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RESEARCH ARTICLE

Identification of promising hybrids and opportunities for rapid selection through trait association, combining ability and gene action in the pearl millet (*Pennisetum glaucum* L. R. Br) gene pool under rainfed conditions

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Abstract

The ICRISAT pearl millet B-line gene pool, crucial for Indian NARs partners and private seed companies, was assessed through 218 Line × Tester crosses using an alpha-lattice design alongside four hybrid checks. The study explored combining ability, gene action, hybrid selection and accelerated product advancement using trait associations and interdependencies. ANOVA revealed strong genotypic and location effects and genotype × environment interactions were significant. Grain yield correlated positively with plant height, panicle length, threshing ratio and days to 50 % flowering. Panicle yield per plot had a strong direct effect (0.962) on grain yield, with very high phenotypic (0.95) and genotypic (0.94) correlations. Key yield traits, including days to 50 % flowering (0.164), plant height (0.491) and panicle length (0.414), influenced grain yield indirectly through panicle yield per plot. Significant genetic variability among parental groups emphasized the role of both additive and non-additive genetic variance. Narrow-sense heritability was highest for productive tillers (84.00 %), days to 50 % flowering (65.67 %) and panicle girth (62.81 %). Inbreds ICMR 08888 (2.87), ICMB 10555 (2.81), ICMB 01666 (2.71), ICMB 08888 (2.41) and ICMB 11111 (2.16), exhibited strong positive GCA for grain yield. Hybrids ICPH213, ICPH265, ICPH273, ICPH321 and ICPH166 exhibited high SCA for grain yield and reduced days to 50 % flowering, indicating superior per-day productivity. A total of seventeen hybrids including ICPH033, ICPH189, ICPH197 and ICPH206, have been identified for large-scale evaluation based on their high yield potential and desirable market-specific traits, such as adaptation to the A1 Zone, medium maturity, dual-purpose suitability, short plant type suited for the B Zone, large panicle size and excellent fodder yield. To optimize selection efficiency, "Product Rating," a metric combining flowering duration and grain yield, is proposed for assessing broader adaptability. Additionally, prioritizing panicle yield per plot and threshing ratio over direct grain yield measurements is suggested, particularly in early-generation hybrid evaluations.

Keywords: correlation; gene action; general combining ability (GCA); Line × Tester; path-coefficient analysis; per day productivity or product rating; rapid selection; specific combining ability (SCA)

Introduction

Pearl millet (*Pennisetum glaucum* L.R. Br) is a highly adaptable, small-grained C4 cereal with exceptional photosynthetic efficiency, superior water-use capacity and remarkable resilience to climate change. As one of the most widely cultivated millet species globally, it thrives under moisture stress and salinity while producing stable yields even at temperatures exceeding 40 °C. Grown across nearly 30 million hectares in 30 countries spanning five continents, pearl millet serves multiple purposes, including staple grain production, grazing, silage, hay, green chop, bird feed, fodder and lignocellulosic feedstock for biofuel. It is particularly valuable in mixed crop-livestock farming systems. In regions where it is a dietary staple, especially in arid and semi-arid tropics, pearl millet contributes up to 35 % of daily energy, protein, iron and zinc intake, making it the most cost-effective micronutrient source for rural communities.

Its rich nutritional profile includes a broad spectrum of bioactives and antioxidants (carotenoids, anthocyanidins, flavonoids, lignans and phytoestrogens), anti-inflammatory compounds (benzoic and cinnamic acids), complex carbohydrates, dietary fibres, essential amino acids and key minerals that support nerve function and immune health (phosphorus, magnesium, iron and zinc).

Given its dense nutrient composition, pearl millet plays a crucial role in addressing "hidden hunger" and combating micronutrient malnutrition on a global scale.

India accounts for 31.5 % of the global pearl millet cultivation area and 46.7 % of total production (1). It ranks as the fourth most extensively grown cereal after rice, wheat and maize. Nearly 90 % of India's pearl millet production comes from Rajasthan, Maharashtra, Gujarat, Uttar Pradesh and Haryana. The crop is cultivated on approximately 6.703 million hectares, yielding an average production of 9.624 million tonnes with a productivity of 1436 kg/ha (2). Rajasthan leads with 3.751 million tonnes, followed by Uttar Pradesh (1.949 million tonnes), Haryana (1.12 million tonnes), Gujarat (1.056 million tonnes), Madhya Pradesh (0.869 million tonnes), Maharashtra (0.475 million tonnes), Karnataka (0.171 million tonnes) and Tamil Nadu (0.157 million tonnes), making it a key crop for these states. Recognizing its significance, the Government of India designated 2018 as the “Year of Millets,” while the FAO declared 2023 the “International Year of Millets” through the COAG forum. Given pearl millet’s adaptability, resilience and nutritional benefits, scientific research on this crop is more crucial than ever. India's pearl millet production predominantly relies on single-cross hybrids due to their heterotic advantage and cost-effectiveness in commercial deployment of cytoplasmic-genetic male sterility systems, a practice initiated in the 1960s (3). ICRISAT has played a pivotal role in developing breeding lines and hybrid parents, distributing them globally since the 1980s (4). ICRISAT-bred seed parents have significantly contributed to genetic gains in India's hybrid breeding programs. Notably, 60-70 % of the 175 hybrids notified by the Ministry of Agriculture until 2020 were derived from ICRISAT-developed A-lines or proprietary lines based on ICRISAT materials (5), underscoring their impact on product development and genetic progress.

Estimating combining ability, both general (GCA) and specific (SCA), is fundamental to hybrid breeding. However, these estimates depend not only on the chosen mating design but also on the genetic materials under evaluation. Consequently, each breeding program must periodically assess combining ability and gene effects within newly incorporated or developed breeding materials. This study, therefore, focused on deciphering combining ability and gene action in ICRISAT-bred seed-parent gene pools, given their critical role in both public and private Indian millet breeding programs.

The Line × Tester mating design (6), a modified version of the top-cross method and a refinement of NCD-II, is the most widely employed approach in both public and private pearl millet hybrid breeding programs. It serves as a fundamental tool for studying trait inheritance, genetic gain, gene action, combining ability, breeding material selection, inter-population improvement, heterotic pattern analysis and advancing parental lines or hybrids within the product development pipeline. Unlike designs limited to multi-flowered crop species, the Line × Tester method offers greater flexibility. It enables the use of multiple testers, accommodates a large set of test lines, simultaneously generates full-sibs and half-sibs and provides robust estimates of general combining ability (GCA), specific combining ability (SCA) and gene action essential for quantitative trait expression. This design facilitates the evaluation of material across two heterotic pools, enhances heterosis breeding efficiency, supports cytoplasmic-genetic male sterility (CMS) systems and balances population coverage with comprehensive genetic insights. Additionally, it streamlines hybrid selection for direct commercialization, making it an indispensable strategy in pearl millet breeding.

Grain yield, being a primary trait of interest, has long driven researchers to explore strategies for enhancing genetic gain in its selection. However, its polygenic, quantitative and complex inheritance poses significant challenges. The correlation of yield with other traits and understanding impact of environmental factors on their inheritance is important. This helps in identification of additional traits that can be co-selected with yield to accelerate genetic progress (7). The concept of linear correlation between two datasets, or the Pearson’s correlation coefficient measures the direction and strength of a linear relationship between paired variables, offering critical insights for selecting appropriate breeding methods and parental lines by identifying key component traits contributing to yield (8-10). Trait associations at both phenotypic and genotypic levels play a crucial role in breeding programs. Since heritability influences genotypic correlations, these were also analyzed as part of this study. To further dissect trait relationships and distinguish between direct and indirect effects, a path coefficient analysis was conducted, following the methodology established by Wright (11) and refined by Dewey and Lu (12), to establish cause-and-effect relationships among yield-related traits.

Considering critical role of pearl millet as a climate-resilient crop, the genotype-specific nature of combining ability estimates, the significance of both additive and non-additive gene interactions in heterosis breeding and the central contribution of ICRISAT-bred seed parents to hybrid development, this study was undertaken to evaluate combining ability and gene action within the ICRISAT-derived seed-parent gene pool using the Line × Tester design. To enhance research impact and accelerate advancements through early performance predictions based on trait interdependencies, correlation and path coefficient analyses were conducted prior to identifying promising genotypes and evaluating combining ability or gene effects. These methodologies are instrumental in establishing high-throughput, cost-efficient hybrid selection pipelines and driving progress in commercial breeding programs.

Materials and Methods

2.1. Genetic materials

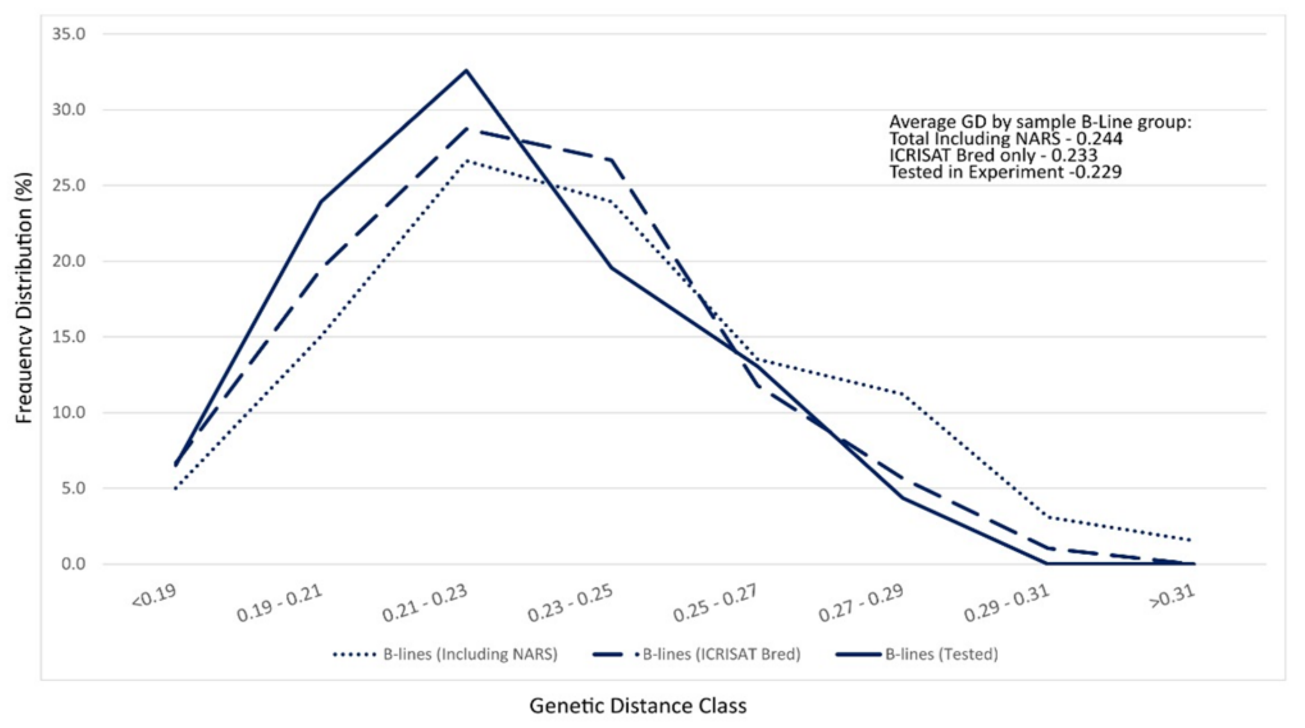
This study aimed to analyze trait correlations, combining ability and gene effects for grain yield and related traits while exploring rapid selection strategies to enhance decision-making and reduce costs, particularly in early-generation top-cross analysis. A representative set of 46 seed parents (B-lines) and five testers (R-lines) was selected from six B-line and five major R-line groups, derived from 18 groups identified through Restriction site Associated DNA - Genotyping by Sequencing (RAD-GBS) diversity analysis, which enabled genome-wide, high-resolution mapping of genetic variation for population structure assessment. These lines were exclusively chosen from the 391 ICRISAT-bred lines within a larger set of 580 lines, examined for heterotic pool formation using the high-density SNP dataset generated through RAD-GBS (4). To preserve genetic diversity within the B-line pool despite the reduced sample size, the 46 sampled B-lines were selected to represent the allelic variation present in the full breeding pool (Fig. 1). The genetic distance (GD) of the 46 selected inbred parents ranged from 0.179 to 0.299, with a mean GD of 0.229, closely approximating the mean GD of 0.233 in the original set of ICRISAT-bred female lines. The correlation coefficient between the GD frequency distributions of the original and sampled B-lines was highly significant (0.954, $p = 0.00023$). These 46 female lines were crossed using the Line × Tester mating design, with five restorer lines as testers (Annexure 1). Since some lines were designated inbreds with established A/B-pairs while others were advanced-generation B-lines without corresponding A-lines, only B-lines were used for crossing to ensure consistency in comparison.

Maintainer (B-lines/females) and restorer (R-lines/males) were planted in the crossing block, where manual bagging and pollination were performed to produce hybrid seed. Since B-lines, like male parents, produced viable pollen, the protogynous nature of pearl millet was leveraged to prevent self-pollination and ensure true hybrid formation. A staggered planting method synchronized stigma receptivity in females with pollen shedding in males, optimizing cross-pollination. The number of rows per female or male inbred was determined based on the required panicle count for crosses. To prevent open pollination, seed-parent panicles were covered with parchment paper bags at the boot-leaf stage. At full flowering, when ~95 % of florets had mature stigma, manual pollination was conducted using pollen from the target R-line in parchment paper bags, ensuring hybrid seed production. Crossing was conducted during the 2020 rainy season and the 2021 summer season. However, 12 of the 230 planned hybrid combinations could not be produced due to female to male flowering time mismatch (nicking issues), plant population constraints, or seed set failure, leaving 218 hybrids with adequate seed for hybrid yield trials. These hybrids were evaluated for combining ability, genetic effects and trait correlations, alongside four nationally notified commercial hybrids used as checks (Annexure 2).

2.2. Experiment design and field evaluation

The field trial included 218 test hybrids alongside four nationally notified commercial checks: PRO9444 Gold, Kaveri Super Boss, 86M88 and 86M84, which are used in coordinated ICAR crop improvement trials. Conducted during the 2021 rainy season from July to October under rainfed conditions, the experiment employed an alpha lattice design with two replications to replicate farmers' field environments for accurate phenotypic assessment. Plot designs were generated using GenStat, 17th edition, VSN International, UK, with unique randomizations for each trial location. To ensure uniformity, pre-measured seed amounts were packed into labelled envelopes corresponding to designated plot rows. Randomized plot numbers were assigned to each seed packet, ensuring precise field layout execution.

The trials were conducted at four locations, representing two distinct agro-climatic zones classified by the All India Coordinated Research Project on Pearl Millet under ICAR, Government of India. These zones include A-zone (Alwar and Jaipur) and B-zone (Aurangabad and Ahmadnagar), recognized as separate mega-environments (13) based on annual rainfall and pearl millet adaptation. Testing across diverse environments ensured the study captured variability affecting hybrid performance. Despite being in two mega-environments, the four locations exhibited significant variation in soil type, rainfall and temperature. The geo-environmental specifics are detailed in Table 1. Soil types and pH levels varied: sandy loam (pH 7.5) at Alwar, sandy (pH 8.3) at Jaipur, medium black (pH 7.9) at Aurangabad and deep black (pH 8.2) at Ahmadnagar.



Restrictionsite-associated DNA (RAD) sequencing, 580 inbreds (Gupta et.al.,2020) resequence data available at https://www.ncbi.nlm.nih.gov//sra/?term=SRP063925

Fig. 1. Frequency distribution (%) by class - Mean genetic distance of each pearl millet hybrid parent over all lines in the sampled B-line pool.

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 temp. range in rainy season														
				June			July			August			September			October		
				Rain (mm)	Temp °C Min	Temp °C Max	Rain (mm)	Temp °C Min	Temp °C Max	Rain (mm)	Temp °C Min	Temp °C Max	Rain (mm)	Temp °C Min	Temp °C Max	Rain (mm)	Temp °C Min	Temp °C 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

Each entry was planted in a two-row plot of 5.0 meters length with a 1.4-meter alley width. Row spacing was 45 cm, with plants spaced 15 cm apart. During the 2021 rainy season, seed sowing was carried out by dibbling on ridges at Alwar, Jaipur, Aurangabad and Ahmadnagar. The crop received a basal fertilizer dose of 65 kg DAP (18 % N, 46 % P) and a top dressing of 105 kg Urea (46 % N) per hectare, meeting the recommended 60 kg N and 30 kg P_2O_5. Only lifesaving irrigation was provided during prolonged dry spells to maintain natural rainfall conditions and ensure realistic farming representation. Overplanted plots were thinned 15 days after sowing to maintain a single plant per hill with ~15 cm spacing. Standard intercultural practices were implemented to maintain weed-free and healthy crops, including pre-emergence application of atrazine at 0.5 kg/ha, followed by hand weeding at 15 and 35 DAS. Additionally, insect pest management was carried out using a foliar spray of profenophos (0.05 %) at 20 and 40 DAS, complemented by pheromone traps (5 traps/ha) for effective pest control. Other seasonal measures were applied as needed to sustain optimal crop health.

Phenotypic data was recorded for eight yield and ancillary traits: days to 50 % flowering (days) [DF], plant height (cm) [PH], productive tillers plant^{-1} (count) [PT], panicle length (cm) [PL], panicle girth (mm) [PG], panicle yield plot^{-1} (kg) [PY], threshing ratio [TR] and grain yield (q ha^{-1}) [GY]. Observations for PL, PG and PT were based on the mean of five random plants, while DF, PH, PY, TR and GY were recorded on a per-plot basis. Data classification and the times of measurement followed Pearl Millet DUS trait guidelines (14) to facilitate interpretation and inference.

2.3. Statistical analysis

2.3.1. Analysis of variance (ANOVA)

Line × Tester analysis was conducted following Kempthorne (6) to estimate combining ability variances and effects using the formulae described by Singh and Chaudhary (15). Pooled analysis of variance across locations was performed in R Statistical Software v4.4.0, (16) using the "ASReml-R" package (v4.2.0.267, VSN International Ltd.). Location, genotypes and replication were treated as fixed effects, while blocks were considered random. Following data quality control, individual location variances were modelled using residual maximum likelihood (REML) to ensure homogeneity of error variance, utilizing available data without imputing missing plots (17).

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

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

Where μ is the grand mean; y_i is the fixed effect of location *i* ; g_l is the fixed effect of genotype *l*; $(y/r)_{ij}$ is the fixed effect of replication *j* nested within location *i*; $(y/r/b)_{ijk}$ is the random effect of block *k* nested with in replication *j* and location *i* and is ~NID(0, σ^2b); $(yg)_{il}$ is the fixed effect of the interaction between genotype *l* in location *i*; and ε_{ijkl} is the random residual effect and ~NID(0, $\sigma^2\varepsilon$).

Mean squares from pooled analysis of variance were used in the formulae to calculate combining ability variances and effects.

$$\text{COV\_HS\_LINE} = \sigma_l^2 = (MS_{LINE} - MS_{LINEXTESTER})/(Lc*R*T)$$

$$\text{COV\_HS\_TEST} = \sigma_t^2 = (MS_{TESTER} - MS_{LINEXTESTER})/(Lc*R*L)$$

$$\text{Cohrs (Average)} = \sigma_t^2 + \sigma_l^2 = \frac{1}{Lc*R(2LT-L-T)}\left[\frac{(L-1)(MS_{LINE})+(T-1)(MS_{TESTER})}{(L+T-2)} - MS_{LINEXTESTER}\right]$$

$$C1 = ((MS_{LINE}-MSE) + (MS_{TESTER}-MSE) + (MS_{LINEXTESTER}-MSE))/(3*R*Lc)$$

$$C2 = ((6*R*\text{ VAR\_GCA\_HS}) - (R*\text{ VAR\_GCA\_HS}*(L+T))/(3*R*Lc)$$

$$\text{COV\_FS}=C1+C2;$$

$$\sigma^2_{GCA} = \frac{(MS_{LINE} + MS_{TESTER} - 2*MS_{LINE*TESTER})}{Lc*R*(L+T)} = \frac{(1+F)}{4}\sigma^2_A$$

$$\sigma^2_{SCA} = \frac{(MS_{LINE} - \text{MSE})}{\text{Lc}*\text{R}} = \left(\frac{1+F}{2}\right)^2 \sigma^2_D$$

$$\text{GCA effect (lines)} = g_i = (xi/LcTR) - (x\ldots/LcLTR) \text{ and}$$

$$\text{GCA effect (testers)} = g_t = (xj/LcLR) - (x\ldots/LcLTR)$$

$$\text{SCA effect} = s_{ij} = (xij/LcR) - (xi\ldots/LcTR) - (xj/LcLR) - (x\ldots/LcLTR)$$

Where, "*i*th line", "*j*th tester" and "*ij*th cross".

$$\text{SE (gca for line)} = \sqrt{}(MSE/LcRT) \text{ and SE (gca for tester)} = \sqrt{}(MSE/LcRL)$$

$$\text{SE (sca)} = \sqrt{}(MSE/LcR)$$

$$\text{SE } (g_i\text{-}g_j) \text{ line} = \sqrt{}(2MSE/LcRT) \text{ and SE } (g_i\text{-}g_j) \text{ tester} = \sqrt{}(2MSE/LcRL)$$

$$\text{SE } (S_{ij}\text{-}S_{kl}) = \sqrt{}(2MSE/LcR)$$

Standard errors used for “*t*-test” of combining ability effects were calculated using the following formulae:

2.3.2. Correlation and path coefficient

Phenotypic and genotypic correlation coefficients were calculated following Wright (11) and Singh and Chaudhary (15). Correlation coefficients were further partitioned into direct and indirect effects using path coefficient analysis (11, 12, 15). Data analysis was conducted in R Statistical Software v4.4.0 (16), using the “Path. Analysis” package v0.1 (18), and “GGally” v2.2.1, (19). Schematic representation of direct and indirect effects in path coefficient analysis was created using MS Excel®. Correlation and path coefficient analysis were performed for three locations, as threshing percentage and grain yield data were unavailable for one location. The formulae used are detailed below:

Phenotypic covariance $COV_{pi.j} = COV_{gi.j} + COV_{ei.j}$

Genotypic covariance $COV_{gi.j} = (GMP - EMP)/R$

Environmental covariance $COV_{ei.j} = EMP$

Where, MP: environmental mean product; GMP: genotypic mean product; “*i*” and “*j*” are the two variables.

Genotypic correlation coefficient =

$$r_{gi.j} = \left((COV_{gi.j})/\sqrt{(\sigma_{gi}^2)(\sigma_{gj}^2)}\right)\ x\ 100$$

Phenotypic correlation coefficient =

$$r_{pi.j} = \left((COV_{pi.j})/\sqrt{(\sigma_{pi}^2)(\sigma_{pj}^2)}\right)\ x\ 100$$

Where, $r_{gi.j}$ and $r_{pi.j}$ are “genotypic” and “phenotypic” correlation between characters “*i*” and “*j*”. $COV_{gi,j}$and COV_{pij} are the genotypic and phenotypic covariance between characters “*i*” and “*j*”.σ^2_{gi}or σ^2_{pj} Are the examples of Genotypic variance of character “*i*” or Phenotypic variance of character “*j*” respectively. The significance of the phenotypic and genotypic coefficient were tested by using *t*-test as per the formula given in Singh and Chaudhary (15).

To decipher the comparative importance of direct and indirect effects of the different component traits and thereby establish a cause-and-effect relationship. Simple process of conducting path co-efficient analysis expressed in terms of correlation coefficients (*r*) using Wright’s path analysis equations are given below.

The “direct effect” of an independent variable X_i on Y is :

$$P_{X_iY} = r_{X_iY} - \sum P_{X_jY} * r_{ij}$$

Where, P_{xjY} = Path-coefficients of other “*j*” variables that also influence *Y* (yield),

r_{XiY} = Correlation coefficient between independent variable X_i and dependent variable *Y*

r_{ij}= Correlation coefficient between independent variable X_i and other “*j*” variables

The “indirect effect” of X_i on *Y* through an intermediate variable X_j = $P_{X_iX_j} * P_{X_jY}$

Where,

$$P_{X_iX_j} = \left(r_{X_iX_j} - \sum P_{X_kX_j} * r_{ik}\right)/\left(1 - \sum P_{X_kX_j} * r_{kj}\right)$$

and P_{xjY} can be calculated using direct effect formula.

So, the total effect of X_i on Y = $P_{X_iY} + \sum(Indirect\ Effects)$

The unexplained variance in *Y* is captured by the residual effect

$$= Re = \sqrt{1 - \sum P_{X_iY} * r_{X_iY}}$$

The test of significance for direct effects was calculated as per Wright (10, 11) and Sobel test is used for calculation of test of significance for indirect effects or mediation (20).

2.3.3. Product rating

The critical role of per-day productivity in pearl millet improvement has been well acknowledged (21-23). However, this study uniquely attempts to prescribe a method for quantifying it, providing a new perspective on productivity evaluation. To measure per day productivity of pearl millet hybrids and promote products that require comparatively less time to deliver a given level of grain yield, we propose a product rating index based on DF and GY. This formula has been in use by a few private seed companies for the purpose of identification of products with higher per day productivity because such products are expected to deliver stable performance and wider adaptability. Despite different units of measurement for GY and DF, this index incorporates both, by using a unit free calculation procedure as per given formula:

Product Rating Index =

(% Mean Yield) - (% Mean Days to 50% Flower)

$$= ((GYi/\overline{GY})x100) - ((DFi/\overline{DF})x100)$$

Where, “*i*” is the *i*th entry mean for yield or flowering, $\overline{DF}$ and $\overline{GY}$ are the experiment means for GY and DF, respectively.

The sensitivity index of the proposed formula was calculated and tested across the full range of input values to identify nonlinearities or threshold effects critical for accurate interpretation. Descriptive statistics (mean, standard deviation and range) for Grain Yield (GY) and Days to 50 % Flowering (DF) were used, with standard deviations normalized as a percentage of the mean to account for differences in trait heritability. Monte Carlo simulations generated 10000 data points within a ±2SD range and the simulated ranges were divided into five equal intervals. Scatterplots were used to analyze product rating index (PRI) against simulated GY at each DF interval and vice versa. Correlation coefficients (*r*) were calculated and their significance tested using a *t*-test.

We propose to use a similar formula for per day productivity measurement for dry or green fodder for dry forage yield.

Results and Discussion

3.1. Genetic variability

The ANOVA was conducted for yield and ancillary traits, including DF, PH, PL, PG, PT, PY, TR and GY (Table 2). This analysis dissects the sources of variation in the Line × Tester experiment across four diverse environments, providing insights into the genetic architecture of these traits. It highlights the contributions of additive and non-additive genetic variance and assesses trait stability across environments, aiding in parental and hybrid selection. Significant mean square values for grain yield and other traits indicate distinctness of trait expression among evaluated hybrids, thereby indicating substantial diversity among respective parental lines, validating the feasibility of combining ability analysis and further genetic studies (24).

The mean trait values ranged from 3 to 15 times higher than their respective LSDs for instance DF (range = 45.8 - 57.5 days; LSD = 1.12) or GY (range = 14.2 - 41.4 q ha^{-1}; LSD = 4.69) highlighting substantial genetic variation. Differences between the lowest and highest values were: 11.7 days for DF, 112 cm for PH, 12.4 mm for PG, 16.3 cm for PL, 1.3 for PT, 1.6 kg for PY, 18 % (0.18) for TR and 27.25 q ha^{-1} for GY (Table 3). These variations underscore the genetic diversity in the study material, supporting the selection of superior parental lines and hybrids for breeding advancements.

Locations significantly contributed to total variation which is evident through highly significant trait mean squares (MS) of all traits for instance DF (3503.2***), PY (307.23***) and GY (80006.96***). This could be primarily due to environmental differences between Zone A and Zone B and varying rainfall regimes, despite uniform agronomic practices. The significance of "Location.Rep" and "Location.Rep.Block" for most traits indicates substantial micro-environmental variations within sites, typical in rainfed conditions. This reinforces the appropriateness of the alpha-lattice design over RCBD, effectively accounting for environmental heterogeneity across and within locations. Significant interactions between locations and treatments (Locs × Treatments), hybrids (Locs × Hybrids) and lines/testers (Locs × Lines/Testers) indicate environmental influence on trait expression. Non-elite or early-stage breeding materials as well as germplasm collections may encounter inconsistencies in trait expression across diverse regions. Likewise, geo-adapted geography specific materials such as landraces may perform variably when introduced into new agro-climatic zones, reinforcing the importance of wide-area testing in breeding pipelines aimed at wide adaptability. ICRISAT-bred materials, developed under an Afro-Asian adaptability mandate, are organized into regionally targeted adaptation nurseries. This contrasts with the narrower genetic base of India adapted commercial breeding programs and may partly explain the pronounced genotype × environment (G × E) interactions observed. AMMI and GGE biplot models can be implied for identifying the most suitable genotypes for specific agro-climatic zones, as well as determining the optimal environments for genotype performance evaluation. Experimental hybrids exhibited broader variations than standard checks indicated by higher and significant MS values, primarily for PL (67.78***), PG (44.89***), PT (0.35***), PY (0.48***) and GY (95.7***). The "hybrid *vs.* checks" contrast was significant for DF, PG, PT, PY and GY, indicating substantial phenotypic deviations both superior and

Table 2. Pooled analysis of variance for Line × Tester over four environments during rainy season 2021

Source	DF	Days to 50 % Flower	DF	Plant Height (cm)	DF	Panicle Length (cm)	DF	Panicle Girth (mm)	DF	Productive Tillers (Count)	DF	Panicle Yield Plot^{-1} (kg)	DF	Threshing (%)	DF	Grain Yield (q ha^{-1})
Locations	3	3503.21***	3	24750.29***	3	674.27***	3	1458.33***	2	42.01***	3	307.23***	2	0.256***	2	80006.96***
Reps in Locs	4	34.27***	4	881.86***	4	28.36***	4	45.48***	3	1.29***	4	0.24**	3	0.005	3	11.91
Block (Loc × Rep)	104	3.45***	104	202.35***	104	1.41	104	14.20***	78	0.16*	104	0.18***	78	0.006***	78	45.77***
Treatments	221	41.13***	221	1623.41***	221	67.05***	221	44.65***	221	0.35***	221	0.50***	221	0.008***	221	95.32***
Hybrids	217	41.06***	217	1605.99***	217	67.78***	217	44.89***	217	0.35***	217	0.48***	217	0.008***	217	95.70***
Lines	45	128.31***	45	4087.18***	45	151.96***	45	109.29***	45	0.70***	45	0.83***	45	0.008	45	161.90***
Testers	4	568.96***	4	17794.26***	4	1739.93***	4	953.36***	4	5.74***	4	5.60***	4	0.054***	4	950.64***
Line × Tester	168	5.00***	168	556.35***	168	5.42***	168	6.01***	168	0.13	168	0.26***	168	0.007***	168	56.79***
Checks	3	53.92***	3	3392.89***	3	36.68***	3	31.95***	3	0.31*	3	0.17	3	0.009	3	17.26
Hybrids vs. Checks	1	17.58***	1	94.77	1	0.18	1	30.10**	1	0.85**	1	5.15***	1	0.049***	1	246.44***
Locs × Treatments	662	3.35***	662	211.49***	663	2.98***	663	5.69***	442	0.16***	662	0.19***	442	0.005***	442	46.99***
Locs × Hybrids	650	3.36***	650	211.79***	651	2.97***	651	5.68***	434	0.16***	650	0.19***	434	0.005***	434	47.58***
Locs × Lines	135	5.60***	135	370.39***	135	4.05***	135	9.28***	90	0.21***	135	0.29***	90	0.005*	90	63.91***
Locs × Testers	12	46.61***	12	1172.61***	12	11.69***	12	6.74**	8	0.94***	12	0.85***	8	0.020***	8	179.32***
Locs × Line × Tester	503	1.76***	503	144.46***	504	2.47***	504	4.69***	336	0.12	503	0.15***	336	0.005**	336	40.39***
Locs × Checks	9	0.75	9	127.01	9	3.33**	9	7.58**	6	0.07	9	0.17*	6	0.002	6	15.36
Locs × (Hybrids vs Checks)	3	8.85***	3	401.48**	3	5.04**	3	3.59	2	0.22	3	0.11	2	0.000	2	13.86
Average Residual	758	1.30	663	67.76	780	1.23	779	2.63	585	0.11	710	0.07	536	0.004	512	17.12
CV		2.19		3.76		4.51		5.42		20.37		13.18		7.876		14.10

Note: *, **, *** @ 0.05, 0.01, 0.001 levels of significance, respectively.

Table 3. Pooled mean performance and "product-rating" of selected and trait range identifier pearl millet hybrids evaluated during rainy 2021

S. No.	Variety	Cross	Product Rating	GY % of Exp. Mean	DF % of Exp. Mean	DF**	GY	PH	PG	PL	PT	PY	TR
1	ICPH342	B188/R25	36.8	144.8	108.0	56.2***	41.44***	245.5**	30.2	26.1	1.40	2.70	0.80***
2	ICPH344	B188/R48	28.0	132.0	103.9	54.1	37.78*	239.1	33.9**	24.8*	1.40	2.49	0.82***
3	ICPH307	B126/R25	25.3	128.5	103.2	53.7	36.79	221.2*	31.9	28.9***	1.40	2.47	0.79***
4	ICPH296	B115/R25	23.8	128.3	104.5	54.4	36.74	224.9	28.3***	29.1***	1.90***	2.37	0.81***
5	ICPH265	B92/R48	33.4	127.0	93.6	48.7***	36.35	221.6	29.8	25.5	1.50	2.39	0.80***
6	ICPH286	B107/R25	17.2	125.0	107.8	56.1**	35.78	240.7	24.6***	27.4**	2.20***	2.28	0.80***
7	ICPH277	B99/R25	17.3	124.7	107.4	55.9**	35.69	254.4***	27.8***	31.9***	1.30	2.33	0.77**
8	ICPH189	B184/R22	31.2	122.9	91.6	47.7***	35.17	199.2***	26.6***	24.3**	1.80**	2.20**	0.84***
9	ICPH254	B87/R25	26.2	121.8	95.7	49.8***	34.88	212.0***	27.8***	24.8*	1.60	2.29	0.84***
10	ICPH239	B54/R25	20.4	121.6	101.2	52.7*	34.82	236.3	24.0***	24.1***	1.70**	2.41	0.74
11	ICPH093	B75/R22	22.6	120.7	98.2	51.1***	34.56	214.6***	31.0	24.2***	1.60*	2.29	0.77**
12	ICPH215	B29/R25	20.9	120.4	99.5	51.8***	34.46	223.1	25.5***	25.5	1.60	2.27	0.80***
13	ICPH321	B152/R25	16.1	120.4	104.3	54.3	34.46	227.9	25.7***	27.1	1.50	2.41	0.80***
14	ICPH327	B166/R25	14.3	120.0	105.7	55.0	34.34	239.6	29.9	26.2	1.40	2.45	0.74
15	ICPH206	B12/R25	18.3	119.2	100.9	52.5**	34.12	225.2	28.0***	26.9	1.80**	2.11**	0.82***
16	ICPH332	B180/R48	16.7	117.5	100.9	52.5**	33.65	233.5	32.3	23.6***	1.70*	2.01***	0.84***
17	ICPH273	B96/R48	22.1	117.0	94.9	49.4***	33.50	227.7	32.9*	24.6**	1.40	2.18**	0.78**
18	ICPH293	B111/R25	15.1	116.4	101.2	52.7**	33.32	227.8	25.8***	27.6**	2.00***	2.20**	0.83***
19	ICPH295	B111/R48	20.2	116.3	96.1	50.0***	33.29	218.0**	29.0**	23.7***	1.60*	2.06***	0.82***
20	ICPH324	B153/R25	10.9	115.6	104.7	54.5	33.09	231.3	25.8***	27.5**	1.50	2.15**	0.78**
21	ICPH335	B182/R48	14.6	112.2	97.6	50.8***	32.12	227.4	30.3	24.2***	1.70**	2.24*	0.76*
22	ICPH033	B29/R22	16.7	104.7	88.0	45.8***	29.97	203.2***	27.3***	24.7*	1.60*	2.08***	0.79**
	Mean					52.1	28.63	218.9	29.9	24.6	1.63	1.99	0.77
	Min					45.8	14.2	149	24.0	17.4	1.1	1.10	0.67
	Max					57.5	41.4	261	36.4	33.7	2.4	2.70	0.85
	LSD					1.12	4.69	8.08	1.59	1.09	0.38	0.26	0.069

*Test of significance vs most relevant check 86M84 @ level of significance 0.05, 0.01 and 0.001.

**DF: Days to 50 % Flower; GY: Grain Yield (q ha^{-1}); PH: Plant Height (cm); PG: Panicle Girth (mm); PL: Panicle Length (cm); PT: Productive Tillers (count); PY: Panicle Yield (kg ha^{-1}); TR: Threshing Ratio.

inferior from commercial checks. Trait interdependencies should be leveraged as a co-selection tool for identification of promising hybrid-parent combinations with greater efficiency, thereby increasing genetic gain and cost efficiency.

3.2. Inter-trait dependencies - opportunity for rapid advancement and productivity improvement

Trait correlation studies have long been a fundamental approach in selecting effective breeding methodologies for improving complex quantitative traits like GY. Numerous studies highlight their role in co-selection strategies to enhance genetic gain in pearl millet and other crops (7). By leveraging trait interrelationships, breeders can refine selection criteria, improve genetic efficiency and accelerate the development of superior hybrids with optimized agronomic traits. Strong correlations often suggest co-localized quantitative trait loci (QTLs) (25), such as the QTL linking ear length and flowering time in pearl millet. Physiological mechanisms like improved light interception and photosynthetic efficiency may also explain positive correlations between yield, plant height and the number of leaves per plant (7). Given their importance in GY determination, these traits dependencies can be leveraged as:

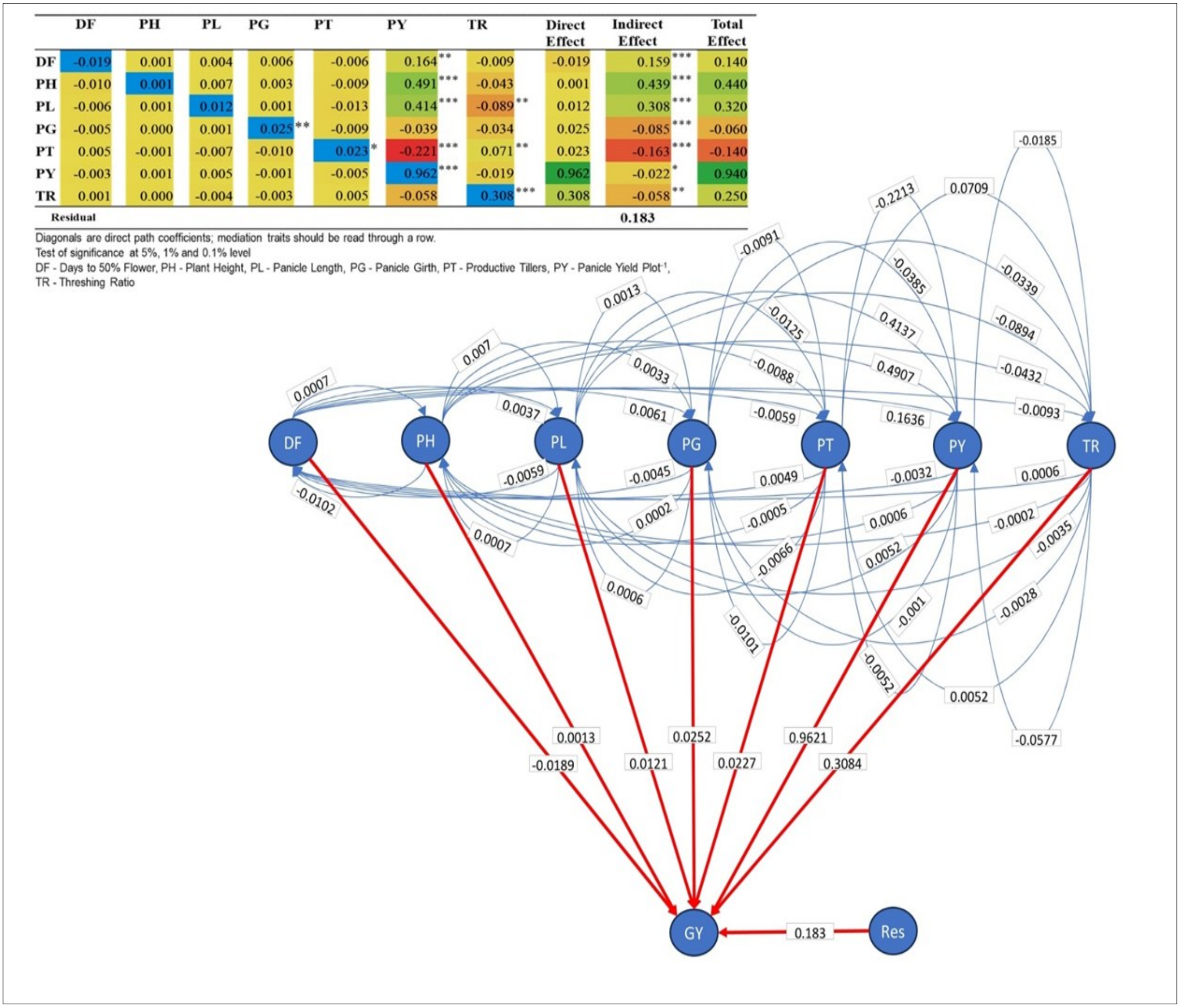
- a preliminary selection tool for early-stage screening,
- a rapid advancement strategy reducing the need for immediate yield validation,
- cost-effective, time-saving approach for early-generation selection in large populations and
- a simultaneous performance validation mechanism to enhance yield predictability before large-scale testing and commercialization.

Phenotypic and genotypic correlation coefficients were calculated (11, 15, 26) and are presented in Fig. 2. To further understand cause-and-effect relationships, the direct and indirect effects of ancillary traits on GY were assessed using path coefficient analysis (15), with significance test conducted as outlined in the methodology and results illustrated in Fig. 3.

DF showed significant positive phenotypic and genotypic correlations with PH (0.54, 0.54), PL (0.31, 0.31) and PG (0.22, 0.24), while exhibiting a significant negative correlation with the number of PT (-0.25, -0.26). The delayed flowering observed in tall genotypes is likely due to resource competition required for vertical growth. Taller plants may need additional nodes and greater biomass accumulation before transitioning to the reproductive phase, regulated hormonally, particularly through gibberellins, which may prioritize vegetative growth over early flowering. In environments where an extended growing season benefits yield potential; genetic and adaptive factors may drive selection for delayed flowering. This correlation between DF, PH and GY has been widely reported in multiple crops, indicating potential genetic linkage or pleiotropic control mechanisms (27).

Early maturing genotypes tend to exhibit higher tillering ability, likely because they transition to the reproductive phase at a shorter plant height without allocating excessive resources to main stem elongation. This enables more efficient use of light, nutrients and developmental time for tiller growth by flowering. The genetic adaptation to rainfed environments, where early flowering helps escape terminal drought stress and high tillering compensates for a shorter growing season, reinforces the observed negative correlation between DF and PT (28, 29). To utilize this correlation for yield improvement, selection strategies should prioritize tall genotypes with shorter

Fig. 2. Genotypic and phenotypic trait correlations in 222 pearl millet hybrids produced in a 46 × 5 Line × Tester and evaluated during rainy 2021at 4 locations under rainfed conditions. *Phenotypic correlations are in (). Test of significance "*t*-test" at 0.05, 0.01 and 0.001 level of significance.



	DF	PH	PL	PG	PT	PY	TR	Direct Effect	Indirect Effect	Total Effect
DF	-0.019	0.001	0.004	0.006	-0.006	0.164**	-0.009	-0.019	0.159***	0.140
PH	-0.010	0.001	0.007	0.003	-0.009	0.491***	-0.043	0.001	0.439***	0.440
PL	-0.006	0.001	0.012	0.001	-0.013	0.414***	-0.089**	0.012	0.308***	0.320
PG	-0.005	0.000	0.001	0.025**	-0.009	-0.039	-0.034	0.025	-0.085***	-0.060
PT	0.005	-0.001	-0.007	-0.010	0.023*	-0.221***	0.071**	0.023	-0.163***	-0.140
PY	-0.003	0.001	0.005	-0.001	-0.005	0.962***	-0.019	0.962	-0.022*	0.940
TR	0.001	0.000	-0.004	-0.003	0.005	-0.058	0.308***	0.308	-0.058**	0.250
Residual									0.183	

Diagonals are direct path coefficients; mediation traits should be read through a row.
Test of significance at 5%, 1% and 0.1% level
DF - Days to 50% Flower, PH - Plant Height, PL - Panicle Length, PG - Panicle Girth, PT - Productive Tillers, PY - Panicle Yield Plot^{-1},
TR - Threshing Ratio

Fig. 3. Direct and indirect trait association effects on grain yield (GY) at genotypic level at ICRISAT B-line pearl millet gene pool.

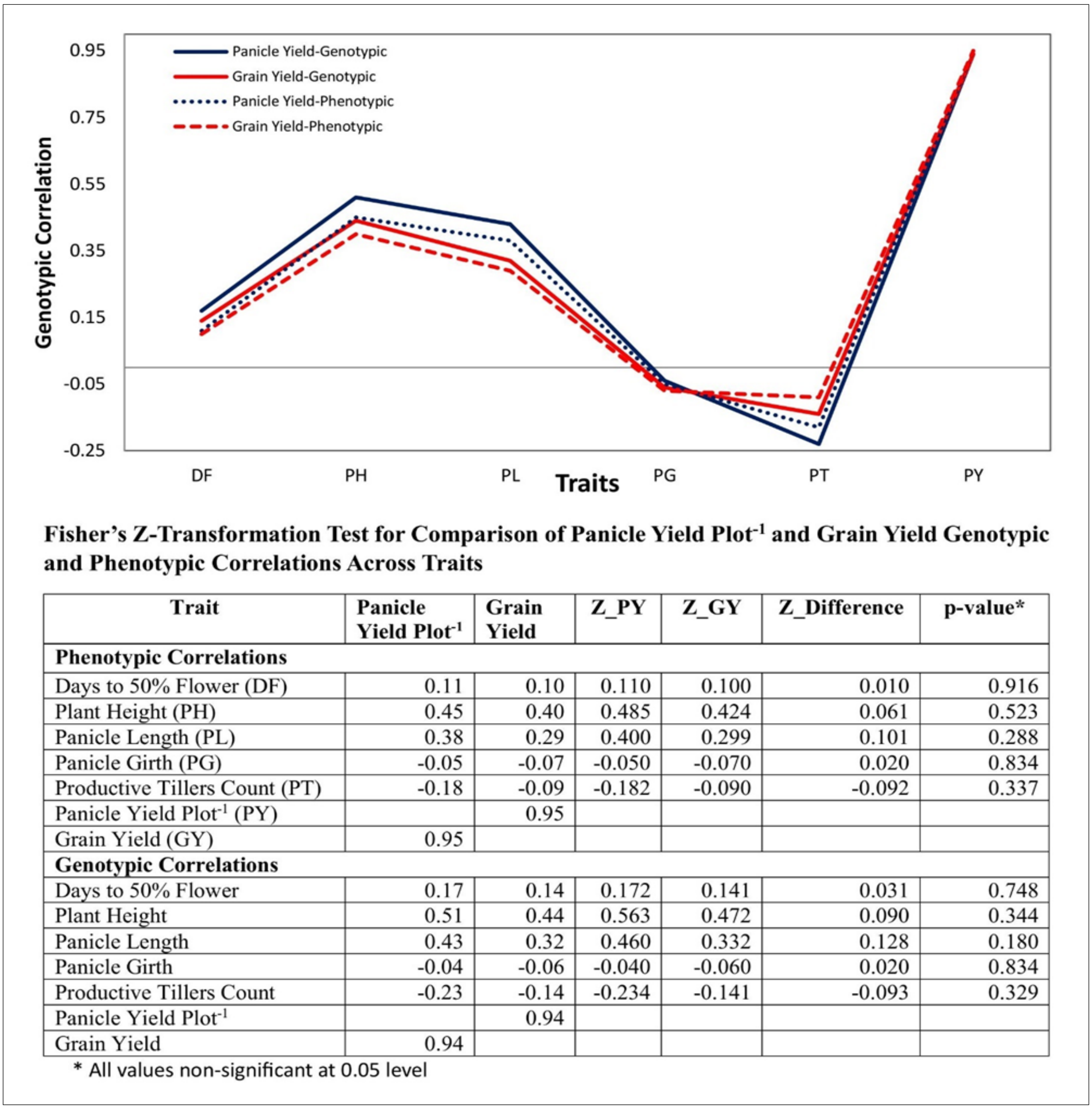
flowering durations and emphasize per-day productivity as a key criterion. Additionally, breeding programs may benefit from selecting late flowering plants with enhanced tillering ability to improve yield stability under diverse environmental conditions.

GY exhibited a significant positive correlation with PH at both phenotypic (0.40) and genotypic (0.44) levels, likely due to an increased photosynthetic area and greater resource accumulation before flowering, which facilitates enhanced biomass partitioning and grain filling (30, 31). This relationship was further supported by a strong positive total indirect effect (0.439) of PH on GY, emphasizing its contribution through intermediary physiological and morphological traits. Additionally, GY showed a significant positive correlation with PL at the phenotypic (0.29) and genotypic (0.32) levels, with a significant total indirect effect (0.308) mediated through other traits. PG also exerted a direct positive effect (0.025) on GY, highlighting the role of panicle morphology in determining sink strength and grain production capacity. While PL contributes positively to yield, its effect may be limited by panicle compactness and grain set efficiency.

TR (or threshing percentage), an indicator of panicle compactness in the absence of abiotic and biotic stresses, exhibited a highly significant positive correlation with grain yield at both phenotypic (0.27) and genotypic (0.25) levels. This suggests that denser, well-packed panicles are more efficient in grain production and yield realization. However, TR also contributed a significant negative indirect effect via PL (-0.089), indicating that as panicles become longer, they tend to lose compactness. This highlights the need for a balanced selection approach in breeding programs. Breeding efforts aimed at optimizing panicle architecture should consider both length and compactness to maximize grain yield improvements. While selecting for longer panicles to enhance grain yield, it is essential to concurrently select for a higher threshing ratio to maintain compactness. Excessively long panicles may suffer reduced compactness, leading to inefficient grain filling and increased vulnerability to panicle breakage, bird picking and shattering. Therefore, an optimized balance between panicle length and compactness can maximize sink strength and grain retention, improving yield potential and harvest efficiency.

Although DF did not exhibit a significant phenotypic correlation with GY, the genotypic correlation (0.14) was positive and significant (7), along with a significant positive indirect effect (0.159) mediated through various other traits (Fig. 3). This suggests that while flowering time may not have a direct impact on GY at the phenotypic level, its genetic influence operates through its effects on other yield-contributing traits. Late-maturing genotypes typically attain greater PH, allowing for a prolonged vegetative phase, enhanced photosynthetic efficiency and increased assimilate accumulation. This is corroborated by the significant positive indirect effects, which contribute to higher yield potential. However, the overall magnitude of this correlation remained low, likely due to the simultaneous selection pressures in breeding programs that aim to improve yield while maintaining early flowering for broader adaptability. In rainfed ecologies, where terminal drought stress is a major limiting factor, early flowering genotypes often exhibit superior yield performance compared to late-flowering ones (29, 30). This dual selection pressure favouring high-yielding lines while ensuring early flowering dilutes the overall association between flowering time and GY, making strategic selection crucial for optimizing performance across diverse environments.

Since GY is derived from PY by excluding non-grain components, a strong correlation between the two is expected. However, grain yield is also influenced by threshability, panicle architecture and grain filling efficiency, which become crucial under biotic and abiotic stress conditions. Despite these factors, our study found an exceptionally strong phenotypic (0.95) and genotypic (0.94) correlation between PY and GY under rainfed conditions. Furthermore, PY per plot exhibited the highest direct effect (0.962) on GY, establishing it as the primary determinant of productivity. Key yield-related traits, including DF (0.164), PH (0.491) and PL (0.414), had significant positive indirect effects on grain yield through PY. This suggests that increases in these traits contribute synergistically to GY, reinforcing the importance of PY as a selection criterion in pearl millet breeding. Additionally, PY and GY exhibited nearly identical correlation trends with all investigated traits. Fisher's Z-transformation test (32) and graphical representation of correlation coefficients (Fig. 4) confirmed that their differences were statistically insignificant (*p*-values: 0.288-0.916 for phenotypic and 0.180-0.834 for genotypic correlations), validating the interchangeable use of PY as a key predictor of GY.



Fisher's Z-Transformation Test for Comparison of Panicle Yield Plot^{-1} and Grain Yield Genotypic and Phenotypic Correlations Across Traits

Trait	Panicle Yield Plot^{-1}	Grain Yield	Z_PY	Z_GY	Z_Difference	p-value*
Phenotypic Correlations						
Days to 50% Flower (DF)	0.11	0.10	0.110	0.100	0.010	0.916
Plant Height (PH)	0.45	0.40	0.485	0.424	0.061	0.523
Panicle Length (PL)	0.38	0.29	0.400	0.299	0.101	0.288
Panicle Girth (PG)	-0.05	-0.07	-0.050	-0.070	0.020	0.834
Productive Tillers Count (PT)	-0.18	-0.09	-0.182	-0.090	-0.092	0.337
Panicle Yield Plot^{-1} (PY)		0.95				
Grain Yield (GY)	0.95					
Genotypic Correlations						
Days to 50% Flower	0.17	0.14	0.172	0.141	0.031	0.748
Plant Height	0.51	0.44	0.563	0.472	0.090	0.344
Panicle Length	0.43	0.32	0.460	0.332	0.128	0.180
Panicle Girth	-0.04	-0.06	-0.040	-0.060	0.020	0.834
Productive Tillers Count	-0.23	-0.14	-0.234	-0.141	-0.093	0.329
Panicle Yield Plot^{-1}		0.94				
Grain Yield	0.94					

* All values non-significant at 0.05 level

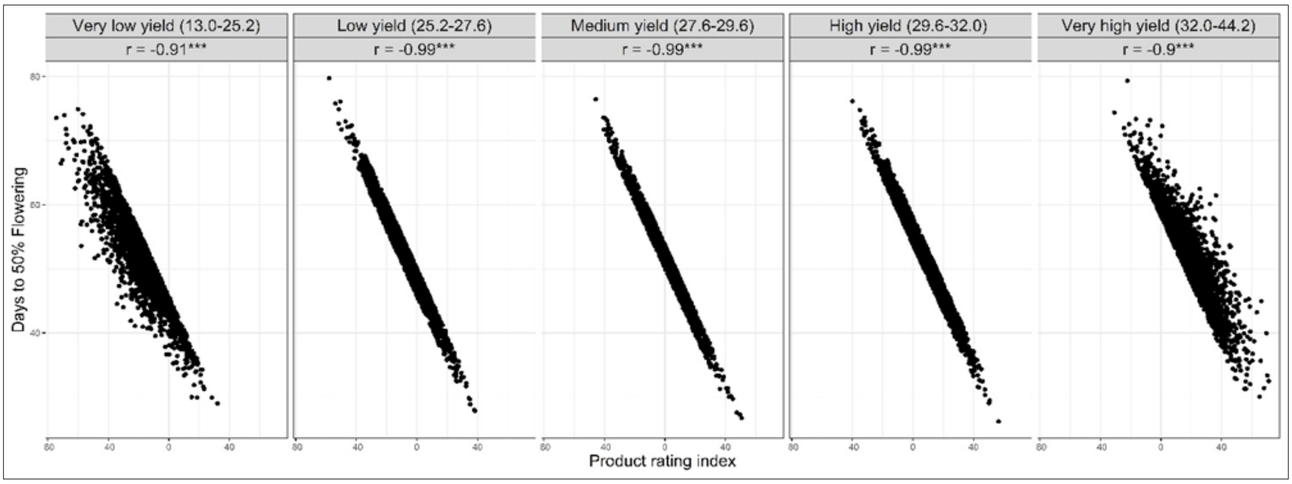
Fig. 4. Comparison of Panicle Yield plot^{-1} (PY) and Grain Yield (GY) genotypic and phenotypic correlations across traits in 222 pearl millet hybrids evaluated during 2021.

These findings have strong implications for optimizing breeding efficiency. The near-perfect correlation between PY and GY suggests that selective data recording can streamline the breeding process, reducing time and resource investments. In early-generation general combining ability (GCA) testing and advancement trials conducted under optimal conditions, breeders can prioritize key traits-DF, PH, PL and PT-alongside PY while omitting direct GY measurements. Further precision can be achieved by incorporating the TR, which showed a significant positive correlation with GY and exerted a strong direct effect (0.308) (Fig. 3), reinforcing its utility in yield estimation. This approach aligns with multiple studies supporting panicle yield as a proxy for GY in pearl millet breeding (29, 33). By leveraging PY as a primary selection criterion and using TR as a correction factor, breeders can enhance selection efficiency, accelerate hybrid development and improve genetic gain in pearl millet breeding programs.

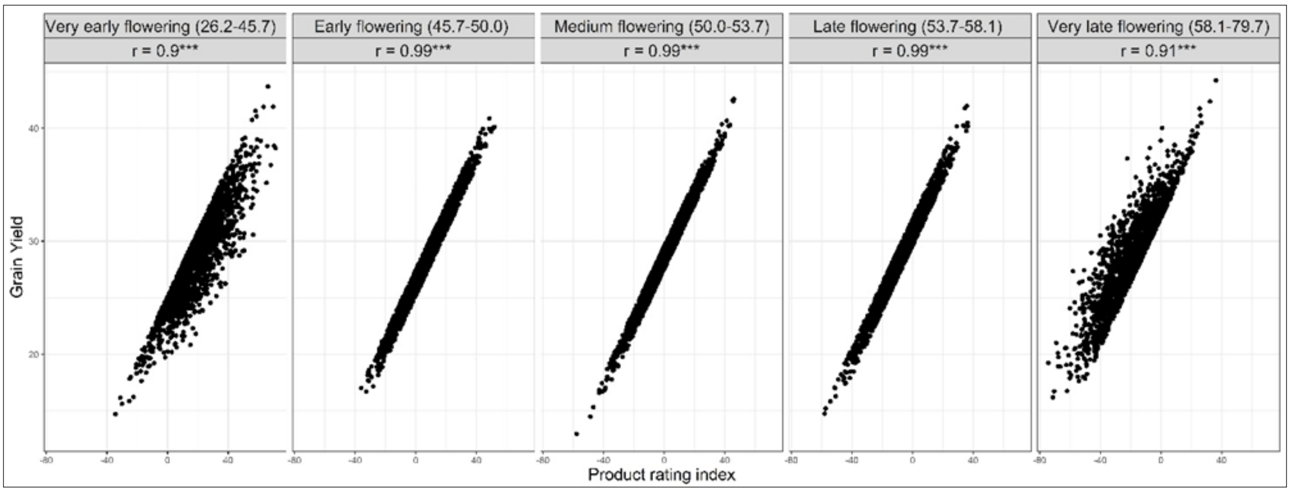
Apart from the previously discussed traits, PH exhibited a significant positive phenotypic and genotypic correlation with PL (0.58 each) but a significant negative correlation with TR (-0.14 each) and PT (-0.38, -0.39). The relationship between PH and both PL and PT has been elaborated earlier. Several studies (34) have attributed the negative correlation between PH and TR to factors such as increased non-grain biomass, stronger grain attachment, panicle compactness, delayed maturity, or harder glumes in late-maturing crops. In this study, rainfed conditions may have further influenced TR, as supported by its significant negative correlation with PL (-0.30, -0.29) and its highly significant positive correlation with PT (0.25, 0.23). Late-maturing genotypes generally produce longer panicles, whereas high-tillering genotypes tend to mature early. The latter benefit under rainfed conditions, where early flowering enhances yield potential before terminal drought stress sets in. This analysis suggests that incorporating threshing ratio as a selection criterion could enhance selection efficiency, making it more representative of the selection environment compared to PL, PG or PT. Additionally, for breeding dual-purpose cultivars, selecting genotypes with a higher TR alongside taller PH would be advantageous.

3.3. Product rating index (PRI)

Per day productivity (PDP) refers to the yield-whether biomass, fruit, or grain-produced per unit area per day by a crop. Biologically, it serves as a key survival and climate-resilience-readiness trait. Genotypes that achieve higher yields in shorter durations often perform better under biotic and abiotic stresses, such as drought, by escaping adverse conditions. For this reason, this trait is particularly valuable in crops like pearl millet, traditionally grown under rainfed conditions and is well recognized in breeding programs (21-23). However, the absolute value of PDP (expressed as yield per unit time) is not easily comparable across breeding programs targeting different maturity durations (early, medium, or late), or across diverse environments, locations and seasons. To address this



DF vs PRI at respective grain yield levels



GY vs PRI at respective flowering levels

Fig. 5. Sensitivity analysis of product rating index (PRI) to Days to 50 % Flowering and Grain Yield using Monte Carlo Simulation (i = 10000).

limitation, the Productivity Rate Index (PRI) was developed. PRI normalizes PDP by referencing it to the experiment mean, making it a unit-free metric suitable for cross-program and cross-season comparisons. PRI values for selected hybrids are presented in Table 3 and the full dataset is available in Annexure 3. PRI, calculated using 10000 data points generated through Monte Carlo simulations for sensitivity index evaluation, showed strong and highly significant correlations with both grain yield (GY: 0.7036***) and days to flowering (DF: -0.7064***). The similar magnitude of these coefficients indicates that GY and DF exert a comparable influence on PRI. Minor non-linear deviations were observed at the extreme ends of both traits, as shown in Fig. 5. These findings highlight PRI's robustness and relevance, especially under climate change scenarios. Further research could enhance its application in breeding for resilience and productivity.

3.4. Mean performance and identification of promising hybrids

Pearl millet is vital for marginal and rainfed lands, where enhancing per-day productivity is crucial. Thus, breeding programs must prioritize earliness alongside grain yield. To accelerate advancement and improve productivity in dual-purpose pearl millet trials the following key strategies are recommended based on discussed inter-trait dependencies and PRI:

- PY and TR as selection criteria - Prioritize PY and TR to identify high-yielding genotypes, enables elimination of plot-level threshing and yield measurements. This approach significantly reduces cost and time in hybrid advancement decisions.
- Optimize flowering time relative to plant architecture - Always select for higher value of PRI. Select hybrids with shorter days to flowering (DF) for a given plant height (PH) or panicle length (PL) and ensure that TR is comparable to or exceeds checks, especially in long-panicle or tall hybrids.
- Favor higher tillering in late-maturity hybrids - enhances overall yield potential and stress adaptability.
- Target short-statured hybrids - amenable to mechanized harvesting, offer improved lodging tolerance and suitable for markets in Zone-B where pearl millet fodder is not required.
- Emphasize TR in high head-volume selections - ensure TR remains a key criterion to maintain grain recovery efficiency while selecting for high head-volume.

The pooled mean performance of selected pearl millet hybrids, based on rapid selection and productivity improvement criteria, along with range identifier entries, is summarized in Table 3, while complete trial results are provided in Annexure 3. The tested hybrids displayed significant variation in flowering time, ranging from 45.8 days in ICPH033 to 57.5 days in ICPH339, with a pooled mean of 52.1 days (Table 3). ICPH033 was classified as early-maturing (43-46 days), while 53 test hybrids and the check PRO9444 Gold fell into the medium-maturity category (47-50 days) (14). In contrast, 45 hybrids and two checks, Kaveri Super Boss and 86M84, flowered beyond 54 days and were classified as very late-maturing. Among these, ICPH277, ICPH296, ICPH321, ICPH324, ICPH327, ICPH342 and ICPH344 stood out as promising candidates for assured irrigation areas due to their superior GY potential (33.09-41.44 q ha^{-1}), higher PT (1.3-1.9) and favourable performance for PL, PH and TR. The wide variation in flowering time among hybrids highlights the need for environment-specific selection. Early flowering is crucial for maintaining productivity under terminal water stress, enabling plants to complete reproduction before moisture depletion-a well-documented advantage in drought-prone environments (13). Conversely, late-maturing hybrids benefit from extended vegetative growth, leading to greater biomass accumulation and higher yield potential under favourable moisture and nutrient conditions. These findings emphasize the importance of selecting hybrids based on agro-ecological conditions to optimize productivity in pearl millet breeding programs.

Plant height in pearl millet is influenced by planting time, precipitation, soil fertility, moisture stress and the genotype's inherent growth potential. Among the tested hybrids, PH ranged from 148.5 cm to 260.8 cm, with a pooled mean of 218.9 cm (Table 3). Based on DUS classification (14), ICPH214 was the only short hybrid (101 to 150 cm), while four hybrids, ICPH232, ICPH123, ICPH277 and ICPH278, were categorized as very tall (greater than 250 cm). Notably, many of the tallest hybrids were derived from ICMB 08888 (B99), emphasizing its genetic influence on plant stature. It is noteworthy that a few such hybrids surpassed the check hybrid 86M84 in height while maintaining superior or comparable grain yields, making them strong candidates for dual-purpose cultivation or biofuel production. Conversely, ICPH190, a shorter hybrid at 176.4 cm with early-maturity and grain yield comparable to 86M84, presents an option for mechanized harvesting. While tall hybrids offer advantages in fodder yield and biomass production, particularly if lodging resistant, shorter hybrids are better suited for mechanical management and efficient harvesting (35).

PL, a key determinant of panicle volume and grain yield potential, ranged from 17.4 cm (ICPH048) to 33.7 cm (ICPH300), with a mean of 24.6 cm and an LSD of 1.09 cm. Panicle thickness ranged from 24.0 mm (ICPH239) to 36.4 mm (ICPH340), averaging 29.9 mm and LSD of 1.59 mm. Based on DUS classification, 16 hybrids had small panicles (11-20 cm), while only six hybrids had long panicles (31-40 cm). Most hybrids, along with the check varieties, had medium-sized panicles (21-30 cm). Notably, eight hybrids-ICPH099, ICPH263, ICPH277, ICPH286, ICPH293, ICPH296, ICPH307 and ICPH324-exhibited significantly greater PL than 86M84 and outperformed it in GY. Longer panicles provide more space for grain development, directly enhancing yield potential.

Among the tested entries, 105 hybrids and three of the four check varieties (49 % of the total) had thick panicles (>30 mm). Panicle thickness in check varieties ranged from 28.3 mm in PRO9444 Gold to 32.0 mm in Kaveri Super Boss. Several hybrids, including ICPH344, ICPH328, ICPH273, ICPH318 and ICPH332, exhibited PG between 32.0 and 33.9 mm, combined with high grain yields of 32.9 to 37.78 q ha^{-1}, indicating their potential for enhanced seed set and grain production. Additionally, hybrids ICPH041, ICPH244, ICPH281, ICPH303, ICPH147, ICPH307, ICPH308, ICPH339 and ICPH197 displayed both greater panicle length and girth compared to 86M84, with comparable grain yields. These "high head volume hybrids" demonstrated impressive panicle traits and superior grain yield potential, making them strong candidates for multi-location testing to identify regionally adapted hybrids. Breeding programs focused on developing novel plant types suitable for mechanized harvesting have emphasized improving panicle volume, leading to the selection of lines with long, thick panicles and bold seed sizes to enhance yield potential and adaptability to modern farming practices (31, 34).

Tillering is a crucial adaptation trait that enhances grain and fodder yields, especially in drought-prone regions. The check varieties had productive tiller counts of 1.2 to 1.7, while test hybrids ranged from 1.1 to 2.4, showing 3.5 times the LSD (0.38) variation. ICPH148 and ICPH048 recorded the highest tiller counts (2.4 and 2.3, respectively). Sixteen medium-maturity hybrids matched or exceeded PRO9444 Gold in tillering and achieved grain yields comparable to or higher than 86M84. Notably, nine hybrids-ICPH217, ICPH220, ICPH241, ICPH113, ICPH261, ICPH298, ICPH187, ICPH189 and ICPH200-had tiller counts of 1.8-2.1 (*vs.* 1.7 in PRO9444 Gold) and yields of 28.39-35.17 q ha^{-1} (*vs.* 28.15 q ha^{-1} in PRO9444 Gold). These hybrids offer strong potential for drought-prone regions where high tillering enhances yield (36).

In India, pearl millet is harvested using two primary methods: (1) cutting entire plants, drying them in the field and later shearing panicles, preferred in regions where fodder is valued and (2) shearing panicles first, followed by chopping stalks later. Since PY is the first step in grain production, it serves as a key indicator of hybrid performance (33). This study confirms a strong correlation (0.94) and a significant direct effect (0.962) of PY on final GY. PY ranged from 1.1 kg (ICPH188) to 2.70 kg (ICPH342), with a mean difference exceeding six times the LSD (0.26 kg) value. Notably, 20 hybrids performed on par with commercial hybrids 86M88 and 86M84, with ICPH093, ICPH099, ICPH215, ICPH239, ICPH254, ICPH265 and the check 86M88 flowering earlier yet yielding more than 86M84. Additionally, these hybrids exhibited high per-day productivity and superior TR, suggesting broader adaptation potential. Meanwhile, later-maturing hybrids ICPH277, ICPH286 and ICPH342, with taller plant heights and superior product ratings, show promise as dual-purpose candidates for large-scale testing. The importance of per-day productivity in advancing pearl millet hybrids is well established (21, 22, 37, 38).

The TR, indicating the proportion of grain to panicle weight, reflects panicle compactness and grain-bearing capacity under optimal conditions. Influencing factors include panicle size, compactness, shape (conical *vs.* blunt), grain development under stress and susceptibility to rust, blast, or green ear. Pooled mean values ranged from 0.67 (86M84) to 0.85 (ICPH203, ICPH269), averaging 0.77 (Table 3). A total of 165 test hybrids showed significantly higher TR than 86M84, while 72 hybrids matched or exceeded its GY with superior threshing efficiency. Among them, ICPH286 and ICPH342 (very late-maturing), nine late-, 11 medium- and one early maturing hybrid (ICPH033), outperformed 86M84 in both product rating and TR. While threshing efficiency can be affected by machine speed, moisture content and post-harvest losses, this study used controlled conditions with properly dried panicle samples threshed using Wintersteiger LD180 research threshers, ensuring minimal losses. Efficient threshing is key to reducing post-harvest losses and maximizing grain recovery.

GY exhibited substantial variability, ranging from 14.19 q ha^{-1} (ICPH214) to 41.44 q ha^{-1} (ICPH342), with mean value of 28.63 q ha^{-1} and LSD of 4.69, which clearly highlights significant genetic variability and selection potential (36, 39). Several medium-maturity hybrids (ICPH254, ICPH265, ICPH273, ICPH295, ICPH189) flowered earlier (47-50 days) yet outperformed the later-maturing check 86M84 (32.81 q ha^{-1}, 54.3 days) with yields of 33.29-36.35 q ha^{-1}, making them ideal for rainfed regions. Additionally, ICPH206, ICPH239, ICPH293, ICPH332 and ICPH335 stood out as dual-purpose hybrids, combining grain yields comparable to 86M84 with higher PT (1.7-2.0) and earlier flowering (50.8-52.7 days). Notably, 43 hybrids had superior product ratings to Kaveri Super Boss and significantly higher TR than 86M84 while maintaining comparable GY, warranting further multi-location testing.

Wide-area testing is essential for selecting hybrids suited to specific agronomic goals, market needs, adaptation, grain yield, disease resistance and fodder production. Promising hybrids for targeted geographies in A1, A and B-zones (13) include:

- ICPH033 - for A1-zone, early-maturity
- ICPH273 - medium-maturity, all-India adaptation
- ICPH189 and ICPH197 - short-statured, grain-type for B-zone
- ICPH342, ICPH286 and ICPH277 - dual-purpose, grain and fodder
- ICPH344 - high head volume, dual-purpose
- ICPH342 and ICPH277 - tall, high-fodder-value for Madhya Pradesh and South Rajasthan
- ICPH278 - late-maturing, high-biomass for forage, fodder, or biogas production

3.5. Gene action, degree of dominance, heritability and contribution to the total variance

Partitioning total hybrid variance into “Lines”, “Testers” and “Line × Tester” interactions (Table 2) revealed significant genetic variability, confirming both additive and non-additive genetic influences on key traits. Significant variation in DF, PH, panicle traits (both PL and PG), PY and GY highlights the necessity of integrating heterosis breeding with *perse* line selection for optimal genetic gain. For PT, significant “line” and “tester” variances but a non-significant interaction indicates predominant additive gene action, favouring selective breeding of high-tillering parental lines. Line × Tester analysis showed GCA variance exceeding SCA variance for DF, PL, PG and PT, with high GCA/SCA ratios (3.64-8.81) (Table 4), supporting improvement through recurrent selection and pure -line breeding. Conversely, grain yield and threshing percentage exhibited lower GCA/SCA ratios (0.49 and 0.30), suggesting hybrid breeding as the optimal strategy (39, 40). While these trends were generally consistent across locations, some exceptions were observed: SCA variance exceeded GCA for PT at the Jaipur location, likely due to moisture stress, whereas GCA variance was higher for threshing ratio (TR) at Aurangabad, which experienced the most favourable weather conditions among the four test sites during the crop season.

Table 4. Estimates of genetic components as measured in Line × Tester evaluated over four environments during Rainy season - 2021

Variable	DF*	PH	PG	PL	PT	PY	TR	GY
$\sigma^2_{gca\,lines}$ [GCA variance - Lines]	3.08	88.27	2.58	3.66	0.02	0.01	0.00	3.50
$\sigma^2_{gca\,testers}$ [GCA variance - Testers]	1.53	46.84	2.57	4.71	0.02	0.01	0.00	3.24
σ^2_{gca} [GCA variance]	1.68	50.90	2.58	4.61	0.02	0.01	0.00	3.26
σ^2_{sca} [SCA variance]	0.46	61.07	0.42	0.52	0.00	0.02	0.00	6.61
$\sigma^2_{gca}/\sigma^2_{sca}$ [GCA/SCA Ratio]	3.64	0.83	6.09	8.81	8.48	0.60	0.30	0.49
σ^2_A [Additive Genetic Variance]	3.37	101.81	5.15	9.22	0.04	0.03	0.00	6.53
σ^2_D [Dominance Genetic Variance]	0.46	61.07	0.42	0.52	0.00	0.02	0.00	6.61
σ^2_D / σ^2_A [Dominance var/Additive var Ratio]	0.37	0.77	0.29	0.24	0.24	0.91	1.29	1.01
h^2_{ns} [Narrow sense heritability]	65.67	44.14	62.81	84.00	26.07	23.38	7.03	21.58
Contribution of Lines	64.81	52.78	50.49	46.49	41.69	35.62	21.58	35.08
Contribution of Testers	25.54	20.42	39.15	47.32	30.27	21.31	12.40	18.31
Contribution of Line × Tester	9.43	26.82	10.36	6.19	28.05	42.06	66.37	45.94

* DF: Days To 50 % Flower; GY: Grain Yield (Q Ha^{-1}); PH: Plant Height (Cm); PG: Panicle Girth (Mm); PL: Panicle Length (Cm); PT: Productive Tillers (Count); PY: Panicle Yield (Kg Ha^{-1}); TR: Threshing Ratio.

The degree of dominance was lowest for PG (0.29) and PL (0.24), emphasizing additive genetic effects, while GY (1.01) and TR (1.29) showed higher dominance variance, reinforcing ($\sqrt{\sigma^2_D/\sigma^2_A}$) the need for heterosis exploitation. Narrow-sense heritability (h^2_ns) was highest for PT (84.00 %), indicating strong additive control and high selection potential. High heritability was also observed for DF (65.67 %) and PG (62.81 %), suggesting stability across environments. In contrast, GY (21.58 %) exhibited low heritability, reflecting strong environmental influence, necessitating multi-location trials for reliable selection. Similarly, productive tillers count, panicle yield per plot and threshing ratio require extensive testing due to high environmental dependence.

Female parent lines explained a larger proportion of variance, particularly DF (64.81 %), PH (52.78 %), PG (50.49 %) and PT (41.69 %), indicating a strong maternal influence. However, Line × Tester interaction was dominant for TR (66.37 %), GY (45.94 %) and PY (42.06 %), reinforcing the necessity of multi-environment evaluations to capture genotype-by-environment interactions effectively. These findings suggest that traits like DF, PG and PL can be improved through direct selection, while GY and TR, which are governed by non-additive gene action, require hybrid breeding to exploit heterosis. Leveraging trait interdependencies will enhance genetic gain in product advancements. Hybrids with high GCA effects for early flowering, productive tillers and yield stability should be prioritized, while the significant Line × Tester interactions for TR and GY highlight the need for multi-location testing to identify stable and high-performing hybrids.

3.6. General combining ability effects

The General Combining Ability (GCA) effects reflect additive genetic variance and selection efficiency, which are crucial for parent selection and breeding progress. A preponderance of additive genetic variance suggests that improvement is feasible and fixable through pedigree breeding, ensuring trait stability in subsequent generations. Negative and significant GCA effects for DF were observed for 17 designated female parents, five advanced B lines and two designated male testers, indicating their suitability for breeding early maturing inbreds and hybrids (Table 5). The most notable among them were ICMB 97111 (-3.12), ICMB 07555 (-2.97), ICMB 07999 (-2.66) and ICMB 92777 (-2.41). Notably, ICMB 97111 and ICMB 98555, which exhibited significant negative GCA for DF and PH, hold promise for developing short-statured grain hybrids suited for B zone. Conversely, lines such as ICMB 10333 (4.13), B187 (3.55), B188 (3.02), ICMB 08666 (2.84) and ICMB 08888 (2.57) exhibited strong positive GCA for DF, making them suitable for environments requiring delayed maturity (39, 41). These lines also showed significant positive GCA for PH, suggesting their potential for breeding dual-purpose hybrids. They could be used with early-maturing male inbreds for grain hybrids or late-flowering males for forage hybrids (Table 5).

Among the lines contributing to shorter hybrids, B184 demonstrated the highest negative and significant GCA (-23.9 cm), potentially enhancing lodging tolerance, followed by ICMB 07666 (-15.8), ICMR 07555 (-12.7) and ICMB 08444 (-11.9). In contrast, ICMB 08888 (32.94) and ICMB 10333 (17.50) exhibited large positive GCA effects for PH, highlighting their utility in enhancing biomass yield or production of forage hybrids (42).

Table 5. GCA Effects studied through 218 hybrids based on ICRISAT B-Line gene pool - Rainy 2021

Ent	Code	Identity	DF*	PH	PL	PG	PT	PY	TR	GY
1	B8	ICMB 92111	-1.68**	-8.22**	-0.63**	-2.96**	0.10**	-0.27**	0.00	-3.59**
2	B12	ICMB 92777	-2.41**	-7.51**	-0.38*	-1.43**	0.06**	-0.12**	-0.01	-1.35
3	B15	ICMB 93222	-0.94**	6.40**	-0.97**	-1.32**	-0.01	-0.18**	0.00	-2.14**
4	B16	ICMB 93333	1.32**	-9.50**	-1.82**	-0.07	-0.04	-0.34**	-0.02	-7.95**
5	B29	ICMB 97111	-3.12**	-11.00**	-1.57**	-2.42**	0.04	0.01	0.01	0.47
6	B30	ICMB 97222	-1.36**	-6.06**	-2.45**	-0.03	0.07**	-0.20**	0.01	-3.36**
7	B33	ICMB 98222	-0.15	7.76**	-1.21**	2.22**	-0.11**	-0.03	-0.01	-0.44
8	B36	ICMB 98555	-2.16**	-11.00**	-2.72**	-1.18**	0.11**	-0.15**	0.02	-2.09**
9	B44	ICMB 99666	-0.59**	-6.77**	-0.74**	0.97**	-0.06*	-0.04	0.03**	1.25
10	B48	ICMB 00444	-1.80**	-3.92**	-1.41**	-0.29	0.05*	-0.06	0.00	-1.00
11	B49	ICMB 00555	1.99**	6.99**	1.28**	1.06**	-0.07**	-0.03	-0.02	-1.32
12	B54	ICMB 01666	-0.22	-0.73	-2.80**	-2.29**	0.08**	0.16**	-0.01	2.71**
13	B55	ICMB 01888	1.15**	6.98**	2.27**	-0.08	-0.01	0.12**	0.01	0.98
14	B57	ICMB 02333	-1.53**	-5.73**	-0.86**	1.77**	-0.04	-0.07	0.01	-0.95
15	B75	ICMB 05666	-0.46**	-7.60**	-2.39**	1.13**	0.02	0.03	0.00	0.61
16	B82	ICMB 06777	-0.17	-1.98	0.98**	-0.66*	-0.02	0.12**	-0.04**	-0.28
17	B87	ICMB 07555	-2.97**	-10.40**	-1.78**	-0.50	0.03	-0.01	0.00	0.06
18	B88	ICMB 07666	-0.92**	-15.80**	-1.13**	-0.24	-0.02	-0.03	0.00	-0.22
19	B91	ICMB 07999	-2.66**	-7.81**	-1.22**	-2.27**	0.06*	0.00	0.00	-0.03
20	B92	ICMB 08111	-0.35*	2.01	1.20**	-0.20	-0.05*	0.07	0.01	1.63*
21	B95	ICMB 08444	-1.06**	-11.90**	0.29	1.36**	-0.03	0.00	-0.03**	-1.27
22	B96	ICMB 08555	-0.03	-0.13	-0.12	1.22**	-0.06*	0.05	0.02	0.94
23	B97	ICMB 08666	2.84**	4.38**	-2.46**	1.03**	0.01	-0.03	0.04**	1.04
24	B99	ICMB 08888	2.57**	32.94**	5.42**	-0.47	-0.13**	0.24**	-0.02*	2.41**
25	B101	ICMB 09111	1.05**	1.40	2.26**	3.49**	-0.14**	0.00	0.00	0.16
26	B107	ICMB 09888	2.15**	13.14**	1.36**	-2.94**	0.09**	0.03	0.01	0.99
27	B110	ICMB 10333	4.13**	17.50**	4.53**	1.00**	-0.09**	-0.06	-0.02*	-2.73**
28	B111	ICMB 10555	-1.24**	3.46**	1.16**	-1.86**	0.05*	0.12**	0.01	2.81**
29	B115	ICMB 11111	-0.30	-1.98	2.02**	-0.91**	0.06*	0.11**	0.01	2.16**
30	B118	ICMB 11555	1.41**	8.04**	6.22**	0.51	-0.02	0.19**	-0.05**	-4.14**
31	B120	ICMB 11888	-2.47**	-2.37	-1.18**	-0.97**	0.00	-0.28**	-0.02	-3.63**
32	B126	Adv B line	-0.29	-0.18	1.60**	3.13**	-0.02	0.20**	0.01	3.44**
33	B129	Adv B line	1.98**	6.75**	-0.30	0.70**	0.02	0.03	0.00	-0.41
34	B141	Adv B line	-1.37**	5.57**	-2.03**	-1.96**	0.04	-0.06	0.00	-0.50
35	B145	Adv B line	1.76**	18.51**	1.50**	1.42**	-0.09**	0.14**	0.01	1.89*
36	B150	Adv B line	-1.02**	-9.98**	-2.10**	-0.82**	0.11**	-0.09*	0.02	-1.20
37	B152	Adv B line	1.43**	4.73**	0.50**	-1.38**	-0.01	0.08	0.00	-0.52
38	B153	Adv B line	0.88**	4.95**	0.23	-1.15**	-0.02	0.12**	-0.01	1.53*
39	B166	Adv B line	1.83**	7.85**	-0.13	2.17**	-0.02	0.28**	0.01	4.33**
40	B180	Adv B line	1.86**	6.76**	-1.20**	0.57*	0.02	0.06	0.01	1.61*
41	B182	Adv B line	-0.89**	-4.39**	-0.26	-0.84**	0.03	-0.05	0.00	-0.17
42	B184	Adv B line	-2.90**	-23.90**	-1.97**	-2.17**	0.08**	0.03	0.01	1.50
43	B187	Adv B line	3.55**	2.95*	1.00**	4.08**	0.00	-0.22**	0.03*	-1.70*
44	B188	Adv B line	3.02**	20.38**	0.21	1.63**	-0.04	0.34**	0.02	6.62**
45	B189	Adv B line	2.36**	-8.77**	0.98**	2.37**	-0.01	0.11**	-0.02*	0.39
46	B192	Adv B line	-1.83**	-9.01**	1.17**	-0.20	-0.01	0.10*	-0.01	1.70*
47	R13	ICMR 07555	0.40**	-12.70**	-3.74**	-0.61**	0.10**	-0.21**	0.02**	-1.99**
48	R22	ICMR 08555	-1.41**	-1.48**	1.95**	-0.93**	-0.02*	0.01	-0.01	-0.03
49	R25	ICMR 08888	1.62**	9.76**	2.06**	-1.95**	-0.03**	0.16**	0.01	2.87**
50	R34	ICMR 09888	0.42**	3.47**	0.07	2.14**	-0.04**	-0.01	-0.02**	-1.57**
51	R48	ICMR 11555	-1.43**	-1.69**	-0.69**	1.13**	-0.01	0.03*	0.01	0.47

*DF: Days to 50 % Flower; GY: Grain Yield (q ha^{-1}); PH: Plant Height (cm); PG: Panicle Girth (mm); PL: Panicle Length (cm); PT: Productive Tillers (count); PY: Panicle Yield (kg ha^{-1}); TR: Threshing Ratio.

Panicle length and girth, identified as predominantly additive traits in this study, can be effectively improved through pedigree breeding using parents with positive significant GCA. ICMB 11555 (6.22), ICMB 08888 (5.42), ICMB 10333 (4.53), ICMB 01888 (2.27) and ICMB 09111 (2.26) exhibited the strongest positive effects on PL (41). Similarly, B187 (4.08 mm), ICMB 09111 (3.49 mm) and 19 other inbreds, including testers ICMR 09888 and ICMR 11555, recorded positive GCA for PG. Higher grain yield through high head-volume traits also depend on panicle compactness. Seventeen inbreds, including testers ICMR 08888 and ICMR 11555, showed positive significant GCA for either panicle length or girth, along with positive GCA for TR, a key co-selection trait identified for higher selection gains.

Tillering ability is crucial for rainfed environments with lower effective plant populations, while compact, longer panicles are preferred in high-management ecologies. ICMB 98555 (0.11), ICMB 92111 (0.10) and ICMR 07555 (0.10) exhibited positive GCA effects for tillering, making them ideal for low-input conditions (39, 41). Inbreds like ICMB 09888, ICMB 10555 and ICMB 11111, which showed positive significant GCA for both PT and PL, are valuable across diverse ecological settings. PY demonstrated a strong non-additive genetic component in this study, yet 15 inbreds, including ICMB 01666 (0.16 kg), ICMB 01888, ICMB 06777, ICMB 10555 (0.12 kg), ICMB 08888 (0.24 kg) and testers ICMR 08888 and ICMR 11555, exhibited significant positive GCA for this trait. These lines offer direct potential in breeding for enhanced GY through the fixation of GCA effects. Additionally, ICMB 99666, ICMB 08666, B187 and tester ICMR 07555, with positive significant GCA effects for TR, can be strategically combined with high GCA lines for PL and GY, as supported by trait association studies.

Key inbreds such as ICMR 08888 (2.87), ICMB 10555 (2.81), ICMB 01666 (2.71), ICMB 08888 (2.41) and ICMB 11111 (2.16) exhibited strong positive GCA for GY. Advanced B-line progenies B188 (6.62), B166 (4.33) and B126 (3.44) surpassed designated inbreds in GCA estimates, reinforcing their yield potential in breeding programs. Since newly developed inbreds should outperform previous generations, these high-GCA lines can serve as testers and inbred parents for pyramiding yield genes and optimizing heterosis.

Certain inbreds, such as ICMB 10555, ICMB 08111 and B192, exhibited negative GCA for DF alongside significant positive GCA for GY, making them ideal for achieving high per day productivity. Conversely, ICMB 08888, ICMB 09888, B145 and B188, with significant positive GCA for PH and DF, could be instrumental in developing forage-type hybrids or high-biomass products. The multi-trait superiority of certain inbreds underscores their strategic importance in breeding programs. For instance, B145, with significant positive GCA for flowering (1.76), GY (1.89), PH (18.51), PL (1.5) and PG (1.42), is well-suited for developing dual-purpose hybrids with substantial biomass and strong panicle traits (Table 5). Similarly, ICMB 10555, B188 and ICMR 08888 showed consistently high and significant GCA across multiple traits, making them prime candidates for multi-trait gene pyramiding. GCA results provide essential insights into parental contributions to hybrid performance. Identifying high-GCA inbreds with desirable agronomic traits enables targeted breeding strategies for grain yield, biomass, early-maturity and ecological adaptation. Moreover, exploiting multi-trait superior inbreds ensures genetic gain delivery, reinforcing the role of additive genetic variance in sustainable product development (38, 39).

3.7. Specific combining ability effects

The significant mean squares for lines, testers and their interactions across most traits indicate the involvement of both additive and non-additive gene actions in trait inheritance (43). Consequently, specific combining ability (SCA) effects were estimated to evaluate hybrid performance across traits. A significant SCA effect in the desired direction suggests that a hybrid may outperform its expected performance based on parental general combining ability (GCA), offering potential advantages for environmental adaptability (44). The SCA effects of selected pearl millet hybrids, along with hybrids displaying minimum and maximum values, are summarized in Table 6, while complete trial results are available in Annexure 4 (Supplementary material).

Among 218 test hybrids, 60 exhibited significant SCA effects for DF, ranging from -2.20 to +2.72, highlighting the role of non-additive effects for this trait. ICPH033 (-1.77) and ICPH200 (-2.20) had the most negative SCA effects, indicating potential for early-maturity, while ICPH304 (2.41) and ICPH323 (2.72) had the highest positive SCA effects. 73 hybrids showed significant SCA effects, positive or negative, outlining the importance of non-additive gene interaction for PH. Significant positive SCA effects for PH in ICPH232 (30.72) and ICPH019 (20.61), suggest their suitability for biomass production (38, 45). Conversely, negative SCA for height such as ICPH230 (-11.61) and ICPH306 (-11.72) may offer enhanced lodging tolerance among peer half-sib hybrids. Notably, all hybrids derived from seed-parent B16 showed significant positive SCA for plant height, except ICPH214, which had a strong negative effect (-59.49 cm). This underscores that SCA is specific to hybrid combinations rather than solely dependent on parental GCA.

Twenty-five hybrids displayed significant SCA for either panicle length or girth in positive direction. ICPH094 (2.06) and ICPH174 (2.04) had the best SCA estimates for PL, while ICPH214 (2.18) and ICPH221 exhibited strong significant SCA for PG. SCA for longer or thicker panicle is very desirable as this is closely linked to GY (46). PT contribute to adaptability, particularly in stress-prone environments and rainfed conditions. ICPH148 (0.20), ICPH286 (0.14), ICPH062 (0.13), ICPH159 (0.11) and ICPH187 (0.11) showed positive significant SCA for this trait, which can enhance overall yield stability (43).

Only 10 of 106 hybrids with positive SCA effects for TR had significant values. Among them, ICPH206, ICPH329 and ICPH332 showed significant positive SCA for both threshing ratio and panicle traits, suggesting compact panicles with higher GY. Eighteen hybrids exhibited significant positive SCA for PY, in alignment with GY SCA estimates. ICPH213 (6.49), ICPH099 (5.98), ICPH265 (5.67), ICPH093 (5.40) and ICPH189 (5.11) had highly significant SCA for GY. Hybrids such as ICPH213, ICPH265, ICPH273, ICPH321 and ICPH166 showed positive SCA for GY and negative SCA for days to 50 % flowering, enhancing per-day productivity. ICPH206, ICPH189 and ICPH349 combined significant positive SCA for GY and TR, outperforming parental expectations. ICPH213, ICPH273, ICPH303, ICPH156, ICPH166 and ICPH334 exhibited significant positive SCA for both GY and

Table 6. SCA effects in selected and trait range identifier pearl millet hybrids based on ICRISAT B-Line gene pool evaluated during rainy 2021

S. No	Hybrid	Cross	DF	PH	PL	PG	PT	PY	TR	GY
1	ICPH203	B8/R25	0.50	3.16	-0.82*	0.43	0.04	-0.12	0.07**	0.24
2	ICPH206	B12/R25	1.15**	3.81	0.51	1.45*	0.02	0.09	0.06*	4.02*
3	ICPH019	B16/R22	0.55	20.61**	1.05**	-0.48	0.06	0.18	-0.04	3.04
4	ICPH213	B16/R34	-0.83*	18.72**	1.17**	-0.35	0.06	0.34**	-0.06*	6.49**
5	ICPH214	B16/R48	0.17	-59.49**	-3.50**	2.18**	-0.07		0.02	-6.91**
6	ICPH033	B29/R22	-1.77**	-3.34	-0.36	0.69	-0.01	0.08	0.01	0.94
7	ICPH219	B30/R34	0.31	-1.85	0.00	0.17	-0.04	0.09	0.07**	2.93
8	ICPH221	B33/R25	0.26	-5.87*	-0.83*	1.99**	0.00	-0.43**	0.04	-4.69**
9	ICPH230	B48/R13	0.19	-11.61**	-0.53	0.05	-0.04	-0.05	0.00	0.93
10	ICPH232	B48/R25	0.60	30.72**	0.75	1.39*	-0.01	0.00	-0.04	-0.42
11	ICPH062	B49/R13	-0.11	5.42	0.39	0.33	0.13*	0.20*	0.00	3.35
12	ICPH061	B49/R22	1.49**	0.41	0.26	0.85	-0.07	-0.27**	-0.04	-6.91**
13	ICPH094	B75/R13	-0.17	5.63	2.06**	0.45	-0.10*	0.21*	0.01	2.96
14	ICPH093	B75/R22	0.84*	4.56	-0.04	0.87	-0.01	0.26**	0.00	5.40**
15	ICPH099	B82/R22	0.71	2.66	0.52	0.04	-0.01	0.32**	0.04	5.98**
16	ICPH265	B92/R48	-1.63**	2.13	0.27	-1.07	0.03	0.31**	0.02	5.67**
17	ICPH273	B96/R48	-1.30**	10.33**	0.76	0.60	-0.01	0.11	-0.02	3.51*
18	ICPH275	B97/R34	-0.49	0.07	-0.60	-2.13**	0.03	0.02	0.00	0.07
19	ICPH124	B99/R13	-0.14	4.19	-0.91*	0.29	0.02	0.42**	0.01	4.36*
20	ICPH286	B107/R25	0.25	-1.30	-0.65	-0.39	0.14**	0.11	0.01	3.33
21	ICPH303	B118/R48	-0.65	6.93*	-0.22	0.93	0.05	0.14	0.01	4.06*
22	ICPH304	B120/R25	2.41**	6.62*	-0.51	0.63	-0.03	-0.17	0.01	-2.12
23	ICPH306	B120/R48	-0.66	-11.72**	-1.81**	-0.50	0.04	-0.04	0.02	0.11
24	ICPH148	B126/R13	0.75	15.08**	-0.50	-0.32	0.20**	0.13	-0.01	1.14
25	ICPH156	B141/R13	-0.68	7.20*	1.76**	-0.48	-0.05	0.14	0.04	4.52**
26	ICPH159	B145/R22	0.04	-2.83	-1.04**	0.44	0.11*	-0.02	0.03	-0.06
27	ICPH321	B152/R25	-0.88*	-5.74*	-0.15	-0.90	-0.03	0.18	0.02	3.52*
28	ICPH323	B152/R48	2.72**	6.44*	-0.15	0.68	0.00	-0.16	0.01	-2.83
29	ICPH166	B153/R13	-1.37**	6.07*	-0.36	0.45	0.06	0.14	0.03	3.86*
30	ICPH174	B166/R13	0.24	8.54**	2.04**	-0.24	0.02	0.27**	-0.02	2.82
31	ICPH329	B166/R48	0.22	-0.80	1.21**	0.51	-0.01	-0.25**	0.06*	-3.00
32	ICPH332	B180/R48	-0.01	9.32**	0.78*	0.66	0.01	-0.07	0.06*	2.99
33	ICPH188	B182/R13	-0.06	-41.22**	-1.59**	-0.37	-0.10	-0.62**	0.04	-6.59**
34	ICPH187	B182/R22	-0.65	6.97*	0.55	0.46	0.11*	0.06	0.02	1.09
35	ICPH334	B182/R34	-0.24	9.99**	0.32	-1.13	-0.01	0.26**	0.02	4.03*
36	ICPH189	B184/R22	-0.09	5.44	-0.30	-0.24	0.02	0.17	0.06*	5.11**
37	ICPH194	B187/R13	-0.39	-2.38	-0.26	-0.01	-0.12*	-0.07	-0.04	-2.06
38	ICPH200	B192/R13	-2.20**	9.60**	0.35	-0.39	0.04	0.05	0.00	1.30
39	ICPH349	B192/R34	-0.30	-3.51	-0.31	-0.44	0.00	0.06	0.07**	3.73*
40	ICPH350	B192/R48	2.10**	-7.13*	0.86*	0.04	-0.03	0.08	-0.09**	-1.35
	Min.		-2.20	-59.49	-3.50	-2.13	-0.12	-0.62	-0.09	-6.91
	Max.		2.72	30.72	2.06	2.18	0.20	0.42	0.07	6.49

*DF: Days to 50 % Flower; GY: Grain Yield (q ha^{-1}); PH: Plant Height (cm); PG: Panicle Girth (mm); PL: Panicle Length (cm); PT: Productive Tillers (count); PY: Panicle Yield (kg ha^{-1}); TR: Threshing Ratio.

PH, reinforcing their utility for dual-purpose breeding.

Some hybrids showed highly significant SCA across multiple traits. ICPH273 had desirable SCA for PH (+10.33 cm), early flowering (-1.3 days) and GY (3.51 q ha^{-1}), making it a strong dual-purpose hybrid with superior per-day productivity over the best check 86M84. ICPH206 had significant positive SCA for GY (+4.02 q ha^{-1}), PG (+1.45 mm), DF (+1.15 days) and PT, yet it outperformed 86M84 in earliness and PT while maintaining comparable GY. Despite its positive SCA for flowering time, it was still significantly earlier than 86M84, emphasizing that SCA explains genetic interactions, but practical performance should be evaluated against commercial checks.

ICPH213 exhibited strong positive SCA for GY (+6.49 q ha^{-1}), PL (+1.17 cm) and PH (+18.72 cm) while maintaining SCA effects for early-maturity (-0.83 days), indicating potential as a tall, high-yielding, widely adaptable hybrid. ICPH214 showed positive SCA for PG (+2.18 mm) but negative SCA for PL (-3.5 cm), demonstrating a trade-off between traits. SCA reflects the genetic potential of specific hybrid combinations over and above or lower than the parental GCA performance yet, relevance of its commercial success can still be seen in relation to an existing commercial check only. These findings align with previous studies on hybrid breeding in pearl millet (42-46).

High GCA parents may not always produce the best hybrids, such marked negative SCA effects in good × good crosses suggest a lack of complementation between favourable alleles of the parents involved. Positive SCA in good × poor and poor × poor crosses can possibly be attributed to better allele complementation at the locus in focus. These findings agree with the earlier findings (39, 47). These results highlight the role of epistasis where recurrent selection followed by diallel selective mating or biparental mating may be effective for improving grain yield and associated traits (39).

Conclusion

The study provided meaningful insights into trait associations and genetic interdependencies in pearl millet, leading to the development of a novel "product rating index" for evaluating per-day productivity. It is recommended to prioritize PY coupled with TR instead of GY per hectare for faster and more economical decision-making, particularly in early generation testing and advancement. The combining ability analysis showed role of both additive and non-additive genetic effects in trait manifestation. Inbreds were identified for utilization in breeding program and hybrids were identified for large scale testing with adaptability to different market segments. The strategic selection of parental lines based on GCA and advancement of hybrids based on SCA, coupled with the product rating index, offers a robust approach for developing high-yielding, early maturing and broadly adapted pearl millet hybrids.

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Authors' contributions

SKG provided guidance for work and research materials and corresponding author; AAS provided guidance related to my work at Department of Bioscience and Biotechnology, Banasthali University and corresponding author; AKV & KSK conducted statistical analysis of the experiment; KVK edited the manuscript; SP 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.

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References

1. Bhat BV, Hariprasanna K, Sooganna, Ratnavathi CV. Global and Indian scenario of millets. Indian Farming. 2023;73(1):16-18.
2. Agricultural and Processed Food Products Export Development Authority (APEDA). Pearl Millet Statistics. Jaipur: Directorate of Millets Development; 2024. https://apeda.gov.in/milletportal/files/Statistics_report.pdf
3. Athwal DS. Hybrid bajara-1 marks a new era. Indian Farming. 1965;15(5):6-7.
4. Gupta SK, Patil KS, Rathore A, Yadav DV, Sharma LD, Mungra KD, et al. Identification of heterotic groups in South-Asian-bred hybrid parents of pearl millet. Theoretical and Applied Genetics. 2020;133(3):873-88. https://doi.org/10.1007/s00122-019-03512-z
5. Gupta SK, Patil S, Kannan RL, Pujar M, Kumar P. Characterization of ICRISAT bred pearl millet restorer parents (2006-2019). Patancheru (India): International Crops Research Institute for the Semi-Arid Tropics; 2022. P. 160.
6. Kempthorne O. An introduction to genetic statistics. John Wiley and Sons; 1957.
7. Triki T, Bennani L, Boussora F, Tlahig S, Ali SB, Gasmi A, et al. Characterization and trait association analysis of 27 Pearl Millet landraces in southern Tunisia. Agronomy. 2023;13(8):2128. https://doi.org/10.3390/agronomy13082128
8. Galton F. Regression towards mediocrity in hereditary stature. The Journal of the Anthropological Institute of Great Britain and Ireland. 1886;15:246-63. https://doi.org/10.2307/2841583
9. Pearson K. Notes on regression and inheritance in the case of two parents. Proceedings of the Royal Society of London. 1895;58:240-2. https://doi.org/10.1098/rspl.1895.0041
10. Wright S. Correlation and causation. Journal of Agricultural Research. 1921;20(7):557-85.
11. Wright S. The theory of path coefficients a reply to Niles's criticism. Genetics. 1923;8(3):239-55. https://doi.org/10.1093/genetics/8.3.239
12. Dewey DR, Lu KH. A correlation and path-coefficient analysis of components of crested wheatgrass seed production. Agronomy Journal. 1959;51(9):515-8. https://doi.org/10.2134/agronj1959.00021962005100090002x
13. Gupta SK, Rathore A, Yadav OP, Rai KN, Khairwal IS, Rajpurohit BS, et al. Identifying mega-environments and essential test locations for pearl millet cultivar selection in India. Crop Science. 2013;53(6):2444-53. https://doi.org/10.2135/cropsci2013.01.0053
14. Protection of Plant Varieties and Farmers' Rights Authority (PPVFRA). Pearl millet DUS traits guidelines; 2024 [cited 2025 May 10]. https://plantauthority.gov.in/sites/default/files/revised-pearlmillet.pdf
15. Singh RK, Chaudhary BD. Biometrical methods in quantitative genetic analysis. New Delhi (India); Kalyani Publishers; 1985.
16. R Core Team. R: A language and environment for statistical computing [Internet]. R Foundation for Statistical Computing; 2024. https://www.R-project.org/
17. Clarke RT. Residual maximum likelihood (REML) methods for analysing hydrological data series. Journal of Hydrology. 1996;182(1-4):277-95. https://doi.org/10.1016/0022-1694(95)02929-X
18. Arminian A. Path Coefficient Analysis [R package Path. Analysis version 0.1]; 2024. https://doi.org/10.32614/CRAN.package.Path.Analysis
19. Comprehensive R Archive Network (CRAN). Extension to "ggplot2" [R package GGally version 2.2.1]; 2024. https://cran.r-project.org/web/packages/GGally/index.html
20. Sobel ME. Asymptotic confidence intervals for indirect effects in structural equation models. Sociological Methodology. 1982;13:290-312. https://doi.org/10.2307/270723
21. Satyavathi CT. Project coordinator review. 52nd Annual Group Meeting, PAU Ludhiana. All India Coordinated Research Project on Pearl Millet, Indian Council of Agriculture Research; 2017.
22. Singh S. MPMH 21: A pearl millet hybrid for drought-prone areas. Krishi Jagran; 2024.
23. Gupta SK, Govintharaj P, Bhardwaj R. Three-way top-cross hybrids to enhance production of forage with improved quality in pearl millet (*Pennisetum glaucum* (L.) R. Br.). Agriculture. 2022;12(9):1508. https://doi.org/10.3390/agriculture12091508
24. Pujar M, Govindaraj M, Gangaprasad S, Kanatti A, Shivade H. Genetic variation and diversity for grain iron, zinc, protein and agronomic traits in advanced breeding lines of pearl millet

[*Pennisetum glaucum* (L.) R. Br.] for biofortification breeding. Genetic Resources and Crop Evolution. 2020;67(8):2009–22. https://doi.org/10.1007/s10722-020-00956-x

25. Paterson AH, Damon S, Hewitt JD, Zamir D, Rabinowitch HD, Lincoln SE, et al. Mendelian factors underlying quantitative traits in tomato: comparison across species, generations and environments. Genetics. 1991;127(1):181-97. https://doi.org/10.1093/genetics/127.1.181
26. Johnson HW, Robinson HF, Comstock RE. Estimates of genetic and environmental variability in soybeans. Agronomy Journal. 1955;47(7):314-8. https://doi.org/10.2134/agronj1955.00021962004700070009x
27. Kholová J, Hash CT, Kumar PL, Yadav RS, Kočová M, Vadez V. Terminal drought-tolerant pearl millet [*Pennisetum glaucum* (L.) R. Br.] have high leaf ABA and limit transpiration at high vapour pressure deficit. Journal of Experimental Botany. 2010;61(5):1431-40. https://doi.org/10.1093/jxb/erq013
28. Govindaraj M, Shanmugasundaram P, and Muthiah AR. Correlation, path coefficient analysis and heritability of grain yield and its components in pearl millet. Journal of Plant Breeding and Crop Science. 2015;7(2):55-60. https://doi.org/10.5897/JPBCS2014.0463
29. Dadarwal SL, Rajput SS, Yadav GL. Studies on correlation and path analysis for grain yield and its components in maintainer lines of pearl millet [*Pennisetum glaucum* (L.) R. Br.]. International Journal of Current Microbiology and Applied Sciences. 2020;9(12):1158-64. https://doi.org/10.20546/ijcmas.2020.912.140
30. Yadav OP, Bidinger FR, Hash CT. Quantitative genetic analysis of pearl millet landrace populations for grain and stover yield in arid zone environments. Crop Science. 2004;44(2):442-8.
31. Serba DD, Yadav RS, Gupta SK. Genetic dissection of pearl millet grain yield and related traits under terminal drought stress through association mapping. Plant Genome. 2017;10(3):1-13.
32. Fisher RA. Frequency distribution of the values of the correlation coefficient in samples from an indefinitely large population. Biometrika. 1915;10(4):507-21. https://doi.org/10.2307/2331838
33. Patil KS, Gupta SK, Dangi KS, Shashibhushan D, Balram M, Ramesh T. Panicle traits and plant height are important selection indices to enhance productivity in pearl millet (*Pennisetum glaucum* (L.) R. Br.) populations. International Journal of Current Microbiology and Applied Sciences. 2018;7(12):306-12. https://doi.org/10.20546/ijcmas.2018.712.037
34. Yadav OP, Rai KN. Genetic improvement of pearl millet in India. Agricultural Research. 2013;2(4):275-92. https://doi.org/10.1007/s40003-013-0089-z
35. Wu W, Shah F, Ma B. Understanding of crop lodging and agronomic strategies to improve the resilience of rapeseed production to climate change. Crop and Environment. 2022;1(2):133-44. https://doi.org/10.1016/j.crope.2022.05.005
36. Van Oosterom EJ, Weltzien E, Yadav OP, Bidinger FR. Grain yield components of pearl millet under optimum conditions can be used to identify germplasm with adaptation to arid zones. Field Crops Research. 2005;96(2-3):407-21. https://doi.org/10.1016/j.fcr.2005.08.008
37. Yadav OP, Rai KN. Genetic improvement of pearl millet in India. Agricultural Research. 2013;2(4):275-92. https://doi.org/10.1007/s40003-013-0089-z
38. Pucher A, Sy O, Sanogo MD, Angarawai II, Zangre R, Ouedraogo M, et al. Combining ability patterns among West African pearl millet landraces and prospects for pearl millet hybrid breeding. Field Crops Research. 2016;195:9-20. https://doi.org/10.1016/j.fcr.2016.04.035
39. Mungra KS, Dobariya KL, Sapovadiya MH, Vavdiya PA. Combining ability and gene action for grain yield and its component traits in pearl millet (*Pennisetum glaucum* (L.) R. Br.). Electronic Journal of Plant Breeding. 2015;6(1):66-73.
40. Siddique M, Khanum S, Kamal N, Khan AH, Hayat S, Raza S, et al. Heterosis and combining ability studies in pearl millet. Pakistan Journal of Biotechnology. 2022;19(2):84-8. https://doi.org/10.34016/pjbt.2022.19.2.84
41. Sharma R, Singh J. Assessment of combining ability in pearl millet using line × tester analysis. Advances in Crop Science and Technology. 2014;02(04). https://doi.org/10.4172/2329-8863.1000147
42. Surendhar A, Iyanar K, Ravikesavan R, Ravichandran V. Combining ability analysis in pearl millet [*Pennisetum glaucum* (L.) R. Br.] for yield and yield contributing traits. Electronic Journal of Plant Breeding. 2023;14(2):584-90. https://doi.org/10.37992/2023.1402.070
43. Gajjar KD, Patel MS, Zala HN, Prajapati NN, Patel YN. Towards superior pearl millet [*Pennisetum glaucum* (L.) R. Br.] varieties: unravelling combining ability and heterosis for improved grain yield. Biological Forum An International Journal. 2023;15(11):339-48.
44. Khandagale SG, Sharma V, Lone RP, Khandagale VG, Swamy RV. Combining ability analysis and gene action in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. Electronic Journal of Plant Breeding. 2014;5(3):445-50.
45. Sattler FT, Pucher A, Ango IK, Sy O, Ahmadou I, Hash CT, et al. Identification of combining ability patterns for pearl millet hybrid breeding in West Africa. Crop Science. 2019;59(4):1590-603. https://doi.org/10.2135/cropsci2018.12.0727
46. Jeeterwal RC, Sharma LD, Anju N. Combining ability studies through diallel analysis in pearl millet [*Pennisetum glaucum* (L.) R. Br.] under varying environmental conditions. Journal of Pharmacogncy and Phytochemistry. 2017;6(4):1083-8.
47. Vagadiya KJ, Dhedhi KK, Joshi HJ, Vekariya HB, Bhadalia AS. Genetic architecture of grain yield and its components in pearl millet. International Journal of Plant Science. 2010;5(2)582-6.

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