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Genetic architecture and combining ability of Indian mustard (*Brassica juncea* L.) under climate-induced late sown stress: Insights for climate-resilient hybrid breeding

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Abstract

Delayed sowing in rice-mustard cropping systems frequently pushes Indian mustard (*Brassica juncea* L.) planting beyond optimal windows, exposing the crop to late sown condition associated with terminal heat stress and causing substantial yield reductions. To address the critical gap in late-sown adaptation research, this study evaluated the quantitative genetic basis, combining ability and trait interrelationships of 7 genetically diverse parents and 21 F_1 hybrids developed via a half-diallel mating design. The genotypes were evaluated for 12 agro-morphological traits under very late-sown conditions (December) in Varanasi, Uttar Pradesh. Results revealed significant genetic variability for all traits. Exceptionally high broad-sense heritability and genetic advance as percent of mean (GAM) were observed for seed yield per plant (YPP) (85.77 % and 52.55 %, respectively), test weight (TW) (93.23 % heritability) and the number of siliquae per plant (NSP) (73.39 % heritability and 42.07 % genetic advance). Hybrids generally outperformed parental lines, exhibiting earlier maturity, superior branching and higher yield. Parent P4 exhibited significant positive general combining ability effects for seed YPP and silique number. Additionally, the cross P5 × P6 exhibited the highest specific combining ability for yield and hybrid H17 demonstrated the maximum better-parent heterosis (50.0 %) for seed yield. Path coefficient analysis confirmed that the NSP exerted the strongest direct positive effect (1.045) on seed yield. Furthermore, principal component analysis (PCA) showed that the first four components explained 81.5 % of the total phenotypic variation. These findings demonstrate exploitable genetic variability among mustard genotypes under late-sown stress conditions. Selecting for the NSP and utilising superior heterotic combinations will be highly effective for developing climate-resilient mustard hybrids adapted to delayed sowing environments. Ultimately, deploying these targeted breeding strategies offers a practical pathway to secure crop productivity and stabilise smallholder farm income across late sown rice-mustard cropping systems.

Keywords: *Brassica juncea;* breeding; climate resilience; combining ability; late sown stress

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Introduction

Indian mustard (*Brassica juncea* (L.) Czern. & Coss.) is an amphidiploid species (AABB, 2n = 36) originating from natural hybridisation between *B. rapa* (AA, 2n = 20) and *B. nigra* (BB, 2n = 16) and it is the most widely cultivated rapeseed-mustard species across the Indian subcontinent (1, 2). The crop is cultivated across diverse agro-ecological regions, including South Asia, China, Australia and Canada, reflecting its broad adaptation and economic importance (3). In India, rapeseed-mustard contributes nearly one-third of total oilseed output, with Rajasthan, Uttar Pradesh, Haryana and Madhya Pradesh as the dominant production states (4). Although Indian mustard has a demonstrated biological yield potential of 2500–2700 kg/ha under improved management, the national average yield stagnates around 1443 kg/ha in 2022–23, indicating a wide and persistent yield gap (5). This gap is largely attributed to multiple biotic and abiotic stresses, suboptimal production environments and the limited availability of well-adapted high-yielding varieties and hybrids for diverse sowing situations (6, 7). India continues to depend heavily on edible oil imports to meet domestic demand and this situation underscores the urgency of sustained genetic improvement for enhanced productivity and broader adaptation (8).

While the crop exhibits broad adaptability, intensive selection during domestication narrowed its genetic base and may have reduced its inherent heat

tolerance (9); this vulnerability is now further aggravated by delayed sowing and shifting seasonal patterns. Sowing time is one of the most consequential production factors determining mustard yield in northern India where the recommended sowing window extends from mid-October to early November. In rice-based cropping systems of the Indo-Gangetic Plain, delayed rice harvest, waterlogging and high residual soil moisture routinely delay mustard planting to late November or early December (10, 11). This problem is especially pronounced in eastern Uttar Pradesh and the surrounding alluvial belt, where mustard follows kharif rice and timely land preparation is often not feasible under farmers' conditions. When sowing is delayed well beyond the optimum window, the crop experiences a shortened growth duration and the vegetative and reproductive phases are compressed. As a result, flowering and pod filling may occur under comparatively warmer end-season conditions, which can negatively affect siliqua development, seed set, seed weight and final yield (12, 13). Delayed sowing forces the crop to experience low temperatures and high humidity during the vegetative growth phase, followed by high temperatures and low humidity during seed filling and ripening phase. Documented yield reductions in mustard can reach 30–50 % when sowing is delayed beyond November, with losses intensifying progressively as planting shifts from late to extra-late as reported in different studies around world (10). This trend is broadly observed across regional winter crops such as wheat and chickpea, where late establishment universally exposes reproductive phases to unfavourable end-season stress (14–16). In mustard, this shortened grain-filling duration directly reduces seed weight and final oil yield (17). This growing trend, compounded by increasing climate variability, not only reduces mustard productivity at the field level but also poses a broader threat to national edible oil self-sufficiency.

The genotypic response to delayed sowing, however, is not uniform across germplasm. Evaluation of mustard genotypes under contrasting sowing environments has shown that genetic differences exist for crop duration, branching behaviour, siliqua characteristics and seed yield under late-sown conditions, indicating the presence of exploitable variability for adaptation to this production situation (18). This genetic variation forms the basis for targeted hybrid breeding under delayed sowing. The diallel mating design is a well-established and efficient tool for assessing such variation because it allows simultaneous estimation of general combining ability (GCA) and specific combining ability (SCA) effects, thereby distinguishing the relative contributions of additive and non-additive gene action to trait expression (19–21). Griffing's Method II, Model I (fixed effects) was selected to explicitly evaluate this targeted, non-random set of parents and their crosses, assuming negligible reciprocal effects. In Indian mustard, combining ability and heterosis studies have confirmed that both GCA and SCA effects are significant for seed yield and associated traits, with the relative importance of these components varying across experimental backgrounds and environments (22–24). Estimation of heterosis further supplements combining ability information by quantifying the superiority of cross combinations over parental performance, which is particularly relevant for identifying productive hybrids suited to stress-prone sowing conditions.

Breeding decisions also require a thorough understanding of the quantitative genetic basis and trait interrelationships underlying yield. Seed yield in Indian mustard is not the product of a single process but reflects the combined and sequential contribution of phenology, plant height, branching pattern, main raceme development, siliqua number, seed set and seed weight. Estimates of genetic variability, heritability and genetic advance indicate the scope and efficiency of selection for each trait, while correlation and path coefficient analyses identify which component traits most reliably influence seed yield under a given environment. Multivariate approaches including principal component analysis (PCA) and cluster analysis complement these methods by revealing patterns of genetic divergence among genotypes and grouping parents with complementary trait profiles for more informed cross combinations. Studies in Indian mustard under timely and late-sown conditions have confirmed the usefulness of such integrated analytical approaches in identifying superior parents, defining selection criteria and improving breeding decisions for yield enhancement.

Despite the large amount of breeding literature on Indian mustard, research targeting very late-sown environments (December) is limited compared to studies on standard or moderately late (November) plantings. This represents a significant knowledge gap, because breeding information generated under standard conditions does not reliably translate to the compressed crop durations of December plantings. Furthermore, the eastern Indo-Gangetic Plain (including Varanasi) presents a distinct and challenging agro-ecology. In this region, the delayed harvest of long-duration monsoon rice and the time required for subsequent field preparation frequently push winter crop sowing deep into December. Unlike the gradual spring transition of the traditional northwestern mustard belt, the eastern Indo-Gangetic Plain experiences an abrupt escalation of both day and night temperatures during late February and March. This sudden thermal shift forces the late-sown crop to undergo its critical reproductive and grain-filling phases under intense terminal heat stress, severely reducing seed weight and oil yield. To address this specific regional challenge, the present investigation evaluated 7 parents and 21 F_1 hybrids of Indian mustard, developed through a half-diallel mating design, under very late-sown conditions at Varanasi, Uttar Pradesh.

The specific objectives were: (i) to assess mean performance, genetic variability, heritability and genetic advance for 12 agro-morphological traits; (ii) to estimate

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GCA and SCA effects and identify superior general and specific combiners; (iii) to quantify mid-parent and better-parent heterosis and delineate heterotic groups among parents; and (iv) to examine interrelationships among traits through correlation, path analysis, PCA and cluster analysis. The results are expected to provide practically useful breeding information for developing Indian mustard hybrids better adapted to climate-driven delayed sowing environments in the Indo-Gangetic Plain.

Materials and Methods

Experimental site and agro-climatic conditions

The field experiment was conducted during the rabi season of 2023–24 at the Agricultural Research Farm, Institute of Agricultural Sciences, Banaras Hindu University (BHU), Varanasi, India, which is geographically located in the Middle Indo-Gangetic Plain eco-region (25°18′ N latitude, 83°03′ E longitude; 75.7 m above mean sea level). The soil of the experimental field was sandy loam in texture, neutral to slightly alkaline (pH 7.4) and of moderate fertility with available nitrogen (N) (176 kg ha^{-1}), phosphorus (P) (23.43 kg ha^{-1}), potassium (K) (207 kg ha^{-1}) and organic carbon (C) (0.33 %), making it highly suitable for oilseed cultivation. Based on trial records and weather data from the preceding five rabi seasons at this farm, the site is well-established as representative of very late-sown, post-rice mustard production systems in the region.

During the experimental year, the absolute recorded minimum and maximum temperatures ranged between 6 and 38 °C. The normal monsoon withdraws by the first week of October and about 20 mm of rainfall was received during the crop period, while the relative humidity varied between 57 and 97 %, resulting in relatively dry winter conditions in the region. The late sowing in early December coincided with lower minimum temperatures at the initial stage and exposed plants to terminal heat stress during reproductive growth, a characteristic feature of mustard cropping under delayed sowing in the region.

Genetic material and hybrid development

Seven genetically diverse parental lines of Indian mustard (*B. juncea*) were utilised in this study: IC051151, EC676653, EC597328, RH1222-28, Varuna, Giriraj and RH749. These lines were selected based on their variability for phenological, morphological and yield-related traits recorded during prior germplasm evaluation trials conducted at the BHU research farm. During rabi 2022, hybridisation was carried out in a half-diallel mating design to generate a total of 21 one-way cross combinations, excluding reciprocals (Supplementary Table 1).

Hand emasculation and pollination were performed following standard hybridisation protocols. Emasculation was conducted in the late afternoon (4:00–6:00 PM) prior to anthesis on 7–8 healthy, unopened flower buds per inflorescence across 10 inflorescences per cross combination. Opened flowers and underdeveloped upper buds were excised and emasculated buds were immediately covered with butter paper bags. Concurrently, mature buds of designated male parents expected to open the next morning were bagged to prevent honeybee-mediated pollen contamination and ensure good and pure pollen load. Pollination was performed the following morning (8:00–10:00 AM) using freshly dehisced pollen from these bagged male flowers. Pollinated branches were re-bagged and labeled with jewelry tags detailing parentage and crossing dates. Bags were retained until siliqua initiation. Manual pollination yielded an average of 6–7 viable seeds per crossed silique per cross while exotic crosses show comparatively reduced seed set. All the parents were also selfed with butter paper bag to obtain the pure seed of the parents. All harvested seeds were cleaned, partially retained as a seed reserve and stored separately for field evaluation.

Experimental design and crop management

The field evaluation of the 21 hybrids and 7 parental lines was conducted under very late-sown conditions on December 6, 2023, in a randomised block design (RBD) with two replications. Each genotype was accommodated in a two rows plot of 3 m length with a row spacing of 45 cm and plant spacing of 15 cm. All the recommended crop management practices were taken to raise a good crop.

Data recording and trait measurement

Observations were recorded on 5 randomly selected plants per plot for key agronomic and yield related traits, including: Plant height (cm) (PH), days to 50 % flowering (DFF), days to maturity (DM), number of primary branches (NPB), number of secondary branches (NSB), main raceme length (cm) (MRL), number of siliquae on main raceme (NSMR), number of siliquae per plant (NSP), siliqua length (cm) (SL), number of seeds per siliqua (SS), test weight (g) (TW), seed yield per plant (g) (YPP). Phenological traits, such as DFF and DM, were recorded on a plot basis. For all plant-based traits, individual measurements from the 5 sampled plants were averaged to obtain plot (replication) means prior to statistical analysis.

Statistical and genetic analysis

Data for all traits were subjected to analysis of variance (ANOVA) for a RBD following previous research (25) with significance tested against the ANOVA error term (df = 27). Genotypic and phenotypic coefficients of variation (GCV, PCV), broad-sense heritability (h^2bs) and genetic advance as percent of mean (GAM) at 5 % selection intensity were estimated following previous studies (26–28). Combining ability analysis was performed on the half-diallel data using Griffing's Method II, Model I (Griffing, 1956) to estimate GCA and SCA effects and variances (20). Mid-parent heterosis (MPH) and better-parent heterosis (BPH) were computed based on overall genotype means following

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previous studies (29, 30) and their significance was tested using a *t*-test (df = 27).

Pearson's correlation coefficients were computed among all traits and path coefficient analysis was carried out to partition correlations into direct and indirect effects on seed YPP (31). Principal component analysis and Ward's hierarchical cluster analysis were performed to assess genetic diversity patterns among genotypes. All analyses were performed using R (version 4.3.1; R Core Team, 2023) using the packages agricolae (ANOVA, post-hoc tests and path analysis), DiallelAnalysisR and multcompView (combining ability analysis), factoextra (PCA and hierarchical cluster analysis), ggcorrplot (correlation matrices) and ggplot2 (graphical visualisations).

Results

Analysis of variance (ANOVA) and genetic parameters

The ANOVA was conducted to determine whether significant statistical variation exists among the 28 Indian mustard genotypes for 12 agro-morphological traits (Supplementary Table 2). Although the field evaluation utilised two replications, evaluating 28 genotypes provided 27 error degrees of freedom (df = 27), which represents sufficient statistical power for a robust *F*-test well above the recognised agricultural standard. The results reveal that the mean squares due to genotypes were highly significant ($p < 0.01$) for nine of the twelve characters studied, namely: DFF, NPB, NSB, NSMR, NSP, PH, SS, TW and seed YPP. Additionally, the mean squares for DM, MRL and SL were found to be significant at the 5 % level of probability. These findings confirm the presence of significant statistical variation among the genotypes across all traits under investigation.

Genetic variability, heritability and genetic advance

The estimation of genetic parameters for 12 quantitative traits revealed significant genetic diversity within the studied material (Table 1). Phenotypic coefficients of variation were consistently higher than the corresponding GCV across all evaluated traits (Fig. 1). The margin between PCV and GCV was found narrow for several traits, particularly seed YPP (PCV: 29.74 %; GCV: 27.55 %) and TW (PCV: 16.46 %; GCV: 15.89 %). In contrast, high GCV and PCV values (> 20 %) were observed for YPP, NSP and NSB. In contrast, DM exhibited the lowest genetic variability with a GCV of 1.30 %.

Broad-sense heritability (h^2bs) estimates ranged from 31.97 % (MRL) to 94.18 % (DFF) and high heritability (> 60 %) was recorded for traits of major economic importance, including TW (93.23 %), YPP (85.77 %) and NSP (73.39 %). The highest genetic advance as a percentage of mean (GAM) was recorded for YPP (52.55 %), followed by NSP (42.07 %) and NSB (35.84 %). Traits such as DM and PH showed relatively low GAM values of 1.54 and 7.22 % respectively as depicted in Fig. 2. Notably, while traits like YPP and NSP combined high heritability with high GAM, traits such as DFF and PH exhibited high heritability alongside low-to-moderate GAM, highlighting that high heritability alone does not translate to high selection gain unless accompanied by high GAM. The relationship between the h^2bs and genetic advance is depicted in Supplementary Fig. 1.

Table 1. Genetic variability parameters of quantitative traits in Indian mustard

Trait	GCV	PCV	h^2b	GAM
PH	4.92	6.92	50.64	7.22
NPB	17.86	22.24	64.47	29.54
NSB	21.35	26.20	66.41	35.84
SL	5.19	8.22	39.95	6.76
SS	8.27	11.12	55.32	12.67
MRL	6.95	12.30	31.97	8.10
NSMR	10.82	16.08	45.32	15.01
NSP	23.84	27.82	73.39	42.07
YPP	27.55	29.74	85.77	52.55
TW	15.89	16.46	93.23	31.61
DFF	6.43	6.63	94.18	12.85
DM	1.30	2.27	32.92	1.54

DM: days to maturity; DFF: Days to 50 % flowering; GCV: genotypic coefficients of variation; PCV: phenotypic coefficients of variation; GAM: genetic advance as a percentage of mean; h^2b: broad-sense heritability; NPB: number of primary branches; NSB: number of secondary branches; PH: plant height; SL: siliqua length; SS: number of seeds per siliqua; TW: Test weight; YPP: seed yield per plant; MRL: main raceme length; NSMR: number of siliquae on main raceme; NSP: number of siliquae per plant.

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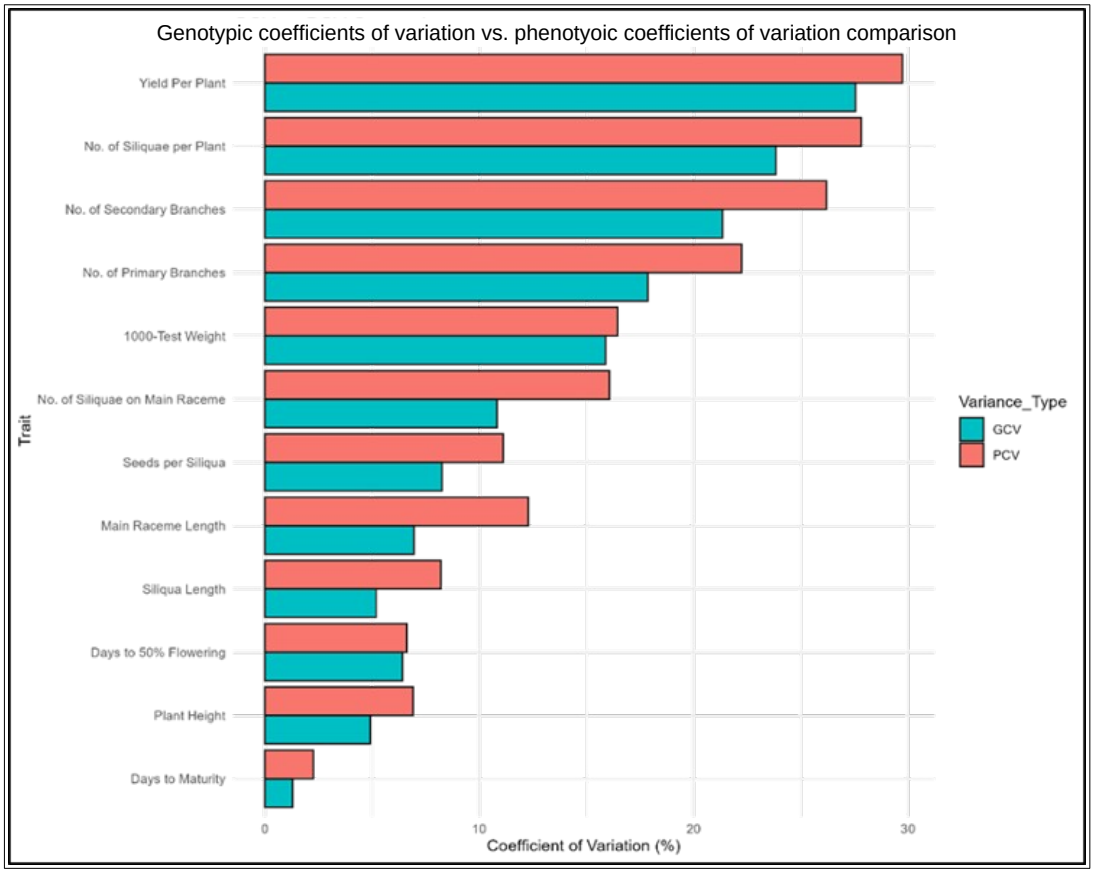


Fig. 1. Comparative bar graph for genotypic coefficients of variation (GCV) and phenotypic coefficients of variation (PCV) among 12 studied traits in Indian mustard.

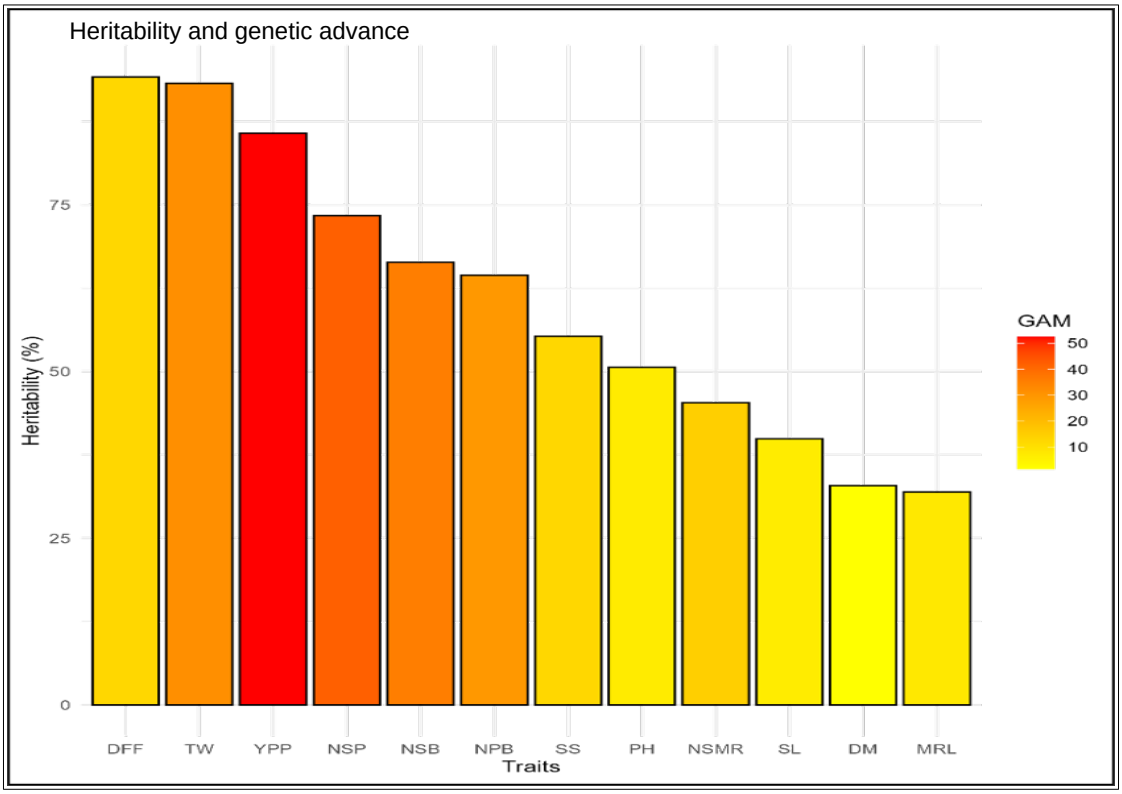


Fig. 2. Heritability and genetic advance of 12 agromorphological and yield traits of Indian mustard.

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Mean performance of genotypes

The comparative evaluation of the mean performance revealed significant differences between the hybrid and parental groups for all 12 agro-morphological characters (Table 2). On average, the hybrid group exhibited earlier phenological traits, with a mean of 57.57 for DFF and 119.24 for DM, compared to the parental means of 60.71 and 122.14 days respectively. Lower values for these phenological traits represent an agronomic advantage in Indian mustard, as earliness facilitates escaping terminal heat stress during late-season seed filling. Hybrid H13 was identified as the earliest flowering genotype (48.0 days), while H11 matured earliest (116.0 days). Regarding architectural traits, the parental group was slightly taller on average (173.47 cm) than the hybrids (168.97 cm). However, hybrids generally showed superior branching patterns; the hybrid group mean for the NPB was 5.62 compared to 5.49 for the parents and the NSB ranged from 6.2 – 15.5. Notably, hybrid H7 recorded the maximum values for both NPB (9.4) and NSB (15.5), establishing it as a key multi-trait architectural performer. The MRL averaged 53.44 cm in the hybrid group and 55.99 cm in the parental group, with hybrid H16 recording the highest individual value of 61.5 cm. For siliquae traits, the number of siliquae on the main raceme reached a maximum of 44.0 in hybrid H2, surpassing the best-performing parent, P2 (40.4). Similarly, the number of seeds per siliquae (SS) peaked at 16.2 in hybrid H18. The NSP showed a significantly wider range among hybrids (115.8–314.0) compared to parents (125.0–195.0), with the hybrid group mean (180.46) surpassing the parental mean (170.65). The seed YPP followed a similar trend, where the hybrid mean was 7.87 g compared to 7.39 g for the parents. Hybrid H17 recorded the maximum seed yield of 12.3 g, which was higher than the best-performing parent, RH1222-28 (8.5 g), consistent with its superior heterotic performance. Furthermore, the TW was higher in hybrids (mean 3.84 g) than in parents (mean 3.56 g), with hybrid H11 exhibiting the maximum seed weight of 4.9 g. The box plot analysis illustrates the phenotypic distribution and overall variability across all twelve quantitative traits in parents and hybrids (Fig. 3).

Combining ability analysis

The ANOVA for combining ability showed significant genotypic variation for all 12 traits, indicating sufficient genetic diversity among the parents and hybrids. Replication effects were significant only for PH, MRL, YPP, TW, DFF and DM, while the remaining traits were unaffected by replication (Supplementary Table 3). Because the complete RBD explicitly partitioned this replication variance out of the total sum of squares, spatial micro-environmental variation across field blocks was isolated from the residual error term (MSE). Consequently, residual error remained low (CV < 15 %), ensuring uninflated error variances and high statistical precision for subsequent GCA and SCA estimations. Therefore, the material was considered suitable for further estimation of GCA and SCA effects.

Table 2. Mean performance and range of hybrids vs. parents in Indian mustard

Trait	Hybrid mean	Hybrid range	Parent mean	Parent range	Top performing genotype
DFF	57.57	48.00 – 61.00	60.71	55.00 – 68.00	H13 (Earliest: 48.0)
DM	119.24	116.00 – 123.00	122.14	120.00 – 126.00	H11 (Earliest: 116.0)
PH (cm)	168.97	139.65 – 184.20	173.47	155.00 – 186.05	RH749 (186.05)
MRL (cm)	53.43	42.80 – 61.50	55.99	48.75 – 61.00	H16 (61.50)
NPB	5.62	3.85 – 9.35	5.49	3.90 – 6.40	H7 (9.35)
NSB	10.04	6.15 – 15.50	9.68	7.50 – 12.65	H7 (15.50)
SL (cm)	5.03	4.47 – 5.65	4.87	4.35 – 5.35	H6 (5.65)
SS	13.92	11.33 – 16.20	12.96	11.10 – 14.50	H18 (16.20)
NSMR	32.76	23.80 – 44.00	34.98	32.00 – 40.35	H2 (44.00)
NSP	180.46	115.80 – 314.00	170.65	125.00 – 195.00	H7 (314.00)
YPP (g)	7.87	5.05 – 12.30	7.39	5.30 – 8.50	H17 (12.30)
TW (g)	3.84	2.75 – 4.85	3.56	3.10 – 4.30	H11 (4.85)

DM: days to maturity; DFF: Days to 50 % flowering; NPB: number of primary branches; NSB: number of secondary branches; PH: plant height; SL: siliqua length; SS: number of seeds per siliqua; TW: Test weight; YPP: seed yield per plant; MRL: main raceme length; NSMR: number of siliquae on main raceme; NSP: number of siliquae per plant.

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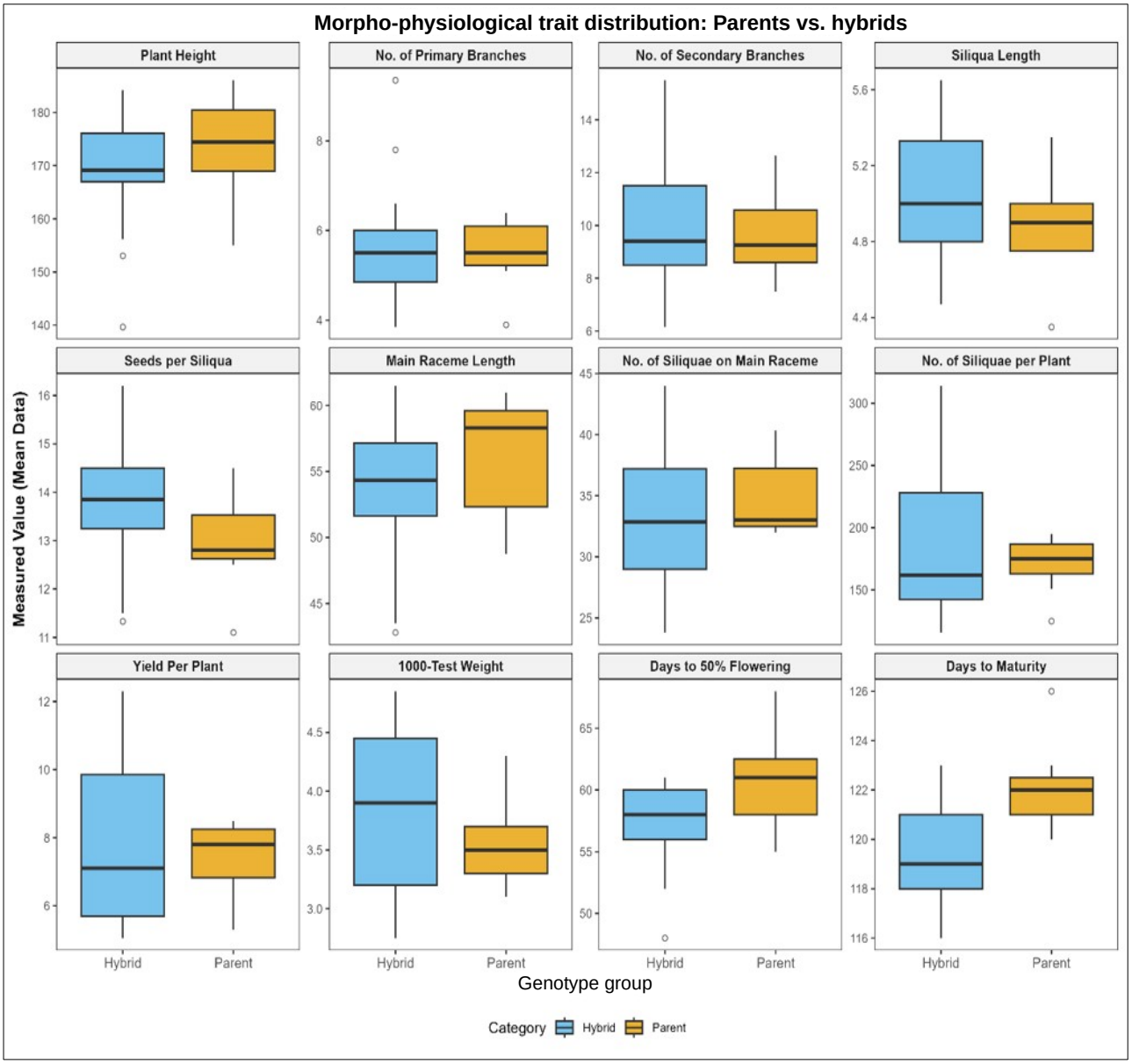


Fig. 3. Comparative distribution of morphological and yield traits in parental lines and hybrids of *Brassica juncea*. Boxplots represent the distribution of 12 quantitative traits in parental lines and hybrids, showing the median, interquartile range and dispersion of observations for each genotype group.

General combining ability and specific combining ability effects

The estimates of GCA effects revealed considerable variation in additive and non-additive gene action across the evaluated traits. (Fig. 4 and 5, Table 3). Parent P4 exhibited the highest positive GCA effects for YPP (1.10) and NSP (24.35), establishing P4 as the best general combiner and primary parental candidate for yield enhancement. Parent P1 proved superior for NSB (2.97), SL (0.48), SS (1.54) and TW (0.74). Parent P6 recorded the maximum positive GCA effect for MRL (4.99), while parent P3 recorded the maximum positive GCA effect for NPB (0.91). Regarding phenological and plant architecture traits, the most negative GCA effects were recorded by P3 for DFF (-5.68) and PH (-18.48), whereas P2 and P6 both recorded the most negative GCA effect for DM (-2.15) (Supplementary Table 4).

Evaluation of specific combining ability highlighted several crosses with high non-additive effects for primary yield components. The cross P3 × P4 recorded the highest positive SCA effects for NSP (161.91), NPB (3.25) and NSB (3.91), while P5 × P6 exhibited the highest positive SCA effects for YPP (5.10) and NSMR (8.99). For yield per plant, maximum positive SCA effects were expressed by cross P1 × P5 (5.27) and P5 × P6 (5.10). The cross P1 × P5 also showed the highest positive SCA effect for MRL (13.90), while P5 × P7 exhibited for seeds per silique (4.04) and P3 × P7 for TW (1.51). For phenological traits, P3 × P4 showed the highest SCA for DFF (9.04), whereas cross P2 × P6 and P6 × P7 exhibited the highest positive SCA effect for DM (5.33) as shown in Fig. 5. The best general and specific combiners along with GCA and SCA effects are mentioned in the Table 3 and Supplementary Table 5.

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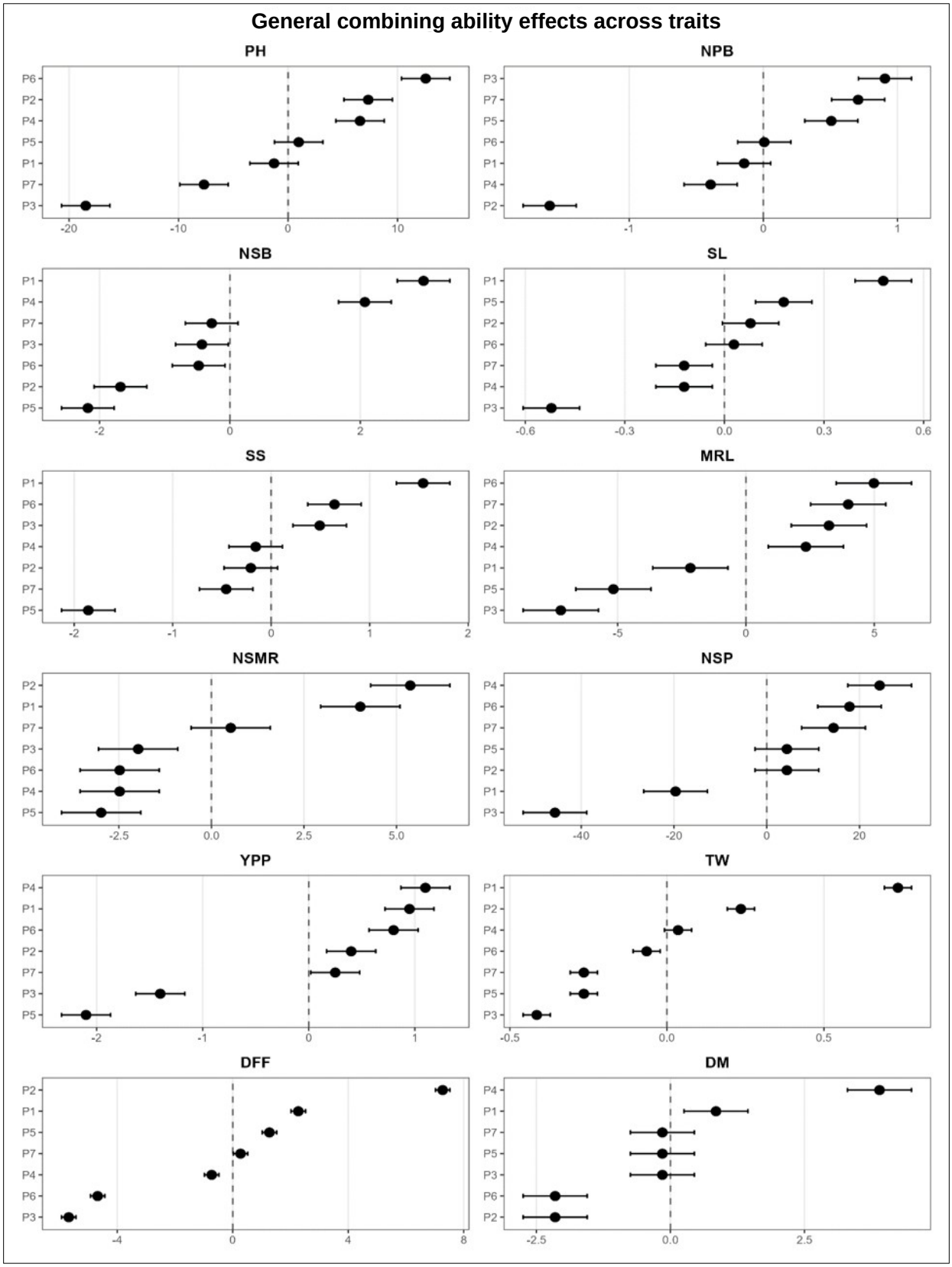


Fig. 4. General combining ability effects of seven parents across twelve traits in Indian mustard. Dot plots show the estimated GCA effects of the parents for PH, NPB, NSB, SL, SS, MRL, NSMR, NSP, YPP, TW, DFF and DM. Points represent GCA estimates, horizontal bars indicate standard errors and the dashed vertical line denotes zero effect. DM: days to maturity; DFF: Days to 50 % flowering; NPB: number of primary branches; NSB: number of secondary branches; PH: plant height; SL: siliqua length; SS: number of seeds per siliqua; TW: Test weight; YPP: seed yield per plant; MRL: main raceme length; NSMR: number of siliquae on main raceme; NSP: number of siliquae per plant; GCA: general combining ability; SCA: specific combining ability.

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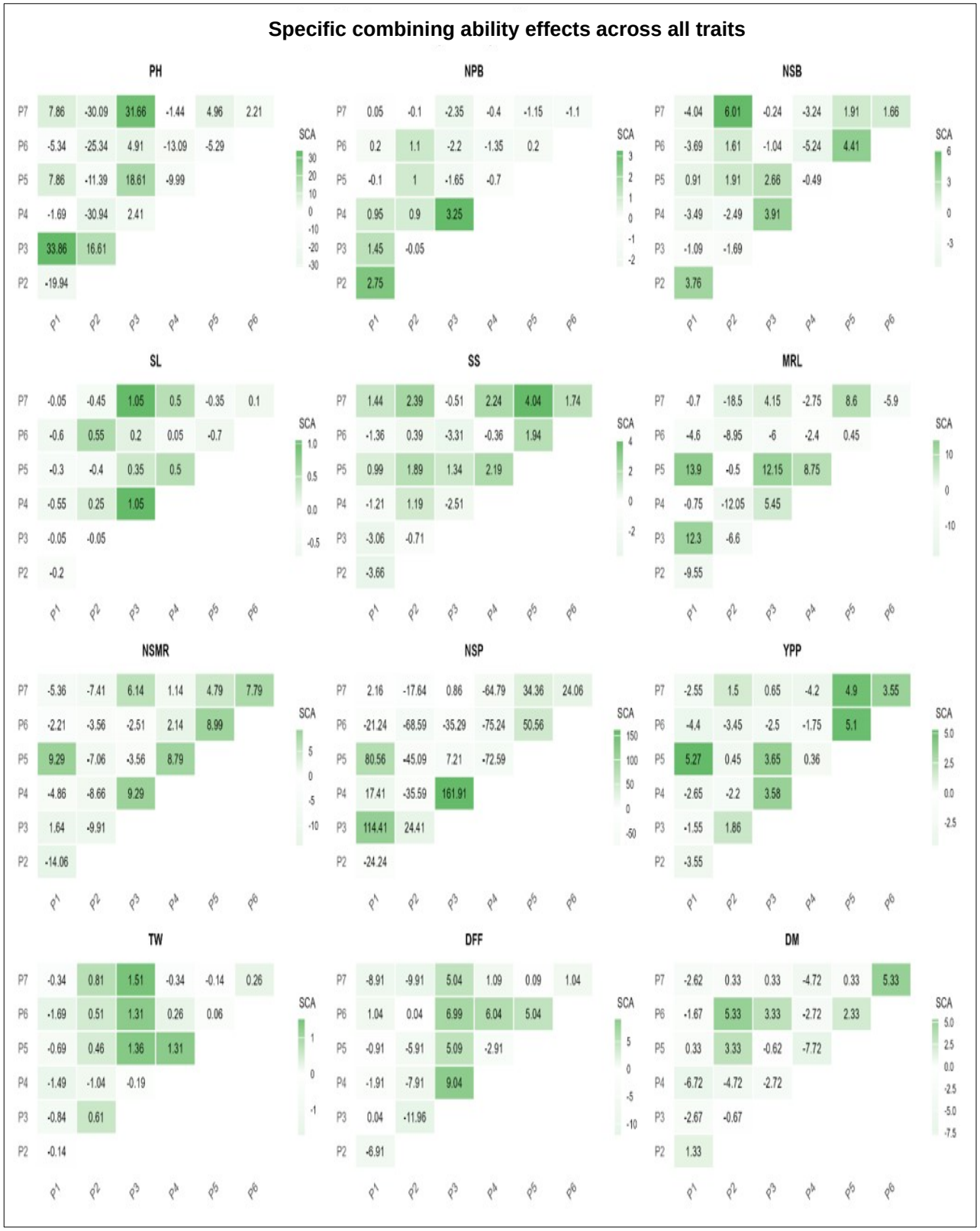


Fig. 5. Specific combining ability effects of parental combinations across 12 traits in Indian mustard. Heatmaps depict the SCA effects of hybrid combinations for PH, NPB, NSB, SL, SS, MRL, NSMR, NSP, YPP, TW, DFF and DM. Cell color intensity represents the magnitude and direction of SCA effects and the numerical values within cells indicate the corresponding SCA estimates. DM: days to maturity; DFF: Days to 50 % flowering; NPB: number of primary branches; NSB: number of secondary branches; PH: plant height; SL: siliqua length; SS: number of seeds per siliqua; TW: Test weight; YPP: seed yield per plant; MRL: main raceme length; NSMR: number of siliquae on main raceme; NSP: number of siliquae per plant; GCA: general combining ability; SCA: specific combining ability.

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Table 3. Best general and specific combiner for 12 traits

Particular	PH	NPB	NSB	SL	SS	MRL	NSMR	NSP	YPP	TW	DFF	DM
Best general combiner	P3	P3	P1	P1	P1	P6	P2	P4	P4	P1	P3	P2 / P6
GCA effect	-18.48	0.91	2.97	0.48	1.54	4.99	5.37	24.35	1.1	0.74	-5.68	-2.15
Best specific combiner	P1 × P3	P3 × P4	P3 × P4	P3 × P4; P3 × P7	P5 × P7	P1 × P5	P5 × P6	P3 × P4	P5 × P6	P3 × P7	P3 × P4	P2 × P6; P3 × P6; P6 × P7
SCA effect	33.86	3.25	3.91	1.05	4.04	13.9	8.99	161.91	5.1	1.51	9.04	5.33

DM: days to maturity; DFF: Days to 50 % flowering; NPB: number of primary branches; NSB: number of secondary branches; PH: plant height; SL: siliqua length; SS: number of seeds per siliqua; TW: Test weight; YPP: seed yield per plant; MRL: main raceme length; NSMR: number of siliquae on main raceme; NSP: number of siliquae per plant; GCA: general combining ability; SCA: specific combining ability.

Heterosis: Trends and distribution

Evaluation of heterotic expression across the 21 cross combinations revealed variation for all 12 quantitative traits. The aggregate heterotic profile (mean heterosis across all evaluated traits) of the experimental population is presented in Fig. 6, while the frequency distribution of heterotic effects is shown in Fig. 7. The distribution pattern indicated predominance of positive heterosis for yield and yield-contributing traits, whereas negative heterosis was more frequent for phenological traits, particularly DFF and DM, a desirable trend for developing early-maturing cultivars to escape terminal heat stress.

For DFF, the highest negative MPH was recorded in H13 (P2 × P3) at -21.95 %, while the highest negative BPH was observed in H18 (P1 × P7) at -14.75 %. For DM, the maximum negative MPH and BPH were both recorded in H11 (P4 × P5) at -6.45 and -4.92 % respectively. Negative BPH for PH was observed in 14 out of 21 hybrids, with the maximum value recorded in H19 (P2 × P7) at -22.76 %. Among the architectural traits, the highest BPH was recorded for NPB in H7 (P3 × P4) at 46.09 %, for NSB in H19 (P2 × P7) at 48.94 % and for main raceme length in H2 (P1 × P5) at 12.69 %.

Seed yield per plant exhibited marked heterotic variation among the hybrids and the comparative performance of hybrids based on MPH and BPH is presented in Fig. 8. Overall, 8 out of the 21 hybrids exhibited significant positive BPH for seed yield. The highest MPH for YPP was observed in H2 (P1 × P5) at 73.82 %, whereas the highest better-parent heterosis was recorded in H17 (P6 × P7) at 50.00 %, followed by H2 at 42.41 % and H15 (P5 × P6) at 40.24 %. While mid-parent heterosis reflects general genetic divergence, BPH remains the crucial metric for commercial hybrid selection, as practical utility depends on outperforming the superior parent. Among the yield contributing traits, the highest BPH was recorded for NSP in H7 at 61.03 %, for NSMR in H7 at 16.67 %, for SL in H6 (P2 × P6) at 14.14 %, for SS in H16 (P5 × P7) at 23.20 % and for TW in H10 (P3 × P7) at 39.39 %.

Parental lines were classified into three heterotic groups via hierarchical clustering (Ward's method, Euclidean distance) on seed yield SCA effects (HSCA approach), as illustrated in Fig. 9. Truncation of the dendrogram at k = 3 assigned the parents into Group I (P3, P1 and P6), Group II (P7) and Group III (P5, P2 and P4). Comparison of parental grouping with heterobeltiosis for seed yield showed that the superior hybrids were derived from inter-group crosses. The highest heterobeltiosis for seed yield was recorded in H17 (P6 × P7), representing a Group I × Group II cross, while H2 (P1 × P5) and H15 (P5 × P6) were derived from Group I × Group III crosses. In contrast, intra-group crosses showed low or negative heterobeltiosis for seed yield.

Correlation and path coefficient analysis

Correlation analysis revealed that YPP had a highly significant positive association with NSP (r = 0.720**), followed by number of siliquae on the main raceme (r = 0.394*) and NSB (r = 0.381*). Number of seeds per siliqua showed a positive but non-significant association with yield (r = 0.303), whereas SL was negatively associated with yield (r = -0.146); the correlation pattern is presented in Fig. 10. Among inter-trait associations, NPB was positively correlated with NSP (r = 0.617**) and NSB (r = 0.577**), while MRL showed strong positive association with number of siliquae on the main raceme (r = 0.685**) and PH (r = 0.588**). The complete inter-trait phenotypic correlation matrix for all 12 quantitative traits is presented in Supplementary Table 6. Path coefficient analysis indicated that the 11 component traits explained 87.23 % of the total variation in seed YPP (R^2 = 0.8723), with a low residual effect (R = 0.3573). Number of siliquae per plant exerted the highest positive direct effect on seed yield (1.045), followed by TW (0.382), number of siliquae on the main raceme (0.155) and SS (0.153). In contrast, NPB (-0.412) and PH (-0.185) showed negative direct effects. Positive indirect effects of NPB (0.645) and NSB (0.537) through NSP contributed substantially to their association with seed yield. The direct and indirect effects are presented in Table 4. The direct path coefficient exceeding unity (1.045) is indicative of multicollinearity, arising from strong inter-correlations between siliqua number and associated branching traits. Nonetheless, this high magnitude establishes the NSP as the principal determinant of seed yield under late-sown conditions.

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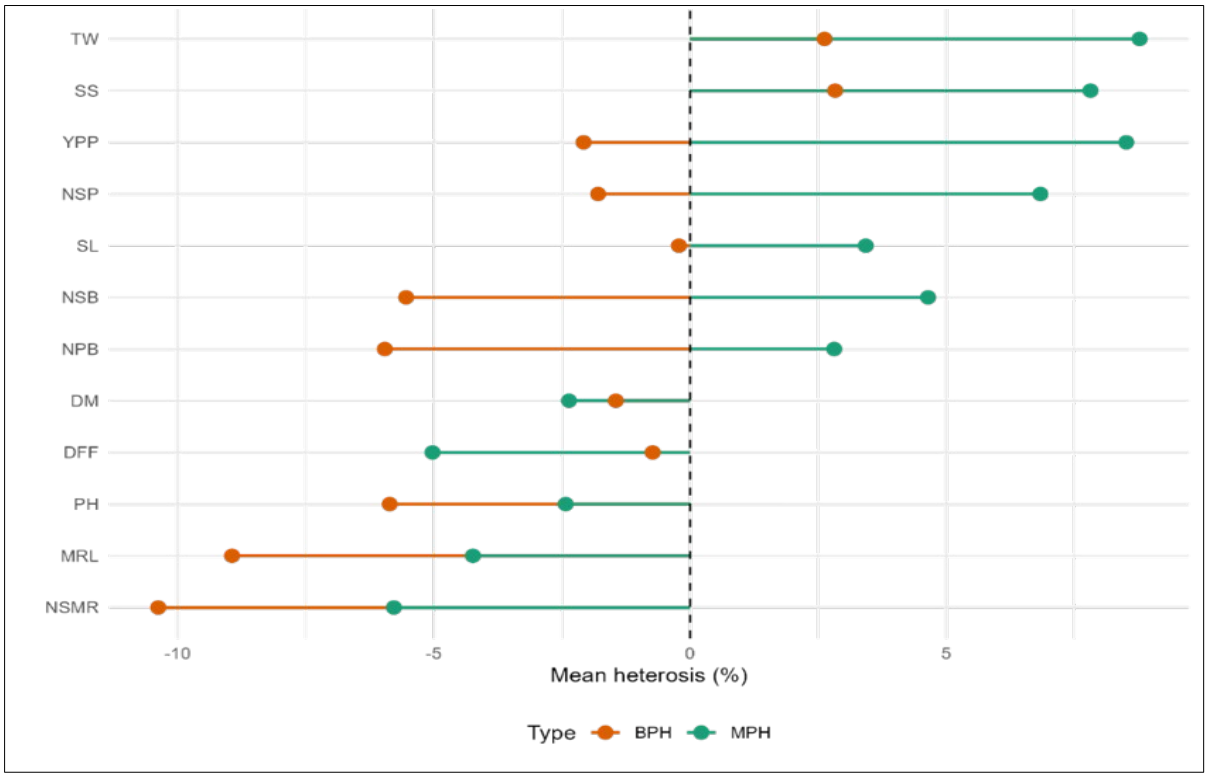


Fig. 6. Heterotic performance of 12 agro-morphological and yield traits in Indian mustard.

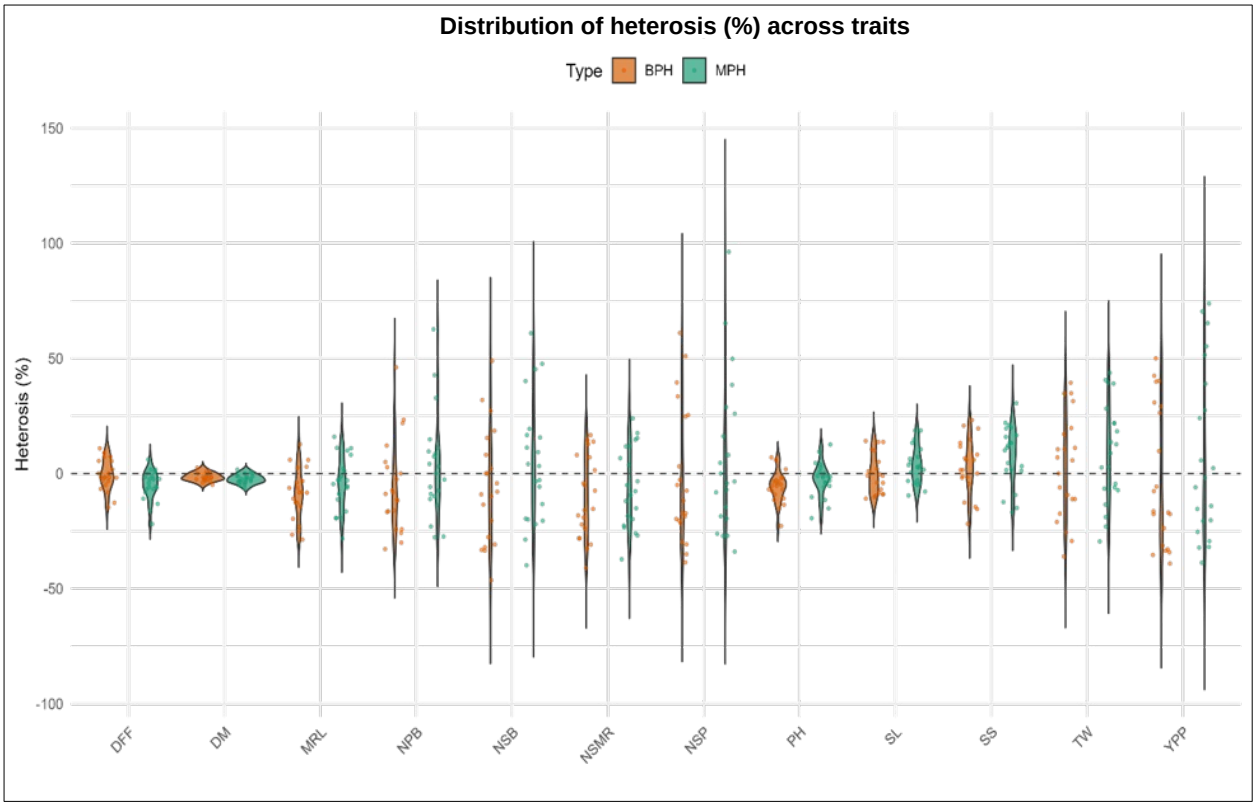


Fig. 7. Distribution pattern of heterosis for 12 agro-morphological and yield traits in Indian mustard.

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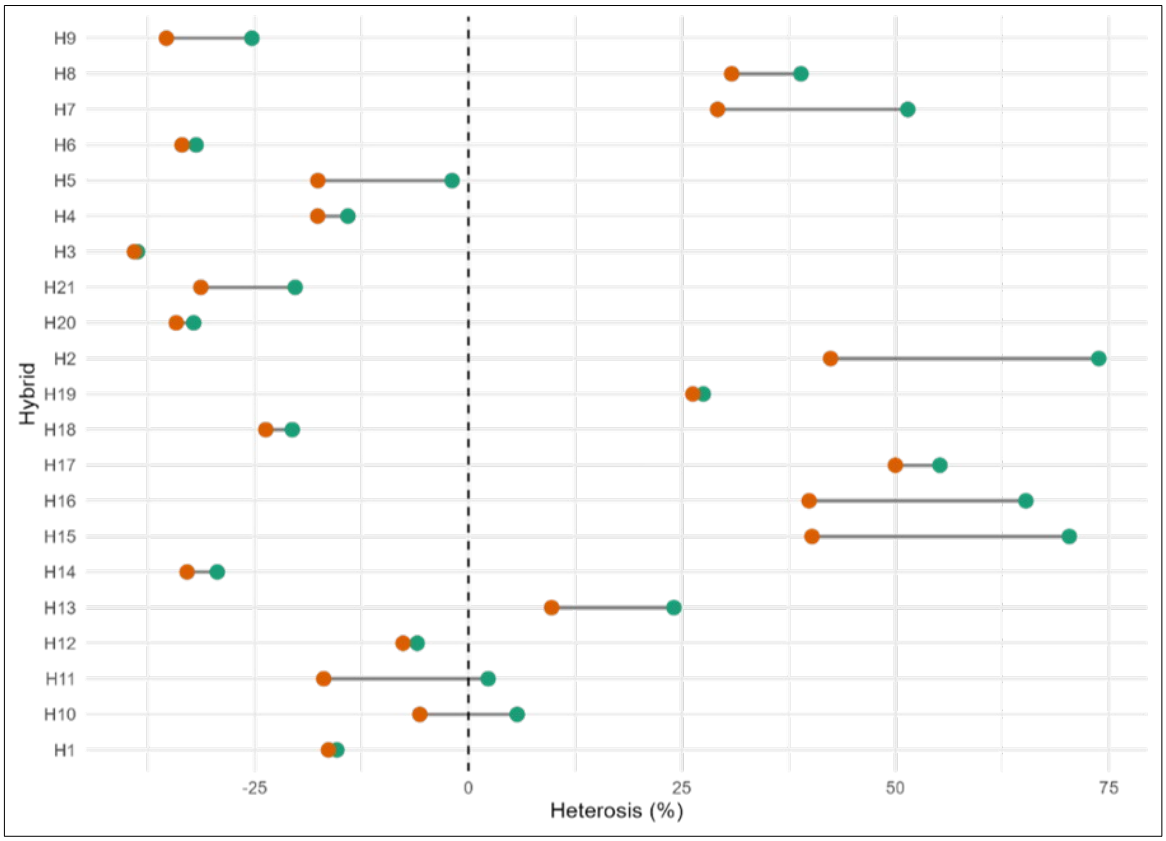


Fig. 8. Comparison of mid-parent and better-parent heterosis for yield per plant across genotypes.

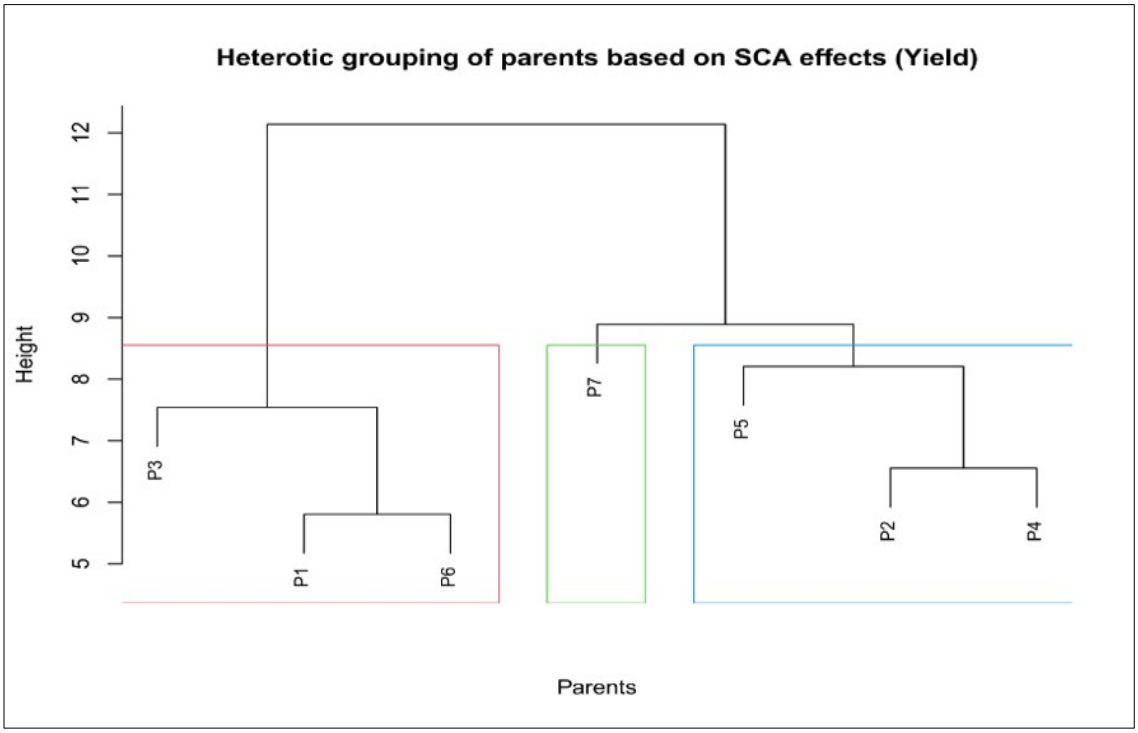


Fig. 9. Heterotic grouping of parents for yield based on specific combining ability.

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Principal component analysis (PCA)

Principal component analysis revealed that the first five principal components had eigenvalues greater than 1.0 and together explained 81.5 % of the total phenotypic variation, as presented in Fig. 11. Among these, PC1 explained the largest proportion of variation (29 %), followed by PC2 (16.7 %), PC3 (14.4 %), PC4 (11.5 %) and PC5 (9.9 %). This retention criterion based on Kaiser's rule was further supported by the scree plot inflection point (Fig. 11), where the curve flattens substantially after PC5. Trait loadings showed that PC1 was mainly associated with yield-related traits, particularly NSP, NSB and NPB, whereas PC2 was primarily influenced by DFF and DM. The PCA biplot (Fig. 12) showed close association among seed yield, NSP and NSB and also indicated wide dispersion of hybrids across the four quadrants.

Cluster analysis

Ward's hierarchical cluster analysis classified the 28 Indian mustard genotypes (21 hybrids and 7 parents) into four distinct clusters on the basis of 12 quantitative traits, as illustrated in Fig. 13. Cluster-wise genotype composition and mean values for all 12 traits are presented in Supplementary Table 7a and b. Cluster I comprised five genotypes (H7, H15, H16, H2 and H17). This cluster recorded the highest mean yield per plant (YPP = 11.46 g against an overall mean of 7.75 g), the highest number of siliquae on the main raceme (NSMR = 38.74) and per plant (NSP = 255.40) and the highest NSB = 11.82, justifying its classification as the superior group of hybrids. Cluster II comprised six genotypes (H19, H13, IC051151, H9, H5 and H8), with a mean PH of 162.92 cm, MRL of 47.73 cm, NSMR of 27.47 and YPP of 7.33 g. Cluster III comprised six genotypes (H21, H4, H1, H3, H14 and H18), with a mean DM of 117.83 days, YPP of 6.15 g and TW of 3.18 g. Cluster IV comprised 11 genotypes (RH1222-28, Varuna, Giriraj, EC597328, H12, RH749, H20, H11, EC676653, H6 and H10), with trait means closest to the overall population mean across most of the 12 characters.

Discussion

The present findings demonstrate that Indian mustard retains meaningful genetic variability for yield and related traits even under very late sowing, a constraint particularly relevant to rice-based cropping systems where delayed field readiness restricts timely establishment (32, 33). The significant variation observed among the evaluated genotypes indicates that very late sowing can discriminate among materials for productivity and associated traits, thereby providing a useful screening environment for identifying parents and hybrids with relatively better performance under delayed establishment. These findings are biologically significant and important because the studies conducted under normal and timely sow conditions often identify high-performing cultivars or parents, yet those rankings may shift substantially when the crop is exposed to delayed sowing and a shortened effective growth period (34–36), where yield penalties can range from 20 % to over 80 % (37–40).

The mean performance and combining ability results further indicate that productivity under very late sowing depends on both parental breeding value and cross-specific complementation. Specifically, parents P4 (GCA = +1.10), P1 (GCA = +0.95) and P6 (GCA = +0.80) were identified as superior general combiners for YPP based on statistically significant positive GCA effects ($p < 0.01$; SE = 0.2309), confirming that these lines contribute favourable additive genetic effects for yield retention under late-sown conditions. Similar importance of general and specific combining ability for yield and its component traits has been reported in Indian mustard under timely-sown conditions, indicating that both parental breeding value and cross-specific complementation are relevant for improvement (41, 42). Concurrently, significant SCA effects observed among top-performing hybrids highlight that non-additive gene action plays an important complementary role in shaping yield expression under delayed planting. In time and heat-constrained environments, specific non-additive complementation between parental lines helps buffer the adverse impacts of a truncated crop duration by optimising developmental timing and reproductive sink strength (43). The heterosis results demonstrate that substantial hybrid advantage can be realised even under a highly constrained late-sown window, as evidenced by hybrids H17, H2 and H15 exhibiting the highest heterotic expression for seed YPP. However, high heterosis expressed within a single late-sown environment does not automatically ensure yield stability across fluctuating micro-environments, necessitating multi-environment testing to verify commercial performance. Comparable yield heterosis under favourable sowing dates has been attributed to high *per se* performance coupled with strong SCA effects. In the present material, the yield advantage was directly supported by strong positive correlation and direct path effects of reproductive sink traits specifically NSP ($r = 0.720$, direct effect = 1.045) in contrast to vegetative traits like PH, which showed negligible direct contribution (-0.185). Furthermore, descriptive evaluation of this heterotic grouping pattern also supported this view, as the best performing hybrids were derived from inter-group combinations (H17-Group I × Group II cross, while H2 and H15- Group I × Group III crosses.) rather than intra-group crosses, suggesting that parental divergence coupled with favourable combining behaviour can improve the probability of identifying useful hybrids for delayed sowing (44).

The correlation and path analyses clarified the trait basis of yield expression under very late sowing. Seed yield per plant showed the strongest positive association with NSP and path analysis confirmed that this trait exerted the highest positive direct effect on yield as presented in Table 4. This agrees with earlier studies in mustard and related *Brassica* material where

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siliquae number has frequently emerged as a major contributor to yield because it directly reflects reproductive sink size (45, 46). Number of siliquae on the main raceme and NSB also contributed positively, but largely through their influence on siliquae production.

Table 4. Direct and indirect effects of traits on seed yield

Trait	Direct effect	Total indirect effect	Total correlation (r)	Percentage contribution
PH	-0.185	0.276	0.091	6.381
NPB	-0.412	0.510	0.098	14.188
NSB	0.020	0.361	0.381	0.695
SL	-0.227	0.081	-0.146	7.815
SS	0.153	0.150	0.303	5.284
MRL	0.114	0.181	0.295	3.913
NSMR	0.155	0.239	0.394	5.337
NSP	1.045	-0.325	0.720	35.995
TW	0.382	-0.463	-0.081	13.172
DFF	-0.073	0.144	0.071	2.516
DM	0.137	0.090	0.226	4.704

DM: days to maturity; DFF: days to 50 % flowering; NPB: number of primary branches; NSB: number of secondary branches; PH: plant height; SL: siliqua length; SS: number of seeds per siliqua; TW: test weight; YPP: seed yield per plant; MRL: main raceme length; NSMR: number of siliquae on main raceme; NSP: number of siliquae per plant.

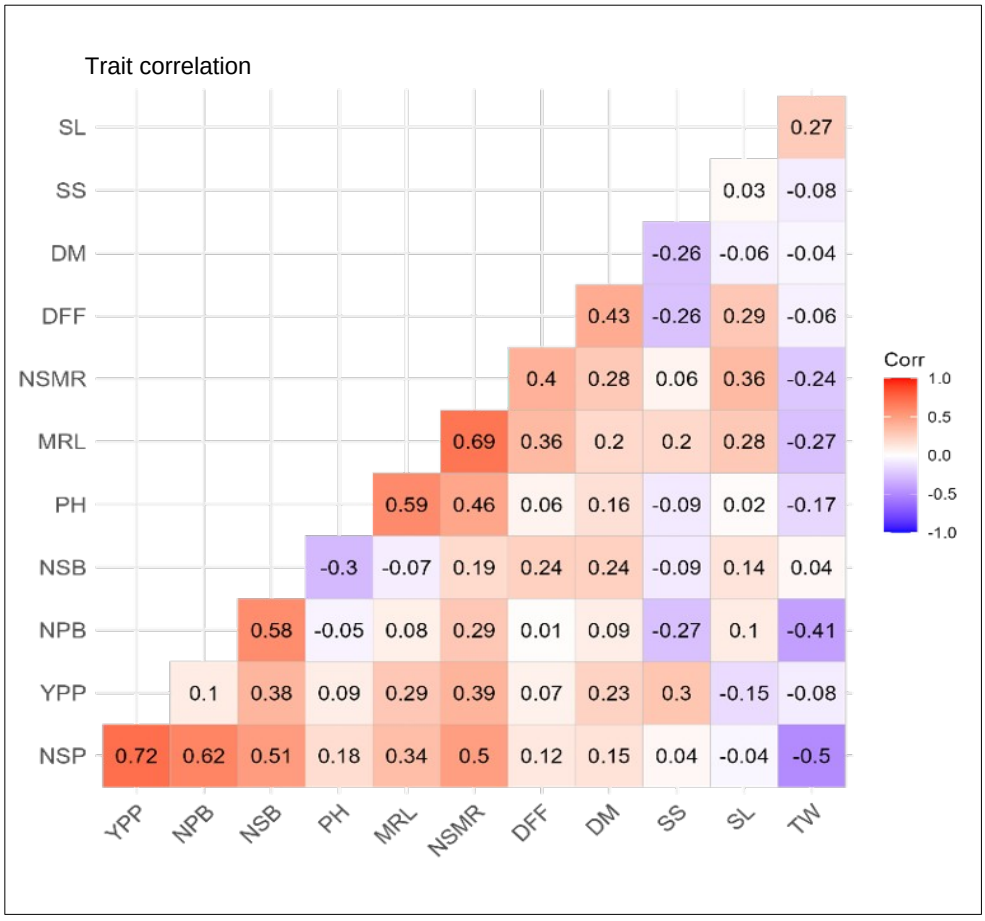


Fig. 10. Correlation heatmap illustrating the inter-relationships between seed yield per plant (YPP) and 12 contributing traits.

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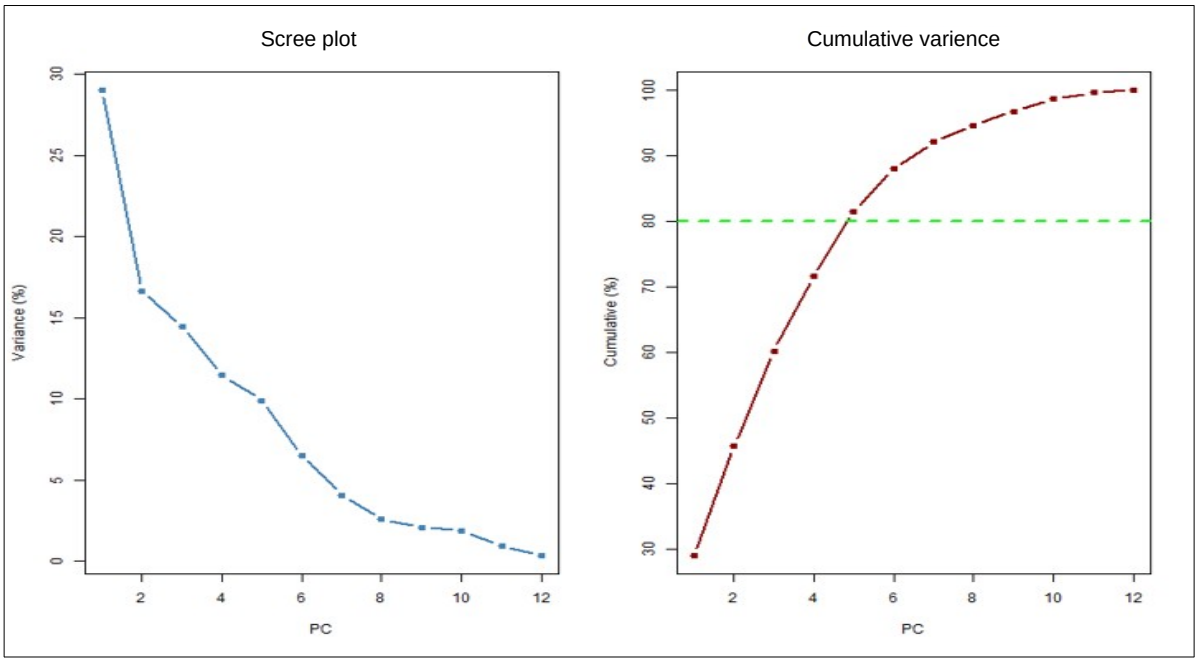


Fig. 11. Scree and cumulative variance plot.

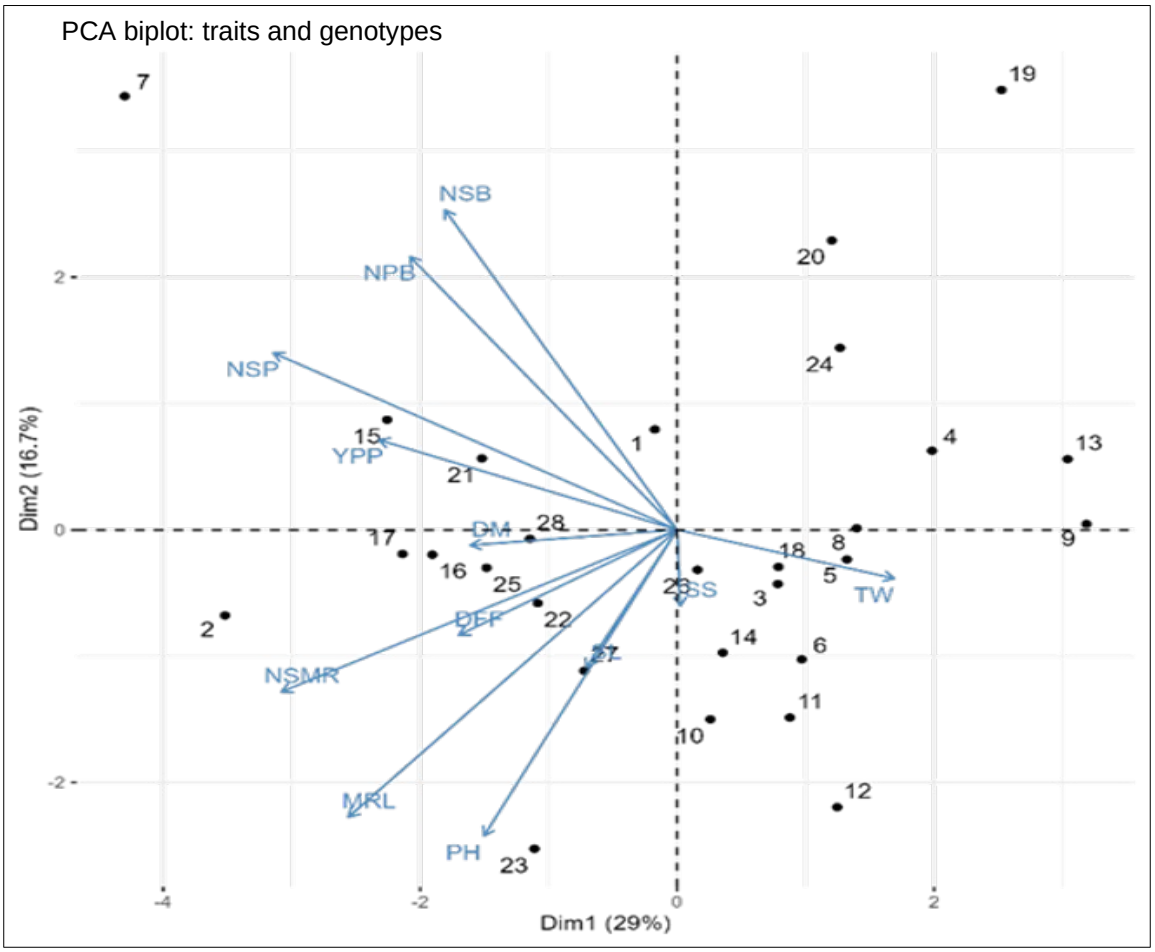


Fig. 12. Principal component analysis (PCA) biplot of 12 agro-morphological and yield traits in Indian mustard.

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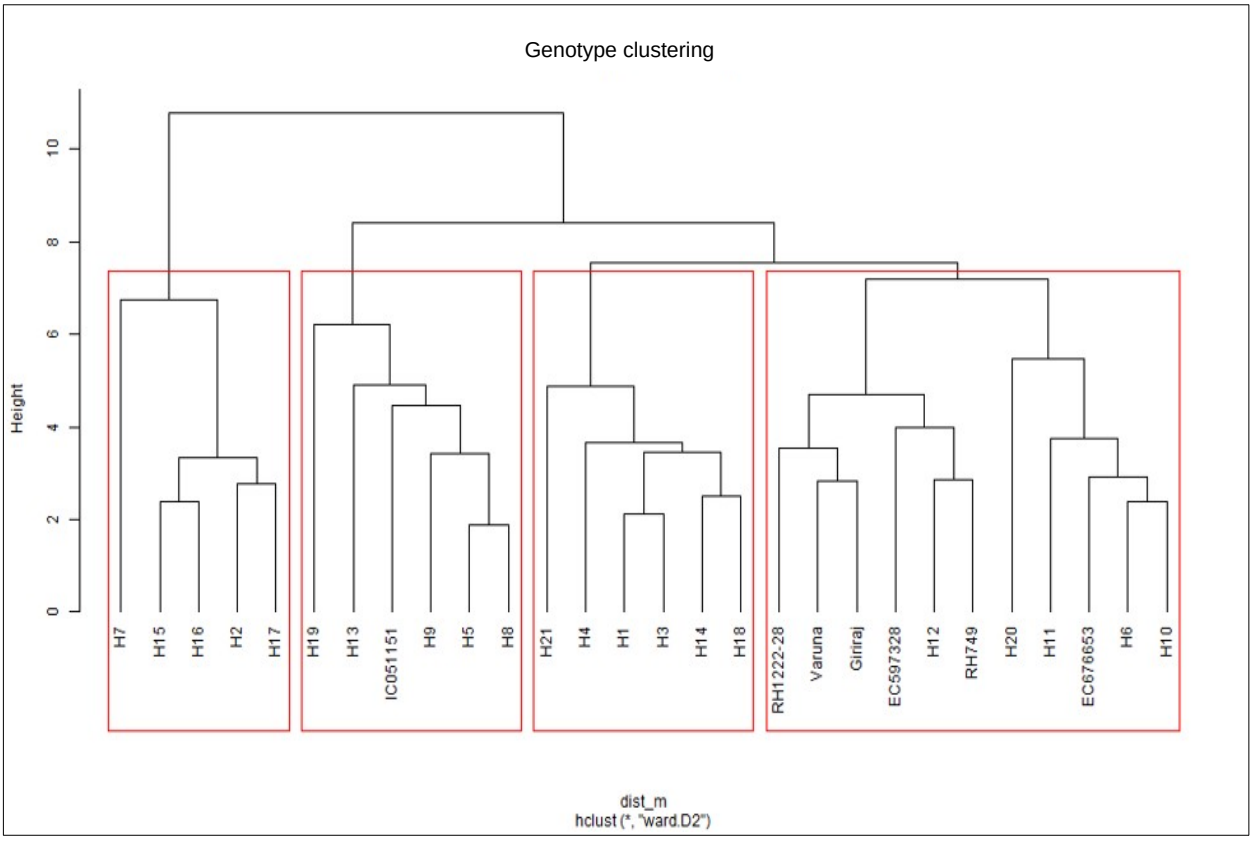


Fig. 13. Hierarchical clustering of 28 Indian mustard genotypes.

In contrast, earlier work under severe late sown heat stress (36) reported that thousand seed weight and SS exerted stronger direct path effects on seed yield than NSP, with a different trait hierarchy emerging relative to timely sowing. The difference in trait hierarchy may reflect variation in the severity and timing of stress, genetic background, environmental conditions and experimental methodology between the two studies. This divergence suggests that the relative importance of yield-determining traits may shift according to the severity and type of sowing delay and that under more moderate delays, seed quality traits such as TW may assume greater relative importance than under an extreme December planting scenario. Under delayed sowing, yield reduction in Indian mustard is closely associated with disruptions in reproductive development and yield-component expression (47, 48) These results indicate that reproductive sink retention is the primary determinant of yield adaptation under very late sowing and underscore the importance of conducting environment-specific path analysis rather than applying trait selection criteria derived from timely sown studies to delayed planting scenarios.

The multivariate analyses provided additional support to these biological insights. Principal component analysis showed that a major proportion of total variation was explained by the first four components, with the first component largely associated with yield-related traits and the second with phenological traits. This pattern indicates that under very late sowing, both reproductive capacity and developmental timing contribute to genotypic differentiation. The close association among seed yield, siliquae per plant and branching traits in the PCA biplot, together with the clustering of H17, H2 and H15 among the superior group (Cluster I mean yield = 11.46 g), confirms that top performing hybrids possessed favourable multivariate trait combinations rather than superiority for a single isolated character. Broad agreement among PCA, cluster analysis, combining ability and heterosis adds confidence to the breeding relevance of the identified material.

Before extrapolating these findings to commercial breeding, important methodological limitations of this study must be noted. Because this trial was structured specifically as a 7 x 7 diallel genetic analysis without commercial check cultivars or multi-location testing, the yield advantages reported reflect relative cross-performance and combining ability rather than agronomic release potential.

An important contribution of the present study is its explicit focus on very late sowing (December), a condition that is less frequently examined in mustard breeding studies than timely or moderately delayed sowing. While previous works reported that trait associations were broadly maintained under late sowing despite environment dependent genotypic shifts, the present diallel evaluation proves that meaningful genetic discrimination remains possible even under severe planting delays (39, 40). This is corroborated by a previous study, which demonstrated that terminal heat stress fundamentally restructures both combining ability patterns and yield component hierarchies (36).

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Furthermore, these findings underscore the complexity of genotypic responses to delayed sowing, necessitating environment-specific selection strategies rather than assuming universal trait stability. By contrast, the present work demonstrates that even when sowing is pushed to early December, meaningful genetic discrimination remains possible and some parents and hybrids still perform relatively better than others. This is valuable for breeding programs targeting rice following and other delayed-establishment ecologies, where the practical question is not whether mustard can survive under late planting, but which genetic combinations can retain better productivity under such conditions.

To translate these findings into practical breeding strategies for delayed-sowing conditions, parents with significant positive GCA effects, specifically P4, P1 and P6 should be used in recurrent selection to accumulate additive genes for yield retention under a shortened season. For hybrid breeding, crossing parents across different heterotic groups proved most effective, as Group I × Group II and Group I × Group III crosses produced the highest-yielding hybrids (H17, H2 and H15) through favourable non-additive gene action. Finally, field selection under late-sown environments should prioritise siliquae per plant and secondary branching rather than PH, as these traits directly govern reproductive sink capacity in late-sown, rice–mustard cropping systems. From an economic standpoint, adopting hybrid mustard under late-sown conditions requires balancing higher seed costs against yield protection for smallholder farmers. Although hybrid seed requires greater upfront investment than open-pollinated varieties, the substantial yield advantage of superior crosses (such as H17 and H2) under late planting easily offsets the seed cost, generating higher net returns per unit area. Consequently, targeted hybrid deployment offers an economically viable and risk-mitigating strategy to secure farm income in late-sown, rice-mustard cropping systems.

Although the present study provides useful evidence on genetic variability, combining ability and hybrid performance under very late sowing, these findings require further validation before wider breeding conclusions are drawn addressing the limitations of this. The promising parents and hybrids identified here should be examined across locations, seasons and sowing windows to determine the stability of their performance under diverse delayed-sowing environments. In addition, integration of physiological, biochemical and molecular analyses would help explain the mechanisms governing adaptation, particularly with respect to heat-stress response, reproductive efficiency and yield stability under terminal stress. Such validation will not only strengthen the present conclusions but also improve the practical use of these materials in climate-resilient hybrid breeding programs for Indian mustard.

Conclusion

This study establishes that planting delays into early December within rice mustard cropping systems do not preclude genetic gain, as high heritable selection potential persists across key agro-morphological traits under late sown conditions. Combining ability analysis and heterotic grouping demonstrate that productivity under late planting relies on strategic parental selection and genetic complementation. Parents P4, P1 and P6 proved to be superior general combiners for seed yield retention, while intergroup crosses involving Group I with Group II and Group III parents generated the top performing hybrids (H17, H2 and H15) exhibiting high mid-parent and better-parent heterosis. Integrating correlation, path coefficient, principal component and cluster analyses reveals that yield expression under delayed planting is governed primarily by reproductive sink capacity-specifically the number of siliquae per plant (NSP) and secondary branching, rather than vegetative height or biomass. A core conclusion of this work is that selection strategies must be specific to the environment rather than assuming universal trait stability across sowing dates, as time and heat constraints in late sown environments alter trait hierarchies. Breeding programs for late sown cropping systems should therefore focus on intergroup hybridisation and field selection for siliqua retention over vegetative growth. While these findings offer valuable preliminary indications for late sown hybrid breeding, multi environment validation across locations and years against standard commercial checks remains necessary to confirm performance stability. Moving forward, integrating physiological, biochemical and molecular analyses will be vital to unravel the underlying heat tolerance mechanisms and reproductive efficiency traits, enabling the effective utilisation of these promising genetic resources within climate resilient breeding programs.

Authors' contributions

SS^1, KS and PS have conceptualised the study and designed the whole experiment. RKV and AP conducted data collection and curation. DGP and GT performed the formal statistical analysis and data visualisation. SS^1 and SS^2 prepared the original draft of the manuscript. KS, AB and SS^1 contributed to the critical revision and editing of the manuscript. KS and PS provided overall supervision and project administration. All authors have read and approved the final manuscript. [SS^1 stands for Sahil Shamkuwar and SS^2 stands for Shivangi Saha].

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Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

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

During the preparation of this work, the authors used Perplexity and Gemini to refine the language, correct grammar and improve the readability of the manuscript. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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