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Genetic architecture and combining ability analysis for forage yield and attributing traits in pearl millet (*Pennisetum glaucum* L.) utilizing a Line $\times$ Tester design

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ABSTRACT

Getting insight into the genetic architecture and combining ability analysis in pearl millet (*Pennisetum glaucum* L.) is the essential step for developing superior and nutritionally rich forage cultivars. This study evaluated 40 F_1 hybrids obtained from a Line $\times$ Tester mating design with their 8 lines and 5 testers during *kharif* 2024 in a Randomized Block Design with three replications. Fourteen distinct morphological, yield, and nutritional traits were analyzed to estimate General Combining Ability (GCA), Specific Combining Ability (SCA) and the nature of gene action. Biometrical analysis revealed that the ratio of general to specific combining ability variance ($\sigma^2_{gca}/\sigma^2_{sca}$) was less than unity for all fourteen evaluated characters, suggesting that non-additive gene action predominantly controls the inheritance of fodder yield and quality. Among the parents, lines AFB-23 and AFB-67, and testers RBB-1 and, were identified as superior general combiners for green fodder yield per plant. For specific combining ability, the hybrid AFB-66 $\times$ RBB-1 showed the highest positive SCA effect for green fodder yield per plant, followed by AFB-25 $\times$ Baif and AFB-23 $\times$ Giant Bajra. The findings emphasize that breeding programs should capitalize on specific non-additive cross combinations to develop commercial heterotic hybrids and select desirable transgressive segregants for enhancing forage biomass and nutritional quality in pearl millet.

Keywords : Combining ability (GCA and SCA), forage nutritional quality, gene action, green fodder yield, Line $\times$ Tester design, pearl millet

INTRODUCTION

India possesses one of the world's largest livestock populations and animal husbandry sector plays an essential role in national development and the prosperity of rural economies (Bhardwaj *et al.*, 2018). In this sector, achieving higher income relies heavily on increasing milk production. This can be achieved by animal feed management and the provision of green fodder. To meet these demands farmers must adopt scientific cultivation methods for fodder crops.

In the regions that have irregular rainfall and poor soil fertility, forage pearl millet (*Pennisetum glaucum* L.) serves as a vital biological crop. As a fast-growing and short-duration cereal crop, it shows robust resistance to water Scarcity and heat, allowing it to thrive across diverse soil types. Pearl millet is known for its rapid growth cycle and high nutritional profile, which yields a substantial amount of dry matter alongside superior crude protein content and

excellent ruminant digestibility (Anonymous 2023). Furthermore, the recent development of specialized multi-cut varieties for green fodder has significantly enhanced its agricultural utility. With its noticeable genome size (~1.79 GB) (Varshney *et al.*, 2017) and an inherent allogamous mating system characterized by protogyny, pearl millet exhibits profound genetic variability.

Despite this vast genetic potential, it is necessary to get a precise understanding of the underlying genetic architecture governing yield and quality traits in addition to phenotypic selection. The success of any hybridization program is intrinsically linked to the careful selection of parental lines capable of transmitting desirable performance to their progeny. Combining ability analysis, as proposed by Sprague and Tatum (1942), provides a biometric framework to evaluate these inbred lines, partitioning genetic variance into General Combining Ability (GCA) and Specific Combining Ability (SCA).

To evaluate a wide array of germplasm efficiently, the Line $\times$ Tester (L $\times$ T) mating design [Kempthorne (1957)] offers a robust biometrical approach to precisely estimate these additive and non-additive gene actions. While the agronomic performance of pearl millet hybrids is well-documented, the specific genetic mechanisms controlling multicut forage biomass and nutritional attributes require further delineation. Consequently, this study utilizes a L $\times$ T mating design with the specific objectives of (1) evaluating the general and specific combining ability effects of selected parental lines, (2) investigating the nature and relative magnitude of gene action governing forage traits, and (3) identifying superior combiners for deployment in future forage pearl millet improvement initiatives.

MATERIAL AND METHODS

Experimental Material

To assess the combining ability and genetic architecture of forage traits, a crossing block was established at the Centre for Forage Research, S. D. Agricultural University, Sardarkrushinagar during the summer 2024. Eight diverse pearl millet lines were crossed with five testers (Table 1) using a Line $\times$ Tester mating framework, generating 40 unique F₁ hybrid combinations. Strict pollination protocols were followed by utilizing butter paper bags to prevent foreign pollen contamination given the protogynous and highly allogamous nature of the crop.

Lines	Testers	Check
L ₁ : 'HC-20'	T ₁ : 'Baif'	'GAFB- 4'
L ₂ : 'AFB-44'	T ₂ : 'Giant Bajra'	
L ₃ : 'AFB-21'	T ₃ : 'ICMO-1604'	
L ₄ : 'AFB-24'	T ₄ : 'RBB-1'	
L ₅ : 'AFB-67'	T ₅ : 'AFB-45'	
L ₆ : 'AFB-23'		
L ₇ : 'AFB-25'		
L ₈ : 'AFB-66'		

Field Evaluation

The 40 experimental hybrids, along with their 13 respective parental lines and check, were evaluated during the *kharif* 2024 in a Randomized Block Design comprising three replications. Genotypes were accommodated in single-row plots of 4.0-meter length, with inter-row and intra-row spacing maintained at 30 cm and 10 cm, respectively. Fourteen distinct yield and nutritional parameters were evaluated (*i.e.* days to flowering, plant height, number of tillers per plant, stem diameter, leaves per plant, leaf length, internode length, leaf width, leaf stem ratio, green fodder

yield per plant, dry matter yield per plant, dry matter content, crude protein content and iron content). Morphological traits (such as plant height, tillering, stem diameter, leaf dimensions, and fodder yield) were recorded from five randomly selected plants per plot, while phenological and biochemical metrics (flowering time, dry matter content, crude protein, and iron content) were analyzed on a per-plot basis.

Biometrical and Genetic Analysis

The partitioning of total genetic variance into general combining ability (GCA) and specific combining ability (SCA) components was executed strictly according to the Line $\times$ Tester biometrical procedure outlined by Kempthorne (1957).

The total variance among hybrids was divided to calculate the variance attributable to females (lines), males (testers), and their interaction. The additive and non-additive gene actions were assessed by calculating the GCA variance (σ^2_{GCA}) and SCA variance (σ^2_{SCA}), respectively. The potence ratio was subsequently determined to ascertain the predominant nature of gene action:

$$Potence\ ratio = \frac{\sigma^2_{gca}}{\sigma^2_{sca}}$$

A potence ratio exceeding unity indicates predominantly additive gene action, whereas a ratio below unity signifies non-additive (dominance/epistatic) gene action. The individual GCA effects for the i^{th} line (g_i) and j^{th} tester (g_j), as well as the SCA effect for the ij^{th} specific cross combination (s_{ij}), were estimated using the standard additive model:

$$X_{ij} = m + g_i + g_j + s_{ij} + e_{ijk}$$

Where m is the population mean and e_{ijk} represents the associated environmental error. The significance of these combining ability effects was tested using standard error estimates and standard 't' tests at the 5% and 1% levels of probability.

RESULTS AND DISCUSSION

The analysis of variance (Table 2) for combining ability revealed highly significant differences for the Line $\times$ Tester interaction across all evaluated traits, confirming that specific combinations of parents behaved distinctly differently than predicted by their independent additive effects. Furthermore, the mean sum of squares for the lines was significant for all characters, while the male testers showed significance for all traits except plant height. A critical biometrical reality observed in this study is that the ratio of general to specific combining ability variance

($\sigma^2_{gca}/\sigma^2_{sca}$) was less than unity for every trait evaluated.

The higher magnitude of σ^2_{sca} compared σ^2_{gca} dictates that non-additive gene actions specifically dominance and epistatic interactions predominantly control the inheritance of fodder yield and nutritional quality in this pearl millet germplasm. This non-additive genetic variance plays a primary role in the inheritance of traits including days to flowering, plant height, number of tillers per plant, stem diameter, leaves per plant, leaf length and width, internode length, leaf:stem ratio, green fodder and dry matter yield per plant, dry matter content, as well as crude protein and iron content. Similar results were also reported by Shinde and Mehetre (2014) and Ashwini *et al.* (2021) for all the traits.

While non-additive variance dominates, identifying strong general combiners remains the foundational step in assembling a successful crossing block. The general combining ability variance estimates for the lines (σ^2_{lines}) were predominantly non-significant for all the characters except crude protein content, whereas the tester variances (σ^2_{tester}) showed significance for specific traits such as iron content. Because the GCA effects were negative for days to flowering, number of tillers per plant, leaves per plant, and dry matter content, these were not counted in the positive directional analysis. For the primary economic trait *i.e.*, green fodder yield per plant, the lines AFB-67 and AFB-23 emerged as the most valuable general combiners, exhibiting highly significant positive GCA effects. Among the testers, RBB-1 and Baif provided the most favorable additive genes for this trait, with RBB-1 additionally

serving as a strong general combiner for dry matter yield per plant.

The estimates of general combining ability (GCA) and specific combining ability (SCA) effects of genotypes for fourteen traits are presented in Table 3. Good, average and poor combinations meant significant positive, non-significant and significant negative gene actions, respectively. Yield is governed by complex inheritance pattern which is noticeable because no single cross exhibited favorable SCA effects for every trait simultaneously. Nevertheless, a significant number of hybrids showed desirable SCA effects for many traits. For example, ten hybrids showed favourable SCA effects for internode length, leaf:stem ratio, and crude protein content; nine for plant height, number of tillers per plant, stem diameter, leaves per plant, and green fodder yield per plant; eight for leaf length; and seven for days to flowering, dry matter yield per plant, dry matter content, and iron content.

While discussing in detail, line AFB-23 emerged as a top good general combiner. Since it showed desirable significant values for GCA for majority of traits namely, plant height (3.75), number of tillers per plant (0.20), number of leaves per plant (2.58), leaf length (2.46), leaf width (0.18), leaf stem ratio (0.03), green fodder yield per plant (14.70), dry matter yield per plant (4.17) and iron content (3.30). This line is followed by line AFB-67 for days to flowering (-2.00), number of tillers per plant (0.49), leaves per plant (2.12), leaf length (2.43), leaf width (0.15), green fodder yield per plant (14.76), dry matter yield per plant (3.59) and dry matter content (1.44).

Table 2: Analysis of variance for combining ability and its component characters in forage pearl millet

Source of variation	df	Days to flowering	Plant height	Number of tillers per plant	Stem diameter	Leaves per plant	Leaf length	Internode length
Replications	2	30.55	17.49	0.06	0.01	1.95	18.06	0.23
Hybrids	39	56.30**	539.25**	1.03**	0.21**	28.36**	61.46**	9.95**
Lines	7	43.05**	897.20**	1.03**	0.28**	41.93**	42.43**	10.50**
Testers	4	60.55**	279.27	0.70**	0.21**	11.61**	101.12**	21.15**
Lines × Testers	27							
Testers		59.01**	486.90**	1.08**	0.19**	27.35**	60.55**	8.21**
Error	78	13.45	119.78	0.10	0.04	2.84	12.47	1.95
ESTIMATES								
σ^2_L		-1.06	27.35	-0.003	0.01	0.97	-1.20	0.15
σ^2_T		0.06	-8.65	-0.015	0.01	-0.66	1.69	0.53
σ^2_{GCA}		-0.36#	5.19	-0.011#	0.01	-0.03#	0.57	0.39
σ^2_{SCA}		15.18**	122.37**	0.326**	0.05**	8.17**	16.02**	2.08**
$\sigma^2_{GCA}/\sigma^2_{SCA}$		-0.02	0.04	-0.033	0.05	-0.01	0.03	0.18

*, ** indicates significant at 5% and 1% levels of probability, respectively.

Table 2 Contd.....

Source of variation	df	Leaf width	Leaf: stem ratio	Green fodder yield per plant	Dry matter yield per plant	Dry matter content	Crude Protein content	Iron content
Replications	2	0.02	0.01	479.43	13.80	5.68	0.03	29.22
Hybrids	39	0.22**	0.01**	1945.88**	139.53**	16.46**	3.26**	288.99**
Lines	7	0.22**	0.02**	1741.92**	128.36**	14.03**	7.84**	87.15*
Testers	4	0.40**	0.01**	2572.78**	186.70**	13.53**	4.35**	1037.69**
Lines × Testers	27	0.19**	0.01**	1907.31**	135.58**	17.49**	1.96**	232.49**
Error	78	0.04	0.01	194.01	12.64	3.17	0.13	35.18
ESTIMATES								
$\sigma^2 L$		0.01	0.00	-11.02	-0.48	-0.23	0.39**	-9.68
$\sigma^2 T$		0.01	0.00	27.72	2.12	-0.16	0.09	33.54**
σ^2_{GCA}		0.01	0.01	12.82	1.12	-0.19#	0.21	16.91
σ^2_{SCA}		0.05**	0.01**	571.10**	40.98**	4.77**	0.60**	65.77**
$\sigma^2_{GCA}/\sigma^2_{SCA}$		0.11	0.06	0.02	0.02	-0.03	0.34	0.25

was not counted in analysis due to negative value.

Table 3 : Summary of promising general and specific combiners along with their significant GCA and SCA effects for forage traits in pearl millet

Traits	Promising Lines (GCA Effect)	Promising Testers (GCA Effect)	Top Hybrids (SCA Effect)
Days to flowering	AFB-67 (-2.00*), AFB-25 (-2.00*)	AFB-45 (-1.72*)	AFB-67 × Baif (-8.61**), AFB-25 × Giant Bajra (-7.15**)
Plant height	AFB-25 (6.63*), AFB-23 (3.75**)	Giant Bajra (5.34*)	AFB-67 × AFB-45 (16.21*), AFB-24 × Giant Bajra (15.99*), AFB-23 × ICMO-1604 (15.27*)
Number of tillers per plant	AFB-67 (0.49**), AFB-23 (0.20*)	AFB-45 (0.22**), Baif (0.13*)	AFB-67 × ICMO-1604 (1.31**), AFB-66 × RBB-1 (1.07**)
Stem diameter	AFB-44 (-0.12*), AFB-24 (-0.11*), AFB-66 (-0.10*), HC (-0.10*)	Giant Bajra (-0.10*)	AFB-25 × Giant Bajra (-0.49**), AFB-23 × AFB-45 (-0.39**)
Leaves per plant	AFB-23 (2.58**), AFB-67 (2.12**)	Baif (0.70*)	AFB-66 × RBB-1 (4.62**), AFB-24 × Baif (4.19**)
Leaf length	AFB-23 (2.46**), AFB-67 (2.43**)	AFB-45 (2.22**), Baif (1.98**)	HC-20 × RBB-1 (7.63**), AFB-24 × AFB-45 (6.41**)
Internode length	AFB-21 (-0.94*)	RBB-1 (-1.35**)	AFB-21 × Giant Bajra (-2.94**), AFB-24 × Baif (-2.06*)
Leaf width	AFB-23 (0.18**), AFB-67 (0.15**)	ICMO-1604 (0.09*), Baif (0.08*)	AFB-25 × Baif (0.49**), AFB-44 × RBB-1 (0.44**)
Leaf: stem ratio	AFB-23 (0.03*), AFB-24 (0.03*), AFB-25 (0.03*)	Baif (0.02*), AFB-45 (0.02*)	AFB-23 × Giant Bajra (0.10**), AFB-21 × ICMO-1604 (0.09**)
Green fodder yield per plant	AFB-67 (14.76**), AFB-23 (14.70**)	RBB-1 (10.35**), Baif (6.43*)	AFB-66 × RBB-1 (53.58**), AFB-25 × Baif (32.36**), AFB-23 × Giant Bajra (30.96**)
Dry matter yield per plant	AFB-23 (4.17**), AFB-67 (3.59**)	RBB-1 (2.91**), Baif (1.45*)	AFB-66 × RBB-1 (15.33**), AFB-23 × Giant Bajra (10.22**)
Dry matter content	AFB-67 (1.44**), AFB-21 (1.05*)	Baif (0.77*), AFB-45 (0.73*)	AFB-23 × AFB-45 (5.74**), AFB-66 × Baif (4.01**)
Crude Protein content	HC-20 (1.20**), AFB-44 (0.49**), AFB-21 (0.41**), AFB-24 (0.29*)	ICMO-1604 (0.47**), AFB-45 (0.34**)	AFB-21 × ICMO-1604 (2.11**), AFB-24 × AFB-45 (1.45**)
Iron content	AFB-66 (3.46*), AFB-23 (3.30*)	ICMO-1604 (5.67**), AFB-45 (5.58**)	AFB-67 × Baif (15.81**), AFB-24 × Giant Bajra (12.70**), AFB-44 × Baif (12.12**), AFB-67 × Giant Bajra (8.56**)

* Significant at 5% level of probability; ** Significant at 1% level of probability. Negative values are desirable for days to flowering, stem diameter, and internode length. Positive values are desirable for all other traits.

While discussing about SCA, the earliness is the desirable character in pearl millet crop since it allows farmers to harvest multiple cut in a season. Desirable value is negative significant for this trait as well as for internode length and stem diameter. Since, less inter node length promote more number of leaves. Specific combining ability effects were found desirable for AFB-67 $\times$ Baif (-8.61**) and AFB-25 $\times$ Giant Bajra (-7.15**) for earliness. Khandagale *et al.* (2014) and Shinde and Meheretre (2014) reported similar results earlier.

Considering the stem properties, plant height is directly related with green forage yield. The cross-combination AFB-67 $\times$ AFB-45 (16.21) recorded highest significant specific combining ability effect in a desirable direction for plant height followed by AFB-24 $\times$ Giant Bajra (15.99) and AFB-23 $\times$ ICMO-1604 (15.27). The earlier findings of Patel *et al.* (2008), Shinde and Mehetre (2014) and Sharma *et al.* (2019) were similar to the present findings. More number of tillers per plant increase the fodder yield. Total nine crosses recorded significant positive SCA effects in desirable direction among which one cross AFB-67 $\times$ ICMO-1604 (1.31) surpassed the other crosses. A study of estimation of general combining ability effects for stem diameter revealed that parent AFB-44 (-0.12), AFB-24 (-0.11), AFB-66 (-0.10) and HC-20 (-0.10) among lines and Giant Bajra (-0.10) among testers showed significant negative general combining ability effects. Therefore, these parents were good combiners for stem diameter. Ashwini *et al.* (2021) also reported similar significant SCA effects earlier for stem diameter. Also, smaller internode is preferred and cross combination AFB-21 $\times$ Giant Bajra (-2.94) recorded highest significant SCA effects for this trait [supported by Govintharaj *et al.* (2021)].

Leaves characteristics are important for fodder since; animal preference is more towards the leaves than stem. Highest SCA effect was 4.62 (AFB-66 $\times$ RBB-1) for number of leaves per plant; 7.63 (HC-20 $\times$ RBB-1) for leaf length; 0.49 (AFB-25 $\times$ Baif) for leaf width; 0.10 (AFB-23 $\times$ Giant Bajra) for leaf: stem ratio. Similar results were also reported by Maitry (2011) and Ashwini *et al.* (2021). The hybrids which showed positive direction for SCA can be directly considered as a best combination. Biomass of plant (specially for fodder plant) is the ultimate character for income generation for farmer. For green fodder yield per plant, the most successful specific crosses consistently involved combinations of Average $\times$ Good, Good $\times$

Average, or Good $\times$ Good GCA parents. The highest positive SCA effect for green fodder yield was recorded by the cross AFB-66 $\times$ RBB-1 ($L_8 \times T_4 = 53.58$), which resulted from an Average $\times$ Good combiner interaction. This was followed by AFB-25 $\times$ Baif ($L_7 \times T_1 = 32.36$) and AFB-23 $\times$ Giant Bajra ($L_6 \times T_2 = 30.96$). This pattern demonstrates that crossing parents with the highest individual GCA does not automatically guarantee the most vigorous hybrid. Instead, selecting crosses that pair at least one strong general combiner, such as AFB-23 or RBB-1, with a genetically divergent partner triggers the highest specific combining ability. Ultimately, breeders must focus on exploiting these specific cross combinations rather than relying solely on the mass selection of parents. Capitalizing on this exclusive non-additive gene action will be highly useful for producing superior, heterotic hybrids at a commercial scale, while also facilitating the production of transgressive segregants to aid in the selection of better recombinants for overall forage yield and associated nutritional traits. Khandagale *et al.* (2014), Shinde and Mehetre (2014) and Bhardwaj *et al.* (2023) also reported similar results earlier.

Mere green fodder yield is not enough; it should be supplemented with dry matter content also. For dry matter yield per plant, the highest SCA effects was 15.33 (AFB-66 $\times$ RBB-1). The highest SCA effects for dry matter content was 5.74 (AFB-23 $\times$ AFB-45). Similar results were previously reported by Ashwini *et al.* (2021) and Bhardwaj *et al.* (2023).

Plant variety or hybrid with only high biomass is not enough nowadays. Fodder with high nutritional quality is necessary for better livestock health. For this, the parents HC-20 (1.20), AFB-44 (0.49), AFB-21 (0.41), AFB-24 (0.29) among lines and ICMO-1604 (0.47) and AFB-45 (0.34) among testers had emerged out as good general combiners for crude protein content. Considering the iron content, the highest SCA effects was 15.81 (AFB-67 $\times$ Baif) followed by 12.70 (AFB-24 $\times$ Giant Bajra), 12.12 (AFB-44 $\times$ Baif) and 8.56 (AFB-67 $\times$ Giant Bajra). The present findings were similar to results reported by Nandaniya *et al.* (2016), Gavali *et al.* (2018).

CONCLUSION

In conclusion, this study demonstrates that the inheritance of all fourteen evaluated forage yield, morphological, and nutritional traits in pearl millet - including crude protein and iron content - is predominantly governed by non-additive gene action, as evidenced by a general-to-specific combining ability variance ratio ($\sigma^2_{gca}/\sigma^2_{sca}$) of less than unity. Among the evaluated parents, lines AFB-23 and AFB-

67, along with testers RBB-1 and Baif, emerged as superior general combiners for green fodder yield per plant, whereas lines HC-20, AFB-44, AFB-21, AFB-24, and tester ICMO-1604 proved to be favorable general combiners for enhancing crude protein content. However, the results indicate that pairing parents with the highest individual GCA effects does not automatically guarantee the most vigorous hybrid. Notably, the top-performing specific combinations for green fodder yield per plant such as AFB-66 × RBB-1, AFB-25 × Baif, and AFB-23 × Giant Bajra—resulted from pairing at least one strong general combiner with a genetically divergent partner. Consequently, future forage pearl millet breeding programs should prioritize capitalizing on specific non-additive cross combinations rather than relying solely on the mass selection of parents. Exploiting this non-additive gene action will be instrumental for developing commercial heterotic hybrids and selecting superior transgressive segregants with enhanced forage biomass and nutritional quality in pearl millet.

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