Mamun, M.Y. Rafii, A.B. Misran, Z. Berahim, Z. Ahmad, M.M.H. Khan, Y. Oladosu, Combining ability and gene action for yield improvement in kenaf (*Hibiscus cannabinus* L.) under tropical conditions through diallel mating design, Sci. Rep. 12 (2022) 9646, https://doi.org/10.1038/s41598-022-13529-y.

[65] P. Priyamedha, K. Arun, Z.A. Haider, R. Bhagirath, V.V. Singh, S. Dhiraj, Estimation of combining ability and heterosis for yield and yield attributing traits in Indian mustard (*Brassica juncea*), Indian J. Agric. Sci. 88 (4) (2018) 546–552, https://doi.org/10.56093/ijas.v88i4.79104.

[66] S.P. Chand, S. Debnath, M. Rahimi, M. Ashraf, P. Bhatt, S.A. Rahin, Contextualization of trait nexus and gene action for quantitative and qualitative characteristics in Indian mustard, J. Food Qual. 1 (2022) 4387318, https://doi.org/10.1155/2022/4387318.

[67] H.S. Meena, A. Kumar, B. Ram, V.V. Singh, P.D. Meena, B.K. Singh, D. Singh, Combining ability and heterosis for seed yield and its components in Indian mustard (*Brassica juncea* L.), J. Agr. Sci. Tech. 17 (2015) 1861–1871.

[68] V.R. Akabari, N. Sasidharan, V. Kapadiya, Combining ability and gene action study for grain yield and its attributing traits in Indian mustard, Electron. J. Plant Breed. 8 (1) (2017) 226–235.

[69] G.F. Sprague, L.A. Tatum, General versus specific combining ability in single crosses of corn, J. Am. Soc. Agron. 34 (1942) 923–932, https://doi.org/10.2134/agronj1942.00021962003400100008x.

[70] M.C. Franco, S.T. Cassini, V.R. Oliveira, C. Vieira, S.M. Tsai, C.D. Cruz, Combining ability for nodulation in common bean (*Phaseolus vulgaris* L.) genotypes from Andean and Middle American gene pools, Euphytica 118 (2001) 265–270, https://doi.org/10.1023/A:1017560118666.

[71] P. Fasahat, A. Rajabi, J.M. Rad, J. Derera, Principles and utilization of combining ability in plant breeding, Biom. Biostat. Int. J. 4 (2016) 00085, https://doi.org/10.15406/bbij.2016.04.00085.

[72] B. Ram, Priyamedha, H.S. Meena, A. Kumar, B.K. Singh, R. Rani, A. Kumar, K.H. Singh, P.K. Rai, Studies on combining ability and gene action for heat stress tolerance traits in Indian mustard (*Brassica juncea* L.), J. Oilseed Brassica (2018) 139–145.

[73] E.Y. Owusu, H. Mohammed, K.A. Manigben, J. Adjebeng-Danquah, F. Kusi, B. Karikari, E.K. Sie, Diallel analysis and heritability of grain yield, yield components, and maturity traits in cowpea (*Vigna unguiculata* (L.) Walp.), Sci. World J. (2020), https://doi.org/10.1155/2020/9390287.

[74] S.B.L. Srivastava, Rajshekhar, M. Singh, M. Rao, Combining ability analysis for yield and contributing characters in Indian mustard (*Brassica juncea* (L.) Czern & Coss.), J. Oilseeds Res. 26 (2009) 58–61, 10.9734/cjast/2020/v39i2030808.

[75] A. Teklewold, H.C. Becker, Heterosis and combining ability in a diallel cross of Ethiopian mustard inbred lines, Crop Sci. 45 (2005) 2629–2635, https://doi.org/10.2135/cropsci2005.0085.

[76] N.N. Wassimi, T.G. Isleib, G.L. Hosfield, Fixed effect genetic analysis of a diallel cross in dry beans (*Phaseolus vulgaris* L.), Theor. Appl. Genet. 72 (1986) 449–454, https://doi.org/10.1007/BF00289525.

[77] D.G. Langham, The high-low method in crop improvement, Crop Sci. 1 (1961) 376–378, https://doi.org/10.2135/cropsci1961.0011183X000100050026x.

[78] C. Lal, K. Hariprasanna, A.L. Rathnakumar, H.K. Gor, B.M. Chikani, Gene action for surrogate traits of water-use efficiency and harvest index in peanut (*Arachis hypogaea*), Ann. Appl. Biol. 148 (2006) 165–172, https://doi.org/10.1111/j.1744-7348.2006.00047.x.

[79] S.K. Yadava Aakanksha, B.G. Yadav, V. Gupta, A. Mukhopadhyay, D. Pental, A.K. Pradhan, Genetic analysis of heterosis for yield influencing traits in *Brassica juncea* using a doubled haploid population and its backcross progenies, Front. Plant Sci. 12 (2021), https://doi.org/10.3389/fpls.2021.721631.

[80] J.L. Jinks, Extra Chromosomal Inheritance, Prentice Hall, London, 1964, p. 177.

[81] V.V. Satyavathi, V. Manga, M.V.S. Rao, M. Chittibabu, Genetic analysis of reciprocal differences in the inheritance of in vitro characters in pearl millet, Genet. Mol. Biol. 39 (2016) 54–61, https://doi.org/10.1590/1678-4685-GMB-2014-0380.

[82] N. Li, Y. Li, Maternal control of seed size in plants, J. Exp. Bot. 66 (2015) 1087–1097, https://doi.org/10.1093/jxb/eru549.

[83] N. Li, W. Peng, J.Q. Shi, X.F. Wang, G.H. Liu, H.Z. Wang, The natural variation of seed weight is mainly controlled by maternal genotype in rapeseed (*Brassica napus* L.), PLoS One 10 (2015) e0125360, https://doi.org/10.1371/journal.pone.0125360.

[84] W.H. Yao, Y.D. Zhang, M.S. Kang, H.M. Chen, L. Liu, L.J. Yu, X.M. Fan, Diallel analysis models: a comparison of certain genetic statistics, Crop Sci. 53 (2013) 1481–1490, https://doi.org/10.2135/cropsci2013.01.0027.

[85] C.B. Kunwar, B. Basnet, S. Sunuwar, D.N. Mahato, R. Chaudhari, J. Upadhya, P. Pokhrel, Multi-model approach for optimizing cold-wave resilient maize selection: unveiling genotype-by-environment interaction and predicting yield stability, CABI Agric. Biosci. 5 (2024) 63, https://doi.org/10.1186/s43170-024-00266-7.

[86] M. Ambrósio, R.F. Daher, R.M. Santos, J.G.S. Santana, A.K.F. Vidal, M.R. Nascimento, C.L. Leite, A.G. de Souza, R.S. Freitas, W.F. Stida, J.E.C. Farias, B.F. de Souza Filho, L.C. Melo, P.R. Dos Santos, Multi-trait index: selection and recommendation of superior black bean genotypes as new improved varieties, BMC Plant Biol. 24 (1) (2024) 525, https://doi.org/10.1186/s12870-024-05248-5.

[87] H. Yue, J. Wei, J. Xie, S. Chen, H. Peng, H. Cao, J. Bu, X. Jiang, A study on genotype-by-Environment interaction analysis for agronomic traits of maize genotypes across Huang-Huai-Hai region in China, Phyton 91 (1) (2022) 57, https://doi.org/10.32604/phyton.2022.017308.

[88] M. Azrai, M. Aqil, R. Efendi, N.N. Andayani, A.T. Makkulawu, R.N. Iriany, M. Yasin, B. Zainuddin, T. Sitaresmi, W.B. Suwarno, A comparative study on single and multiple trait selections of equatorial grown maize hybrids, Front. Sustain. Food Syst. 7 (2023) 1185102, https://doi.org/10.3389/fsufs.2023.1185102.

[89] A. Singamsetti, P.H. Zaidi, K. Seetharam, M.T. Vinayan, T. Olivoto, A. Mahato, K. Madankar, M. Kumar, K. Shikha, Genetic gains in tropical maize hybrids across moisture regimes with multi-trait-based index selection, Front. Plant Sci. 14 (2023) 1147424, https://doi.org/10.3389/fpls.2023.1147424.

[90] W. Yan, GGE Bi-plot: a windows application for graphical analysis of multi-environment trial data and types of two-way data, Agron. J. 93 (2001) 1111–1118, https://doi.org/10.2134/agronj2001.9351111x.

[91] M. Choudhary, B. Kumar, P. Kumar, S.K. Guleria, N.K. Singh, R. Khulbe, M.C. Kamboj, M. Vyas, R.K. Srivastava, Puttaramanaik, D. Swain, V. Mahajan, S. Rakshit, GGE biplot analysis of genotype× environment interaction and identification of mega-environment for baby corn hybrids evaluation in India, Indian J. Genet. Plant Breed. 79 (4) (2019) 658–669, https://doi.org/10.31742/IJGPB.79.4.3.

[92] S.H. Shojaei, K. Mostafavi, M.R. Bihamta, A. Omrani, S.M.N. Mousavi, A. Illes, C. Bojtor, J. Nagy, Stability on maize hybrids based on GGE biplot graphical technique, Agron 12 (2) (2022) 394, https://doi.org/10.3390/agronomy12020394.

[93] Y. Li, H. Bao, Z. Xu, S. Hu, J. Sun, Z. Wang, X. Yu, J. Gao, AMMI an GGE biplot analysis of grain yield for drought-tolerant maize hybrid selection in Inner Mongolia, Sci. Rep. 13 (1) (2023) 18800, https://doi.org/10.1038/s41598-023-46167-z.

[94] P. Senguttuvel, N. Sravanraju, V. Jaldhani, B. Divya, P. Beulah, P. Nagaraju, D. Subrahmanyam, et al., Evaluation of genotype by environment interaction and adaptability in lowland irrigated rice hybrids for grain yield under high temperature, Sci. Rep. 11 (1) (2021) 15825, https://doi.org/10.1038/s41598-021-95264-4.

[95] M.J. Hasan, M.U. Kulsum, U. Sarker, M.Q.I. Matin, N.H. Shahin, M.S. Kabir, S. Ercisli, R.A. Marc, Assessment of GGE, AMMI, regression, and its deviation model to identify stable rice hybrids in Bangladesh, Plants 11 (18) (2022) 2336, https://doi.org/10.3390/plants11182336.