



RESEARCH ARTICLE

Line × Tester analysis for sustainable yield and dry fodder contributing traits in pearl millet (*Pennisetum glaucum* (L.) R. Br.) under rainfed conditions

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Abstract

Selection of parents to maximize hybrid performance requires a clear understanding of the combining ability. 101 ICRISAT bred B-lines and two R-line testers were crossed using a line × tester design to develop 202 F₁ hybrids and evaluated at four locations in an alpha-lattice design. The environments, hybrids and variance partitions due to lines, testers and their interaction (lines × testers) were found significant. Contribution of lines to the combining ability variance was very high for days to 50 % flowering (DF) (84.3 %), plant height (PH) (71.9 %), panicle girth (PG) (89.8 %), blast severity score (BS) (59.4 %), panicle yield (PY) (64 %), grain yield (GY) (61.8 %) and dry fodder yield (FY) (65.2 %). High percentage contribution of line × tester for panicle yield plot⁻¹ (32.6), threshing percentage (43), grain yield (38.1), fodder yield (34.8) and blast score (28) revealed an interplay of additive and non-additive gene action in their inheritance, thereby emphasizing the potential for pedigree breeding in combination with harvesting the heterotic potential of crop for these traits. Several seed- parents were identified as good general combiners for DF (ICMB 88004, ICMB 04222), PH (ICMB 08888), PL (ICMB 09333, ICMB 09555) and GY (ICMB 93222, ICMB 94444, ICMB 07666). Inbreds ICMB 08666, ICMB 08888 and ICMB 09333 were identified good for biomass production. Hybrids like ICPH021, ICPH023, ICPH107, ICPH175, ICPH007 and ICPH083 were identified as top performing hybrids for different segments and agro-ecological zones. Grain and fodder yield showed a significant and positive correlation with GCA and SCA suggesting that combining ability estimates are reliable predictors of hybrid performance, aiding in the effective exploitation of heterosis.

Keywords: disease resistance; gene action; General Combining Ability (GCA); grain yield; Specific Combining Ability (SCA); sustainability; threshing ratio

Introduction

Pearl millet (*Pennisetum glaucum* (L.) R. Br.; 2n=2x = 14) is a cereal grain crop with high nutrient density, abiotic stress resistance and climate resilience. It is extensively produced and consumed as a staple food and fodder in semi-arid and arid regions of Asia and Africa. The grains of this crop are nutrient rich, gluten-free and contain higher dietary fibre compared to other major cereals such as rice, maize and wheat (1). Pearl millet is a rich source of iron (Fe) and zinc (Zn), proteins and carbohydrates. Due to its tremendous nutritional value, pearl millet contributes significantly to food and nutritional security, particularly for resource-poor farmers (2). Pearl millet is a climate resilient crop that can grow in drought prone areas, poor soil conditions and under extreme temperatures where other major cereals often fail to produce desirable yields (3, 4). Despite the high value of pearl millet in food and nutritional security, area of pearl millet has not increased, since it is majorly grown under dry soils of marginal

environments with limited resource inputs. A high degree of genetic gain in grain yield is required to compensate less area (5). Enhancement of genetic gains in pearl millet, particularly for productivity and stress tolerance, depends on the identification of superior parental lines with high combining ability through the integration of conventional and modern breeding methods that leverage existing genomic diversity (6, 7). Hence, it is essential to develop high-yielding pearl millet hybrids with high degree of environmental stresses tolerance.

Estimation of pan-genomic variation supports the development of innovative breeding strategies to accelerate genetic gain (8). Identification of promising parental lines poses a persistent challenge for plant breeders and combining ability estimation offers a strategic solution for selection and incorporation of high-yielding materials into breeding cycle (9, 10). Thus, examining proprietary new inbreds and materials received through germplasm consortiums for their combining ability using either strong or weak testers, has been a key

strategy for heterosis exploitation and germplasm diversification. Line \times tester mating design (11) offers great pollination flexibility, enables multi-tester use, can accommodate large number of test materials and offers robust estimation of combining ability and gene action through both half and full-sibs.

The promising parents would need to be selected using more targeted approaches to breed high yielding, dual-purpose and disease-resistant cultivars. Combining ability together with *per se* performance of parents and hybrids is helpful in selecting suitable parents and hybrids. Diallel analysis has been used by many professionals for identifying parents with high GCA and potential diversity for use in breeding program, while line \times tester analysis has been employed to identify potential parents and specific hybrids combinations (12). Several researchers have reported the estimation and utilization of significant GCA and SCA effects of landraces or inbred parents in pearl millet for a wide range of traits including micronutrients (13), grain quality (14), harvest index and fodder yield (15), compactness of panicles (10), plant height, days to flowering, panicle length and girth, number of productive tillers, thousand-grain weight, panicle and grain yield and downy mildew incidence (16). Often, it has been noted that variables like panicle length, days to 50 % flowering and grain yield were significantly influenced by additive gene action (17). The estimation of combining ability and gene effects is not only dependent on the mating design selected but also on the choice of parental lines (18). Therefore, given the importance of understanding the genetic architecture of traits and the material-specific nature of combining ability estimates, it is essential to investigate combining ability and gene effects for each distinct set of materials (19). Based on the above review it can be stated that the development of high-yielding hybrids with improved traits is one of the prime breeding goals; hence the identification of the promising parents is important step in pearl breeding. Therefore, the present study was undertaken to estimate combining ability and gene action in pearl millet using a line \times tester mating design.

Materials and Methods

Plant materials

A set of 101 maintainer lines (B-lines) and two restorer inbreds (R-lines) bred at ICRISAT, were used in this study. Line \times tester mating design was used to develop crosses. As a result, a total of 202 F1 hybrids were developed and evaluated in yield trials for the study of combining ability and genetic effects using widely adapted and nationally notified commercial hybrids – Kaveri Super Boss, 86M84, 86M88 and PRO9444 as checks (Annexure 1).

Crossing program for hybrid development

Staggered set of B-lines and R-lines was planted in crossing block to ensure proper nicking of receptive stigma on female parent with onset of pollen shedding on the male parents. Both female and male panicles were covered with parchment paper bag at boot leaf stage to avoid contamination with foreign pollen. Panicles when they reached at full stigma stage

(after 95 % of florets had fully emerged with mature stigmas) were pollinated using pollen collected in parchment paper bags from targeted R-line. Target number of 202 hybrids were produced using manual pollination during the rainy season of 2020 and summer season of 2021.

Field trials and experimental design

Field trials were constituted as per alpha-lattice design, utilizing aforesaid plant materials and conducted across four locations (Jaipur, Alwar, Aurangabad and Ahmednagar) representing two different agro-climatic zones (Zone A and Zone B). Geo-environmental parameters of phenotypic evaluation locations during the crop season are presented in Table 1. Each entry was planted in two rows plot of 5-meter length with rows spaced 45 cm apart and 15 cm plant to plant distance was maintained within a row. Experimental field had sandy loam soil with pH 7.5 at Alwar, sandy soil with pH 8.3 at Jaipur, medium black soil with pH 7.9 at Aurangabad and deep black soil with pH 8.2 at Ahmednagar. Plot designs were made using GenStat statistical package “GenStat”, 17th edition (VSN Int., Hemel, Hempstead, UK) and different randomization was used for each of the locations.

Agronomic practices

During rainy season 2021 seed sowing was done by dibbling on the ridge. Post-emergence thinning was done at 15 days after sowing (DAS) to uniformly maintain single plants spaced at \approx 15 cm apart. The crop was supplied with a basal fertilizer dose of 65 kg ha⁻¹ of DAP (diammonium phosphate) at the field preparation time. 105 kg ha⁻¹ of urea (46 % N) was applied as top-dressing in split doses, once at three weeks and other at 35 days after sowing to ensure recommended 60:30 kg ha⁻¹ dose of N and P₂O₅. Trials were irrigated only for lifesaving during long rainfall gaps to keep the crop as close to natural precipitation as possible and to represent real farming conditions. All types of recommended interculture operations were followed to raise a weed-free crop.

Phenotypic observations

Phenotypic observations were recorded for ten agronomic traits which includes days to 50 % flower (days), plant height (cm), productive tillers per plant (count), panicle length (cm), panicle girth (mm), panicle yield per plot (kg), threshing ratio, grain yield (q ha⁻¹), dry fodder yield (t ha⁻¹) and leaf blast severity (scores).

Panicle length (cm) [PL]

Length measured from tip to base of panicle excluding peduncle on 5 random plants at hard dough to maturity stage.

Panicle girth (mm) [PG]

Measured on 5 random plants at the point of maximum panicle girth from the middle part of panicle at maturity using digital Vernier calipers.

Productive tillers (count) [PT]

Only the panicles bearing seeds which contribute to yield were considered for taking count at the time of crop maturity.

Days to 50 % flower (days) [DF]

Observed from date of sowing to date of nearly 50 % of stigma emergence, on the principal panicle of 50 % of plants of each genotype on per plot basis.

Table 1. Geo-environmental parameters of phenotypic evaluation locations - rainy 2021

S. No.	Location	Geo - Position (°E/°N)	Altitude (m)	Monthly rainfall (mm)* & Min-Max temperature range														
				June			July			August			September			October		
				Rain (mm)	Temp °C		Rain (mm)	Temp °C		Rain (mm)	Temp °C		Rain (mm)	Temp °C		Rain (mm)	Temp °C	
					Min	Max		Min	Max		Min	Max		Min	Max		Min	Max
1	Alwar	27.56°/ 76.66°	258	25.2	25.6	44.7	275.8	25.7	43.8	152.1	23.3	35.1	178.4	22.4	32.5	21.3	14.4	35.6
2	Jaipur	26.91°/ 75.78°	431	32.4	24.7	42.8	208.3	24.3	41.4	183.8	22.2	35.2	141.3	21.9	32.6	35.4	14.2	34.3
3	Aurangabad	20.08°/ 75.42°	649	130.5	22.3	35.5	171.2	22.1	34.8	186.9	20.5	34.6	460.3	20.7	31.5	107.3	14.4	30.7
4	A. Nagar	19.84°/ 75.23°	561	120.8	22.0	35.1	125.7	21.8	34.3	122.1	20.0	33.8	216.2	19.9	32.1	122.3	15.1	31.5

Plant height (cm) [PH]

Measured at the time of harvesting from plant base to the tip of panicle of main shoot on 5 randomly selected plants.

Panicle yield plot⁻¹ (kg) [PY]

Productive panicles were harvested from the plants and sun dried for two days to bring down the moisture. Panicles from each plot were weighed to record the panicle yield per plot in kgs.

Threshing ratio [TR]

Immediately after measuring panicle yield per plot⁻¹, a random sample of nearly one kilogram of panicle was collected from each plot and its weight was recorded as sample weight. Sample was well dried in muslin cloth bags to threshing moisture, threshed using Wintersteiger LD180 research sample thresher, grain yield of the sample was recorded and threshing ratio of the genotype was calculated, using the following formula:

Threshing ratio =

$$\frac{\text{Threshed grain yield of sample (g)}}{\text{Initial sample weight (g)}} \quad (\text{Eqn. 1})$$

Grain yield (q ha⁻¹) [GY]

Threshing percentage was multiplied with panicle yield per plot⁻¹ to get grain yield per plot and then converted into q ha⁻¹ using formula:

Grain Yield (q ha⁻¹) =

$$\frac{\text{Grain yield (kg plot}^{-1}\text{)} \times 100}{\text{Plot size (m}^2\text{)}} \quad (\text{Eqn. 2})$$

Dry fodder yield (t ha⁻¹) [FY]:

All plants excluding the panicles from a plot were harvested, bundled and fresh fodder weight for the plot was recorded. One or two full plants from the fodder bundle of the plot were taken as a sample, weight was recorded as fresh sample weight and the sample was kept in a nylon net bag, dried for 10-15 days before recording the sample dry weight. Ratio of dry vs fresh sample fodder weight was used to calculate the plot dry fodder weight in t ha⁻¹ using formulae.

Plot Dry Fodder yield (kg) =

$$\frac{\text{Sample dry weight}}{\text{Sample fresh weight}} \times \text{Plot fresh weight (kg)} \quad (\text{Eqn. 3})$$

Dry fodder yield (t ha⁻¹) =

$$\frac{\text{Plot dry fodder yield (kg)}}{\text{Plot size (m}^2\text{)}} \times 10 \quad (\text{Eqn. 4})$$

Blast severity (score) [BS]

Disease severity was recorded at the hard-dough stage using a 1-9 progressive scale as reported and deployed earlier (20). In the case of present research work we used a scale reverse to that mentioned above, as usually used by key private seed companies for blast disease scoring. As per the scale. Score 1 represents highly susceptible, 9 represents highly resistant.

Statistical analysis**Analysis of variance (ANOVA)**

Pooled analysis of variance was conducted using PROC MIXED (SAS v9.4) as described by SAS Institute Inc. considering the locations, genotypes and the replications as fixed and blocks considered as random. Robin T. Clarke described the use of residual maximum likelihood (REML) procedure to model error distribution, which was employed in this study to estimate and model individual location variances, thereby ensuring that the data could be pooled across locations and error variance was made homogeneous (21).

The phenotypic observations Z_{ijkl} on genotype l in replicate j of block k of location i were modeled as:

$$Z_{ijkl} = \mu + y_i + (y/r)_{ij} + (y/r/b)_{ijk} + g_l + (yg)_{il} + \epsilon_{ijkl} \dots (1)$$

Where μ is the overall mean, y_i is the fixed-effect of the location “ i ”, “ g ” is the fixed effect of genotype “ l ”; “ $(y/r)_{ij}$ ” is the fixed-effect of replication “ j ” nested within location named “ i ”; “ $(y/r/b)_{ijk}$ ” is the random effect of block “ k ” nested within replication “ j ” and location “ i ” and is $\sim \text{NID}(0, \sigma^2_b)$; “ $(yg)_{il}$ ” is the fixed-effect of interaction between the genotype “ l ” in location i ; and “ ϵ_{ijkl} ” is the random residual-effect and $\sim \text{NID}(0, \sigma^2_\epsilon)$.

Linear mixed model for multi-location line \times tester: From Eqn. 1, genotypes were further partitioned into lines (f) and testers (m)

$$Z_{ijklm} = \mu + y_i + R_{j(i)} + B_{k(ij)} + f_l + m_m + (f_m)_{im} + y^*f_{il} + y^*m_{im} + y^*fm_{ilm} + \epsilon_{ijklm}$$

Where Z_{ijklm} is the n^{th} observation of the j^{th} replication for the lm^{th} cross in the i^{th} location;

μ is the overall mean.

y_i is the i^{th} fixed effect of location i , where $i=1$ to t .

$R_{j(i)}$ is the fixed effect of the j^{th} replication within the i^{th} location, $j=1$ to r .

$B_{k(ij)}$ is the random effect of the k th block nested in j th replication and i th location $\sim NID(0, \sigma^2b)$, $k=1$ to b

f_l, m_m is fixed effects of the l th line and the m th testers respectively, where $l, m=1$ to p and $l < m$.

$(fm)_{lm}$ is fixed effect of line by tester effect of the l th line and the m th tester (cross) ($l \neq m$).

$(y^*f)_{il}, (y^*m)_{im}$ is fixed effect of line by location and tester by location interaction respectively.

$(y^*fm)_{ilm}$ is fixed effect of line \times tester by location interaction.

Results and Discussion

Analysis of variance (ANOVA) for Line \times Tester

The pooled ANOVA revealed a highly significant location effect, as evidenced by the F-values (for instance DF = 699.4***), confirming substantial differences among the test environments. Significant effects for most of the traits like fodder yield in replications (18.4***) and nested blocks (0.13***) reflect micro-environmental variation and validate the use of alpha designs. The presence of significant variations among the material used for the study was clearly visible through significant effects for treatments and its variance partitioned into hybrids and checks (Table 2). Among the hybrids total variation was partitioned into lines, testers and interaction between lines and testers (line \times tester). F-values of lines were found significant for all the traits under study (DF, PH, PL, PG, PT, BS, PY, GY and FY) except TR. While tester F-value were found significant for all traits except GY and FY. However, the line \times tester reaction was found significant for the all the traits. This clearly indicates an interplay of additive and non-additive genetic variation. When comparing the hybrids to the checks (hybrids vs checks), significant differences existed for all the traits studied which indicates that the hybrids performed significantly different compared to the checks. The interactions between locations and treatments (Locs \times Treatments), locations and hybrids (Locs \times Hybrids) and locations and lines/testers (Locs \times Lines/Testers) were significant for most traits. This suggests that the expression of these traits varied depending on the environment, materials were sourced from trait-specific or adaptation-specific nurseries and/or the effect of different genetic combinations was not consistent across all locations.

The genetic components analysis revealed that contribution of lines to the total variation in hybrids is greater than tester and line \times tester interaction for all the traits except for PL and PT. As evident from GCA/SCA ratio, the magnitude of SCA variance was found greater for PH (0.52), PG (0.25), PY (0.67), GY (0.0015), FY (0.02) and BS (0.67), whereas, both additive and non-additive gene actions were important for TR (1.0) and DF (0.88). The predictability ratio was also found to be less than 1 for these traits which clearly indicates preponderance of dominant gene action. These results are consistent with findings reported previously (22-27). The magnitude of GCA variance was found higher in case of for PL (7.87) and PT (9.0), which was further corroborated by a predictability ratio approaching 1, representing that these two characters are governed by additive gene action (28, 29).

Pooled mean performance of pearl millet hybrids for agronomic traits

The interaction components of variation for locations \times treatments, locations \times hybrids, as well as locations \times lines \times testers were significant for most traits as observed through ANOVA. This indicates that the expression of these traits varied depending on the environment and the effect of different genetic combinations was not consistent across all locations. Box plots (Fig. 1) for DF showed that there was uniform distribution of flowering around mean at Aurangabad (ABD1) location representing no stress and proper growth as the mean coincided with median and sizes of whiskers on both sides were same and well elongated. Despite normal distribution of flowering for both Ahmednagar (ABD2) and Alwar (AWR) locations, range of data for ABD2 was narrow showing possibly early season stress followed by a sudden flowering time rise in temperature thereby narrowing the total flowering time range. Lower quartile was early by 5 days, median line was lower than the mean value point, box size was larger than other locations, with several outliers present for Jaipur location. This showed that the location was under stress. In pearl millet crop, early flowering hybrids tend to complete flowering early whereas, depending upon the stress resilience of the genotypes, the flowering time for medium and later maturity hybrids tends to get delayed even to the point of economic loss. As PH is a moderate to highly heritable trait; location box plots for PH showed that mean and median PH values for all the locations were nearly identical, with whiskers of equal length on both sides of box showing not only normal distribution of PH, but also uniform expression of trait across locations (Fig. 1). Normal distribution of data was observed for both PL and PG, where mean values nearly coincided with median except for PL at JPR (Jaipur) location. For PT both mean and median values coincided and the data was not skewed. The inter-quartile range and whiskers showed a good spread at ABD1 location, indicating good crop expression. In contrast, the narrow data range and lower mean at JPR reflected a predominance of monoculm hybrids, confirming stress conditions at this site. A few distinct outliers at JPR location for PT represented hybrids with comparatively higher average number of tillers. Genotypes bearing more tillers under stressed environments could be a good indication of their stress resilience or escape. The box plots for the blast disease severity score (BS) showed that in Zone-B (ABD1 and ABD2), the inter-quartile range was low showing good tolerance whereas in Zone-A (AWR and JPR), the inter-quartile range was more with longer whiskers showing sufficient variability in genotypes for blast tolerance. Both locations, AWR and JPR had mean values lower than the median which showed that the data was negatively skewed at these locations and there were some highly susceptible entries that pulled down the mean. For PY, hybrids performance was higher at Zone B locations (ABD1 and ABD2) than at Zone A locations (AWR and JPR). TR was higher at ABD1 and ABD2 locations compared to JPR, likely due to the stressed conditions at JPR location. A shorter inter-quartile range was observed at ABD1 and ABD2, whereas the stress-prone JPR location, showed a wider inter-quartile range with long whiskers. At all 3 locations mean values were less than median due to presence of semi compact panicles, or some low yielding and blast affected hybrids. GY values were observed to be higher at ABD1 and ABD2 compared

Table 2. Pooled analysis of variance and genetic components for line × tester over four environments during rainy season 2021

Source	F	DF	PH	F	PL	PG	F	PT	F	BS	F	PY	F	TR	F	GY	F	FY
F-Values for Type 3 test of fixed effects																		
Locations	3	699.4***	208.2***	3	262.9***	763.1***	2	302.7***	3	45.9***	3	2556.2***	2	72.8***	2	4836.7***	1	72.2***
Reps in Locs	4	7.4***	1.5	4	2.6*	6.7***	3	16.9***	4	4.6**	4	14.8***	3	27.5***	3	23.1***	2	18.4***
Treatments	203	41.3***	22.5***	205	89.5***	15.3***	205	3.6***	205	5***	204	6.2***	204	1.9***	204	4.4***	205	4.3***
Hybrids	199	41***	22.3***	201	91***	15.1***	201	3.4***	201	5***	200	5.8***	200	2***	200	4.1***	201	4.1***
Lines	100	9.4***	3.7***	100	5.2***	9.5***	100	1.9***	100	2.1***	100	1.9***	100	1.1	100	1.6**	100	1.9***
Testers	1	76.7***	46***	1	769.7***	7.7**	1	205.7***	1	44.9***	1	10.2**	1	23.4***	1	0.2	1	0.1
Line × Tester	98	7.3***	8.6***	100	13***	2.8***	100	1.4**	100	2.8***	99	3.8***	99	1.7***	99	3.2***	100	2.9***
Checks	3	34***	30.4***	3	25.5***	3.4*	3	4.6**	3	2	3	2.7*	3	1.1	3	4.2**	3	3.3*
Hybrids vs Checks	1	88.9***	33.4***	1	20.8***	101.2***	1	21.6***	1	12.6***	1	101.5***	1	0.2	1	66.8***	1	35.3***
Locs × Treatments	609	3.3***	2.5***	615	7.2***	3.5***	410	1.3**	615	2.2***	612	2.4***	408	1.7***	408	2.3***	205	1.4**
Locs × Hybrids	597	3.2***	2.5***	603	7.3***	3.5***	402	1.3**	603	2.2***	600	2.3***	400	1.7***	400	2.2***	201	1.3*
Locs × Lines	300	3.4***	1.8***	300	1.6***	1.2*	200	1.2	300	1.6***	300	1.6***	200	1	200	1.6***	100	1.5*
Locs × Testers	3	3.4*	22.1***	3	43***	0.8	2	19***	3	32.6***	3	5**	2	1.1	2	1.6	1	1.9
Locs × Line × Tester	294	1.5***	1.7***	300	4.8***	3.1***	200	1.1	300	1.5***	297	1.8***	198	1.7***	198	1.7***	100	1
Locs × Checks	9	4.3***	1.8	9	3.5***	4.4***	6	0.6	9	0.6	9	3.5***	6	1.9	6	3.9***	3	3.8**
Locs × (Hybrids vs Checks)	3	5.7***	1.9	3	2.8*	13.7***	2	1.1	3	2.1	3	9***	2	0.1	2	14.9***	1	26.7***
Covariance parameters																		
Block (Loc × Rep)	0.2***	5.89***		0.01	0.02	0	0**	0**	0**	0**	0**	0**	0**	0**	0**	0.52		0.13***
Average residual	0.82	59.59		0.78	1.51	0.01	0.01	0.06	0	13.91								0.65
Genetic components																		
CONT_LINE	84.3	71.9		37.5	89.8	38.4	59.4	64.0	46.9	61.8								65.2
CONT_TEST	6.9	9.0		55.3	0.7	41.4	12.6	3.4	10.2	0.1								0.1
CONT_LXT	8.8	19.2		7.2	9.5	20.1	28.0	32.6	43.0	38.1								34.8
VAR_GCA	0.7	35.3		11.8	0.1	0.0	0.0	0.0	0.0	0.0								0.0
VAR_SCA	0.8	67.3		1.5	0.4	0.0	0.0	0.0	0.0	6.8								0.4
Predictability ratio	0.7	0.5		0.9	0.3	0.9	0.6	0.2	0.5	0.0								0.0
CV (%)	2.0	4.0		4.2	4.7	10.7	4.6	13.9	8.6	14.7								14.2
Repeatability	0.9	0.9		0.9	0.8	0.6	0.4	0.5	0.1	0.4								0.7

Note: *, **, *** significant at 0.1, 0.01, 0.001>P levels of probability, respectively. F - Degrees of freedom; DF - Degrees of freedom; PH - panicle height (cm); PL - panicle length (cm); PG - panicle girth (mm); PT - productive tillers (count); BS - blast severity (score); PY - panicle yield plot⁻¹ (kg); TR - threshing ratio; GY - grain yield (t ha⁻¹); FY - dry fodder yield (t ha⁻¹)

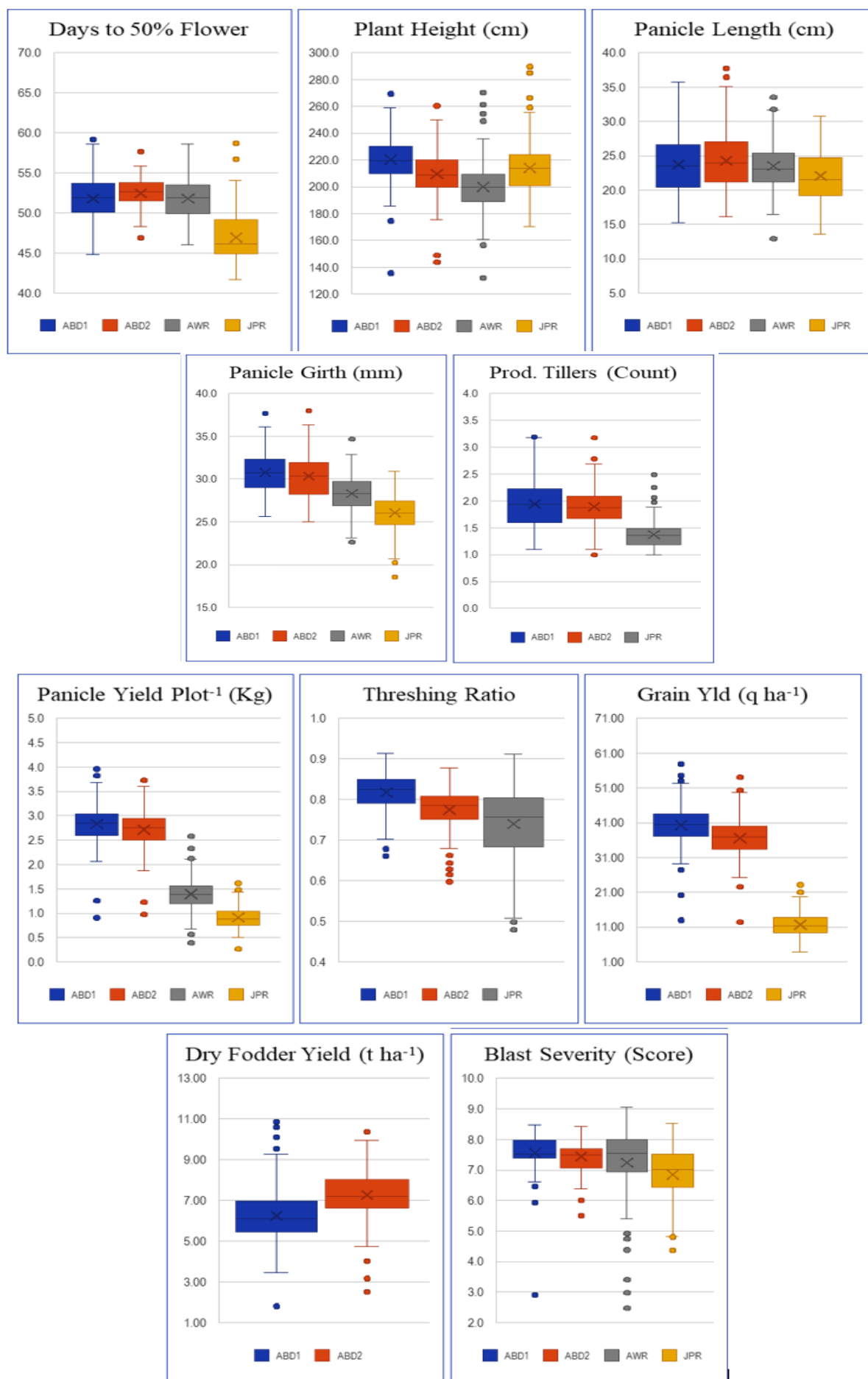


Fig. 1. Boxplot visualization of location wise mean performance of hybrids for each trait.

Note: ABD1 - Aurangabad; ABD2 - Ahmadnagar; AWR - Alwar; JPR - Jaipur

to the JPR location (Fig. 1).

Trait wise pooled mean performance (Annexure 2) of pearl millet hybrids is described below. Earliness is one of the most important advancement and commercialization traits in a crop like pearl millet, which is largely grown on rainfed soils. Early maturing hybrids ensure higher per day productivity and a shorter crop life cycle which reduces drought impact, conserves resources, enhances crop survivability and lowers the risk of crop failure. Among the studied hybrids DF ranged from 45 days (ICPH077) to 57 days (ICPH128) with a mean of 51 days and 36 % or 73 hybrids showed earlier maturity than the earliest check PRO9444 Gold (50 days). Hybrids ICPH009, ICPH018, ICPH021, ICPH023, ICPH029, ICPH031, ICPH067, ICPH083, ICPH107, ICPH131 and ICPH187 were early flowering and showed a yield advantage of 5 – 22 % over PRO9444 Gold (50 days, 32.2 q ha⁻¹). These hybrids show high per day productivity and are earlier than all commercial checks 9444 Gold (50 days), 86M88 (52 days), 86M84 (53 days) and Super Boss (55 days). PH is an important trait in dual-purpose varieties as it contributes to both grain and fodder production (5). Among the studied hybrids PH ranged from 158.4 cm (ICPH085) to 263.3 cm (ICPH007), with a mean height of 211 cm. Tall hybrid ICPH196 (235.6 cm), shows potential for multi-location testing, as it produced significantly high dry fodder yield (9.71 t ha⁻¹) than the best check Kaveri Super Boss (8.97 t ha⁻¹) while maintaining a comparable grain yield. In the hybrid population, the panicle volume traits namely PG (28.9 mm, 25.1 - 33.8 mm) and PL (23.4 cm, 14.5 - 34.0 cm), revealed a good amount of variation. Hybrids ICPH069, ICPH123, ICPH127, ICPH129 and ICPH201 exhibited long panicles (> 30 cm) whereas, 53 test hybrids had thick panicles (>30 mm). Hybrids with long and thick panicles have higher grain-bearing capacity, which directly contributes to increased GY (5, 30). The PT ranged from 1.1 to 2.4, with a mean of 1.7. PT is an environment-resilience trait enabling plant to resume post-drought yield production and indicates ability of genotype to produce multiple grain-bearing shoots, improving overall productivity (31). Among the 18 hybrids that produced greater number of PT and GY than best check PRO9444 Gold, ICPH018, ICPH021, ICPH083 and ICPH187 showed significant earliness (46 – 50 days) and could be recommended for multi-location testing in drought-prone A1-Zone.

PY measures the yield of panicles harvested from a plot, expressed in kilograms. This reflects the potential of the hybrid for grain production and can help determine the best performers in terms of raw panicle output (32). PY ranged from 0.64 kg plot⁻¹ (ICPH179) to 2.58 kg plot⁻¹ (Super Boss), with a mean of 1.96 kg plot⁻¹. Among the test entries ICPH107 (2.43 kg plot⁻¹), ICPH123 (2.43 kg plot⁻¹) and ICPH175 (2.39 kg plot⁻¹) produced high PY. TR indicates the grain density per unit area for a sample of panicles from a specific genotype and is defined by its genetic makeup, while also being influenced by biotic and abiotic stress conditions. TR ranged from 0.68 (ICPH055) to 0.88 (ICPH002), with a mean of 0.78. Threshing Ratio (TR) which also reflects panicle compactness, plays a role in reducing bird damage; notably 33 % of the test hybrids recorded TR values >0.8. Hybrids ICPH022 (88 %), ICPH172 (86 %), ICPH068 (86 %) revealed the best TR. GY ranged from 9.77 q ha⁻¹ (ICPH179) to 39.2 q ha⁻¹ (ICPH107) for test hybrids and from 32.2 q ha⁻¹

(PRO9444 Gold) to 41.1 q ha⁻¹ (86M84) for the checks, with a mean yield of 29.5 q ha⁻¹. ICPH023, ICPH107 and ICPH175 flowered significantly early and produced grain yield at par best check 86M84. In addition to grain, FY is important in regions where pearl millet is grown for livestock feed. The FY, measured in metric tons per hectare, ranged from 2.16 t ha⁻¹ to 10.02 t ha⁻¹, with a mean of 6.76 t ha⁻¹. Hybrids like ICPH121, ICPH007, ICPH196 and ICPH195 exhibited highest FY (9.45 – 10.02 t ha⁻¹) with at par or significantly superior PH than the best check Kaveri Super Boss offering an additional benefit to farmers who prefer both grain and fodder (33). Pearl millet is susceptible to blast disease caused by a fungal pathogen *Magnaporthe grisea*. The blast severity score (BS) ranged from 4.1 to 8.2, with a mean score of 7.3. Among the test entries, hybrids ICPH193, ICPH007, ICPH123 and ICPH183 showed high level of blast tolerance with a score of 8.0. Hybrids with strong disease resistance are crucial for sustainable production in areas prone to blast outbreaks (34).

Estimation of general combining ability (GCA) effects

Combining ability estimates exhibit test material specificity, as they depend on phenotypic observations of full-sibs and half-sibs from which these estimates are derived. The estimates of GCA effects of the lines (female parents) and testers (male parents) are presented in Annexure 3 and the hybrid-parents exhibiting the highest GCA effects are listed out in Table 3. Highly significant GCA estimates were observed for several inbreds across all the traits studied including DF, PH, PL, PG, PT, PY, TR, BS, GY, FY. GCA effects of lines for days to 50 % flower ranged from -4.32** to 5.41**, where negative values indicate early flowering, an important trait for developing early maturing hybrids. Among the lines, ICMB 04222 (-4.32**) ICMB 88004 (-3.48**), ICMB 10666 (-3.35**), ICMB 95111 (-3.14**) and ICMB 98333 (-3.14**) showed a highly significant negative GCA effect indicating that these lines can be used to develop early maturity hybrids and derivation of early maturity materials through pedigree breeding. Advanced B-line B200 (38.65**), ICMB 08888 (34.39**), ICMB 09333 (30.93**) and ICMB 91444 (26.76**) were identified as good combiners for PH. These lines can be effectively utilized to develop taller hybrids, which are desirable for dual-purpose, or forage breeding programs aimed at increasing biomass (35). ICMB 09333 (7.27**), B200 (6.59**), ICMB 09555 (6.03**), ICMB08888 (5.82**) and ICMB 07444 (4.53**) showed highly significant GCA estimates for PL. These lines can be used in pedigree breeding program to develop future line with long panicles thereby increasing hybrid seed production potential of seed-parents and simultaneously to develop high yielding hybrids with long panicles. Advance B-lines, B166 (4.72**), B189 (3.78**), B181 (3.71**) and ICMB 07777 (3.77**) showed highly significant positive GCA estimates for PG. ICMB 91777 (0.14**), ICMB 95222 (0.14**), ICMB 97333 (0.13**), ICMB 07111 (0.13**) and ICMB 94444 (0.12**) showed significant positive GCA effects for PT. ICMB 07777 (0.37**), B220 (0.37**) and ICMB 08888 (0.37**) were identified as good general combiners for PY and GY. ICMB 88004 (0.08**), B169 (0.07**), ICMB 02333 (0.07**) and B163 (0.06**) showed highly significant positive GCA effects for TR, and indicated a great contribution in improving panicle compactness thereby a higher GY and less bird damage (36).

Table 3. Hybrid-parents exhibiting the highest GCA effects in line × tester analysis across environments, rainy 2021

S. No	Code	Identity	Days to 50 % flower	Plant height (cm)	Panicle length (cm)	Panicle girth (mm)	Productive tillers (No)	Blast severity (Score)	Panicle yield plot ⁻¹ (kg)	Threshing ratio	Grain yield (q ha ⁻¹)	Dry fodder yield (t ha ⁻¹)
1.	B1	ICMB 88004	-3.48**	0.68	-1.69**	-1.50**	0.01	-0.03	-0.04	0.08**	0.99	-0.37
2.	B4	ICMB 91222	0.92**	18.13**	-1.84**	-1.44**	0.01	-0.03	-0.08	0.00	-1.47	1.52**
3.	B5	ICMB 91444	3.52**	26.76**	1.11**	0.76*	-0.08	0.07*	0.01	-0.03	-0.60	1.74**
4.	B7	ICMB 91777	-1.91**	1.37	-1.62**	-2.09**	0.14**	-0.01	0.14*	0.00	3.57**	0.12
5.	B15	ICMB 93222	-1.64**	15.33**	0.57*	-0.10	-0.03	-0.02	0.25**	0.02	4.73**	0.95**
6.	B19	ICMB 94444	-0.17	-6.05**	-1.39**	-1.62**	0.12**	0.02	0.23**	0.02	6.60**	1.06**
7.	B27	ICMB 96333	-2.47**	-11.90**	-0.13	-0.57	-0.01	-0.12**	0.15*	0.03	3.85**	0.41
8.	B28	ICMB 96666	-1.58**	0.13	-0.22	0.17	0.08*	0.01	0.18**	-0.02	4.26**	-0.27
9.	B88	ICMB 07666	0.16	-12.40**	0.05	1.62**	0.03	-0.03	0.26**	0.02	5.75**	0.52
10.	B89	ICMB 07777	0.19	-9.09**	1.38**	3.77**	-0.01	0.05	0.37**	-0.02	4.09**	-0.10
11.	B97	ICMB 08666	5.41**	16.02**	-2.80**	1.19**	-0.12**	0.07*	-0.04	0.00	-2.33	2.14**
12.	B99	ICMB 08888	4.36**	34.39**	5.82**	-0.22	-0.15**	0.12**	0.37**	0.00	3.51**	0.98**
13.	B103	ICMB 09333	5.36**	30.93**	7.27**	-2.59**	-0.04	0.10**	0.11	-0.02	0.50	1.12**
14.	B119	ICMB 11666	2.69**	4.05	0.60*	2.29**	0.01	-0.04	0.15*	-0.06**	2.55*	0.70*
15.	B145	Adv B-line	1.82**	25.95**	-0.18	2.19**	0.05	-0.02	0.34**	-0.01	3.48**	1.21**
16.	B155	Adv B-line	3.32**	1.63	0.94**	2.70**	0.02	0.06*	0.17*	0.02	3.13*	1.14**
17.	B169	Adv B-line	1.30**	11.82**	-0.02	0.30	-0.01	-0.06	0.26**	0.07**	6.64**	1.31**
18.	B188	Adv B-line	3.70**	24.83	0.18	1.37**	-0.03	0.10	0.28**	0.02	4.46**	2.85**

Identification of good general combiners for GY is very important to develop high yielding hybrids. Positive GCA values are highly desirable, as they reflect a genotype's ability to enhance trait value in breeding generations, contribute to effective selection through fixable gene effects and lead to increased heritability. Eighteen lines were identified as general combiners for GY. Among them an advanced B-line (B169) exhibited the highest significant positive GCA effect (6.64**) revealing its strong potential as an excellent candidate for improving GY. ICMB 91777, ICMB 93222, ICMB 96333, ICMB 96666 and ICMB 09666 were noted as best general combiners with highly significant negative GCA estimates for DF along with significant positive GCA estimates for grain yield. Lines contributing to higher FY are useful in breeding for dual-purpose hybrids important for both GY and FY. Twenty-one (9.6 %) B-lines were found to have significant positive GCA for FY. Among them B188 (2.85**) was the highest, followed by ICMB 08666 (2.14**), ICMB 91444 (1.74**) and ICMB 91222 (1.52**), making these inbreds a potential candidate for increasing fodder production in hybrids (37). Positive and significant GCA estimates were observed for blast resistance in 26 B-lines. These lines can be used in breeding programs to develop disease resistance and thereby sustainable yield delivery.

Estimation of Specific Combining Ability (SCA) effects

The estimates of SCA effects are presented in Annexure 4. Pearl millet is largely grown on marginal lands across semi-arid tropics, requiring higher per day productivity and consequently

shorter time to flowering. A negative SCA effect for DF indicates earlier flowering relative to the parental mean, making it a desirable attribute in hybrid development. 28 hybrid combinations showed significant negative SCA estimates for DF. Among these hybrids ICPH143, ICPH021, ICPH033 showed highly significant negative SCA effects with mean flowering of 46 days. A total of 26 hybrids showed significant positive SCA effects for plant height, with ICPH187 (25.81**), ICPH086 (21.46**), ICPH007 (21.08**) and ICPH121 (14.17**) showing highest and most significant positive SCA effects for PH. ICPH187 was identified as a potential candidate, showing highly significant SCA effects for both PH and GY (8.61**) (10). Positive SCA estimates for panicle volume traits, namely PL and PG, lead to an increase in panicle surface area, thereby enhancing grain bearing capacity and contributing to the development of high yielding hybrids. Forty-two hybrids and 11 hybrids showed significant positive SCA effects for PL and PG, respectively (38, 39). ICPH187 (0.19**), ICPH082 (0.16**), ICPH168 (0.13*), ICPH148 (0.12*) showed significant positive SCA effects for PT. PY is the first indication of yield estimation immediately after harvest (40) and a total of 13 hybrids showed significant positive SCA effects for this trait. Among them, ICPH180 (0.49**), ICPH187 (0.42**), ICPH128 (0.35*) and ICPH163 (0.25**) were identified as best hybrid combinations for PY. Hybrids ICPH187 (0.06*), ICPH014 (0.06*), ICPH069 (0.06*) and ICPH182 (0.06*) exhibited significant positive SCA effects for threshing ratio.

GY showed considerable variation among hybrids. Hybrids like ICPH187 (8.61**), ICPH180 (7.89**), ICPH107 (3.9*), ICPH014 (3.77*), ICPH053 (3.77*), ICPH126 (3.72*), ICPH172 (3.68*) and ICPH128 (3.66*) were identified as best hybrid combinations with significant positive SCA effects for grain yield. It is important to note that three of these hybrids ICPH107, ICPH126 and ICPH172 were also among the top 15 highest yielding hybrids. These SCA differences highlight the importance of choosing the promising parent-combinations exploiting available inbred GCA to produce hybrids for exploitation of heterosis and then test specific combinations for SCA and standard heterosis to get commercially viable combinations (41). ICPH053 (3.77, 1.15), ICPH172 (3.68, 1.22) and ICPH180 (7.89, 2.01) showed significant and positive SCA values for both GY and FY signifying importance of these combinations both for grain and dry fodder. ICPH170 showed significant positive SCA for FY (1.15*), PH (6.07*) and negative significant SCA for DF (-1.13**) (42) implying greater per day dry fodder productivity of this combination. ICPH180 (0.3**), ICPH149 (0.2**), ICPH082 (0.14**) and ICPH187 (0.12**) hybrids showed significant positive SCA effects for blast score, indicating greater tolerance of these combinations to blast in comparison to their expected tolerance levels based on their average parental performance.

Based on GY, DF, FY and other traits, 20 best hybrids were selected (Table 4). Among these ICPH021 was identified for A1 dry zone as a promising early hybrid (46 days) vs PRO9444 Gold (50 days), that showed significantly better PL (24.7 cm), PT (1.9) and GY (34.47 q ha⁻¹). ICPH023 and ICPH107 are promising options for B-zone with early flowering, good yield and less plant height. ICPH175 is an early dual-purpose hybrid identified for both A1 and A-zone with PH, GY and FY at par 86M84. ICPH196 is another dual-purpose hybrid with at par grain yield with 86M84 and significantly higher FY. Hybrids ICPH007, ICPH121, ICPH195 and ICPH196 showed FY potential ranging between 9.45 - 10.02 t ha⁻¹ which is significantly superior

to 86M84 and even Kaveri Superboss. These hybrids were identified as candidates for higher dry fodder production, total biomass, compressed biogas (CBG) and bioethanol.

Correlation between average parent-pair GCA, SCA and mean performance of hybrids was calculated to assess the extent to which combining ability influences grain yield in hybrids. A highly significant positive correlation was observed between the parent-pair GCA of selected hybrids and their mean grain yield ($r = 0.737^{***}$), as well as between SCA and mean grain yield ($r = 0.622^{**}$). When considering all test hybrids, the correlation between parent-pair GCA and grain yield remained highly significant ($r = 0.757^{***}$) and a strong positive correlation was also found between SCA and grain yield ($r = 0.616^{***}$). We have also observed highly significant positive correlation between parent-pair GCA and dry fodder weight (0.815***) as well as between SCA and dry fodder weight (0.578***) of all test hybrids. In comparison to SCA, the correlation with parent-pair GCA exhibited a higher magnitude for both grain yield and dry fodder yield, which indicates the influence of additive gene action in selection of good hybrids for these two traits. This implies that average of parental GCA effects is a stronger predictor compared to SCA (43). It also implies that selecting good GCA lines for breeding crosses and development of new lines through pedigree breeding is the most effective approach for development of inbreds in a hybrid breeding program. Further SCA can be utilized to maximise heterotic gains. Although GCA values have higher magnitude than SCA, it's noteworthy that SCA is influenced by nonallelic interactions and dominance gene action, similarly heterosis is also primarily driven by nonallelic interactions and dominance gene action. Hence, heterosis should primarily depend on the effect of SCA. Therefore, it is the strength of SCA in each hybrid which plays a critical role in defining the extent of heterosis. In the current study, both GCA as well as SCA are important predictor of heterosis and this can be exploited by developing heterotic groups in the material for GY and FY. It helps in

Table 4. Relationship among GCA, SCA and mean grain yield of top performing hybrids selected for grain yield, fodder yield and key agro-nomic traits in pearl millet

S. No	Hybrid	Identity	Female GCA	Male GCA	Avg GCA_GY	SCA_GY	Mean_GY
1	ICPH107	B88/R22	5.75**	-0.73	2.51	3.99*	39.21
2	ICPH175	B169/R22	6.64**	-0.73	2.95	2.85	38.97
3	ICPH023	B19/R22	6.6**	-0.73	2.93	1.57	37.64
4	ICPH196	B188/R13	4.46**	0.73	2.59	2.98	36.76
5	ICPH173	B166/R22	5.26**	-0.73	2.26	1.19	35.93
6	ICPH126	B100/R13	2.85*	0.73	1.79	3.72*	35.89
7	ICPH009	B7/R22	3.57**	-0.73	1.42	2.81	35.86
8	ICPH018	B15/R13	4.73**	0.73	2.73	1.75	35.79
9	ICPH029	B27/R22	3.85**	-0.73	1.56	2.34	35.67
10	ICPH202	B200/R13	2.93*	0.73	1.83	3.37	35.61
11	ICPH046	B35/R13	3.69**	0.73	2.21	2.54	35.54
12	ICPH172	B163/R13	1.97	0.73	1.35	3.68*	34.97
13	ICPH110	B89/R13	4.09**	0.73	2.41	1.27	34.67
14	ICPH031	B28/R22	4.26**	-0.73	1.76	0.74	34.48
15	ICPH021	B17/R22	2.14	-0.73	0.70	2.85	34.47
16	ICPH024	B19/R13	6.6**	0.73	3.66	-1.56	34.35
17	ICPH131	B106/R22	2.99*	-0.73	1.13	1.63	34.09
18	ICPH007	B5/R22	-0.6	-0.73	-0.66	0.5	29.37
19	ICPH084	B68/R13	1.71	0.73	1.22	-2.86	28.16
20	ICPH121	B97/R22	-2.33	-0.73	-1.53	1.96	29.11

inclusion of other breeding material, tester identification and development of target-oriented breeding populations.

Conclusion

The results of the present study exhibited significant variability among test hybrids for all the traits. ICMB 88004, ICMB 97111, ICMB 93222, ICMB 94444, advanced B-lines B166, B145, B169 and B188 were identified as good general combiners. Hybrids ICPH021, ICPH023, ICPH107, ICPH175, ICPH196, ICPH007, ICPH121, ICPH018 and ICPH083 were identified as the possible candidates for commercialization after further testing. Overall, the findings suggest that selecting superior parental combinations based on GCA and SCA effects, along with considering environmental factors, will be important for developing high-yielding, disease-resistant and widely adaptable pearl millet hybrids. This study provides valuable information for breeders, farmers and researchers working to improve pearl millet production in rainfed agricultural environments.

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Authors' contributions

GSK provided guidance for work and research materials and corresponding author. AA provided guidance related to my work at Department of Bioscience and Biotechnology, Banasthali University and corresponding author VAK & SKK conducted statistical analysis of the experiment. KVK edited the manuscript, PS written the manuscript and conducted the experiment. All authors equally provided inputs in finalising research work direction and concept of manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

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