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Research Article

Assessment of combining ability and gene action for grain yield and its component traits in pearl millet [*Pennisetum glaucum* (L.) R. Br.]

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Abstract
The current study involved the evaluation of 96 pearl millet hybrids synthesized by crossing eight lines with 12 testers using a Line x Tester mating design. The experiment was conducted during the *Kharif* season of 2022 with two replications and included standard checks COH10 and 86M38. Analysis of variance for combining ability revealed that, significant amount of variation was present in all hybrids for studied traits. The contribution of lines to the total variance in hybrid was greater than tester. The ratio between GCA and SCA variance was less than one for all traits and it showed that non additive gene action was predominant and highlighting the potential of heterosis breeding to exploit hybrid vigor. Among the parents, ICMB 02777 and PT 6679 were identified as good combiners, showing positive gca effects and high mean performance for grain yield, test weight, single earhead weight, and single earhead threshed weight. The other parents *viz.,* ICMB 02444, ICMB 93222, PT 6067, and PT 6476 were also recognized as good combiners for grain yield. Out of the 96 hybrids, the cross ICMB 02777 x PT 6679 exhibited significant positive heterosis along with high standard heterosis over both checks for grain yield, test weight and single earhead threshed weight. Additionally, the crosses ICMB 02444 x PT 6679, ICMB 93222 x PT 6067 also recorded significant *sca* effect for grain yield per plant. These promising hybrid combinations hold great potential for heterosis breeding programs and may be suitable for commercial exploitation after thorough evaluation under multi-location trials.

Keywords: Pearl millet, Combining ability, Heterosis, GCA, SCA

INTRODUCTION

Pearl millet (*Pennisetum glaucum* (L.) R. Br.), hardy cereal millet, is a staple food crops in arid and semi-arid regions of the world, playing a crucial role in the food security and livelihoods of millions of people. India holds a prominent position in pearl millet production, contributing significantly to global output. The country accounts for 43.3 per cent of the world's total pearl millet cultivation area and produces 42 per cent of the global yield. The primary cultivation regions for pearl millet in India include the states of Rajasthan, Maharashtra, Gujarat, Madhya Pradesh, Karnataka, Andhra Pradesh, Uttar Pradesh, and Tamil Nadu (Kalagare *et al.,* 2022). The cultivation area of pearl millet in India and Tamil Nadu spans around 7.55 m ha and 59,956 ha respectively, with an average production of 9.22 lakh tones and 1.46 lakh tones, respectively. The productivity of pearl millet in the country and Tamil Nadu is noteworthy, standing at 1747 and 2,437 kg per hectare respectively (DES, Government of India, 2021 and Seasonal crop report 2021). The significant enhancement in pearl millet productivity and overall production occurred with the introduction of hybrids in the 1960s. To address the challenge of productivity and production volatility, it is essential to promote a diverse range of hybrids and varieties. The practical and economical implementation of the CGMS system in pearl millet has made the commercial exploitation of hybrid vigor a reality (Suryawanshi *et al.,* 2021). Hybrid development in pearl millet is of paramount importance, especially in the context of increasing food demand and the need for climate-resilient crops. It offers the promise of enhancing the yield potential, nutritional quality, resistance breeding and overall agronomic performance (Choudhary *et al*., 2023).

To improve the grain yield potential of pearl millet varieties and hybrids, the selection of desirable parents with strong general combining ability (GCA) is essential (Solanki *et al.,* 2017). While phenotypic elimination effectively identifies candidates for various traits, it falls short in identifying poor combining lines based solely on physical characteristics. To optimize hybrid programs, both individual lines and their hybrids need evaluation to identify top cross combinations for yield and quality. General combining ability estimation selects strong parents, and specific combining ability estimation identifies superior cross combinations. These estimates assess variance components, and the GCA/ SCA ratio reveals gene action nature. The significance of GCA and SCA effects on hybrid performance varies, with GCA sometimes more influential. Biometrical mating designs, particularly the line × tester design introduced by Kempthorne in 1957, are widely used and provide reliable estimates of general and specific combining ability in hybrids.

Heterosis breeding is crucial for boosting crop yield and related traits through hybrid development. Identifying the most promising hybrid combinations is of paramount importance in this process, achieved by evaluating new hybrids along with high-yielding checks (Yadav *et al.,* 2021). Standard heterosis is a widely utilized method to pinpoint the best-performing cross combinations. In this study, we primarily focus on exploring combining ability, variance in yield, and its component traits to understand the nature and extent of gene action among lines, testers, and synthesized hybrids.

MATERIALS AND METHODS

Eight lines and twelve testers were used as parents to synthesize 96 hybrids through line × tester mating design. The experimental materials were raised in RBD design with two replications during *kharif* 2022 at Department of Millets, TNAU, Coimbatore. Parents and synthesized hybrids were randomized and evaluated separately in same field. Each entry was raised with two rows with row spacing of 50 x15 cm inter and intra space and 4 m row length. All the recommended agronomic packages and practices were followed for good establishment of crop. Observations were recorded on five randomly selected plants in two replication of parents and hybrids for 14 different quantitative traits *viz.,* days to 50% flowering; leaf blade length (cm); leaf blade width (cm); leaf sheath length (cm); number of economic tillers/plants (no of productive tillers); number of nodes; spike length (cm); spike diameter (cm); plant height (cm); days to maturity; single spike weight (g), single spike threshed weight (g); test weight (g); and grain yield per plant (g). The crop exhibits a protogynous nature, which is harnessed in breeding programs. In these investigations, all the lines employed are characterized by dwarf while restorers displaying tall traits. Additionally, morphological indicators such as anther color and spike shape were employed for identification of true F1 plants under field conditions.

Statistical analysis: The GCA/ (GCA + SCA) ratio was determined by applying a modified equation, which was originally proposed by Baker in 1978 and later adapted by Hung and Holland in 2012.

$$\frac{2\sigma^2 GCA}{2\sigma^2 GCA + \sigma^2 SCA}$$

In this present study, heterosis was estimated based on standard heterosis. The superiority of F_1 hybrid over the commercial hybrid/ variety

$$\text{Standard heterosis} = \frac{F_1 - SH}{SH} \times 100$$

SH – mean value of standard hybrid

The variance and combining ability analysis were performed by using Window stat *ver.* 7.0 and heterosis analysis was carried out in TNAUSTAT software (Mannivannan, 2014). The correlation coefficient was calculated using Microsoft excel 2016.

RESULTS AND DISCUSSION

Analysis of variance was conducted to assess the combining ability for various observed traits, and the estimates of combining ability variance were presented in **Table 1**. The results indicated that the crosses exhibited significant effects for all the traits studied, suggesting the presence of a notable degree of genetic variation in the hybrids. Yadav *et al.* (2022) also observed variation among many traits in pearl millet. The variance was further partitioned into components such as lines, testers, and lines x tester interactions. The lines were found to be significant for all traits, except for test weight, while testers were significant for almost all traits, except for leaf sheath length, leaf blade length, number of economic tillers/ plant and days to maturity. This suggests a significant contribution of both lines and testers to the combining ability variance for yield and related traits. The selection of diverse parental lines in this study resulted in significant differences among them, leading to the generation of substantial genetic diversity in the hybrid crosses.

The predominance of non-additive gene action was evident as the specific combining ability (SCA) variances exceeded over the general combining ability (GCA) variances for all traits (**Table 1**). The baker's ratio $2\sigma^2gca/\sigma^2gca + \sigma^2ca$ was less than one emphasizing the significance of non-additive genetic components in the inheritance of the majority of these traits. It indicated that improvement of these traits through heterosis breeding would be rewarding. This result was supported by Badurkar *et al.* (2018), Reshma *et al.* (2019), Suryawanshi *et al.* (2021) and Surendhar *et al.* (2023). The presence of significant non-additive gene action is crucial for maintaining heterozygosity in the population. Being a cross-pollinated crop, heterosis breeding is a valuable method for hybrid development.

Proportional contribution of lines, testers and line x tester interaction are presented in **table 1 and Fig. 1**. Among the fourteen quantitative traits, lines contributed maximum variance except leaf blade length, leaf blade width, plant height, test weight and grain weight. This implies that lines harbored a higher number of beneficial genetic traits for producing improved hybrids or varieties of pearl millet.

Estimates of combining ability effects in parents: Understanding of *gca* effects helps the breeder to utilize desirable parents to development of high performing hybrids. Estimates of *gca* effects are presented in **table 2**. It showed none of the parental lines displayed significant *gca* effects for all traits studied, making them suitable for specific trait improvement programs. This finding aligns with previous research conducted by Choudhary *et al.* (2023) and Surendhar *et al.* (2023). Among the female lines, ICMB 02777 exhibited a significant GCA effect for grain yield and some of the contributes, including spike length, spike girth, the number of economic tillers per plant, single ear head weight, single earhead threshed weight, and test weight. ICMB 02444 and ICMB 93222 were identified as promising combiners for grain yield and traits related to yield, such as spike length, spike girth, the number of economic tillers per plant, plant height, single ear head weight, and single earhead threshed weight. The remaining lines showed significant *gca* effects specifically for grain yield number of economic tillers per plant, plant height and spike girth. Similar studies were conducted by Aswini *et al.* (2021) for grain yield and the number of economic tillers per plant, Reshma *et al.* (2019) for grain yield, the number of economic tillers per plant, and plant height, as well as Solanki *et al.* (2017) for grain yield, the number of economic tillers per plant, plant height, and spike girth.

Out of 15 testers, PT 6679 had positive significant *gca* effect for important traits like spike length, spike girth, number of economic tillers/plants, single ear head weight, single earhead threshed weight and test weight. followed by PT 6029 and PT 6067 for grain yield, number of economic tillers/plants, single ear head weight, single earhead threshed weight and test weight. Whereas GMR 58, DMR purple and Shoolagiri local lines showed

Table 1. Analysis of variance for combining ability, variance components and proportional contribution of quantitative traits in pearl millet

Source	D50%F	LSL	LBL	LBW	NON	SPL	SPD	NOET	PLH	DTM	SEWT	SETWT	TWT	GYP
Crosses	12.85**	1.83**	50.27**	0.46**	0.77**	12.17**	2.53**	1.53**	261.42**	8.22**	212.96**	145.10**	9.88**	1252.65**
Lines	78.99**	5.72**	120.76**	1.48**	3.67**	66.18**	17.79**	4.66**	514.38*	16.30*	290.99**	970.55**	15.23	4577.37**
Testers	36.17**	2.46	73.61	1.20**	1.30**	22.08**	2.74*	1.32	505.47*	7.97	411.81**	256.64**	23.99**	3300.69**
Line Vs Tester	3.51	1.38**	40.53**	0.26**	0.43**	5.84**	1.15**	1.28**	203.56**	7.53**	86.62**	55.23**	7.38**	657.83**
Error	2.72	0.15	3.46	0.1	0.17	1.37	0.09	0.18	16.05	3.04	7.85	5.81	0.25	40.59
General and specific combining ability variance components for quantitative traits in Pearl millet														
GCA	0.14	0.01	0.14	0.01	0.01	0.10	0.02	0.00	0.88	0.01	1.94	1.39	0.04	9.13
SCA	0.33	0.48	17.92	0.08	0.12	1.65	0.51	0.51	93.41	2.04	39.97	25.09	3.57	310.77
$2\sigma^2GCA/(2\sigma^2GCA+\sigma^2SCA)$	0.46	0.04	0.02	0.20	0.14	0.11	0.07	0.00	0.02	0.01	0.09	0.10	0.02	0.06
Proportional contribution of quantitative traits towards variance in Pearl millet														
Lines	45.29	23.09	17.7	23.61	35.12	40.07	51.76	22.39	14.49	14.6	44.64	48.98	11.35	26.92
Testers	32.6	15.59	16.96	30	19.42	21.01	12.53	9.97	22.39	11.22	22.39	20.35	28.11	30.51
Line Vs Tester	22.11	61.32	65.34	46.38	45.45	38.91	35.71	67.63	63.11	74.18	32.97	30.66	60.53	42.56

*significant at 5 % level ** significant at 1% level

D50%F – days to 50 per cent flowering, LSL- leaf sheath length, LBL – leaf blade length, LSW- leaf blade width, NON – Number of Nodes, SPL – spike length, SPD – spike diameter ,NOET- number of economic tillers/plant, DTM – Days to Maturity,PLH- plant height,SEWT – Single Earhead Weight, SETWT - Single Earhead Threshed Weight , TWT – 1000 grain weight, GYP- Grain yield/ Plant

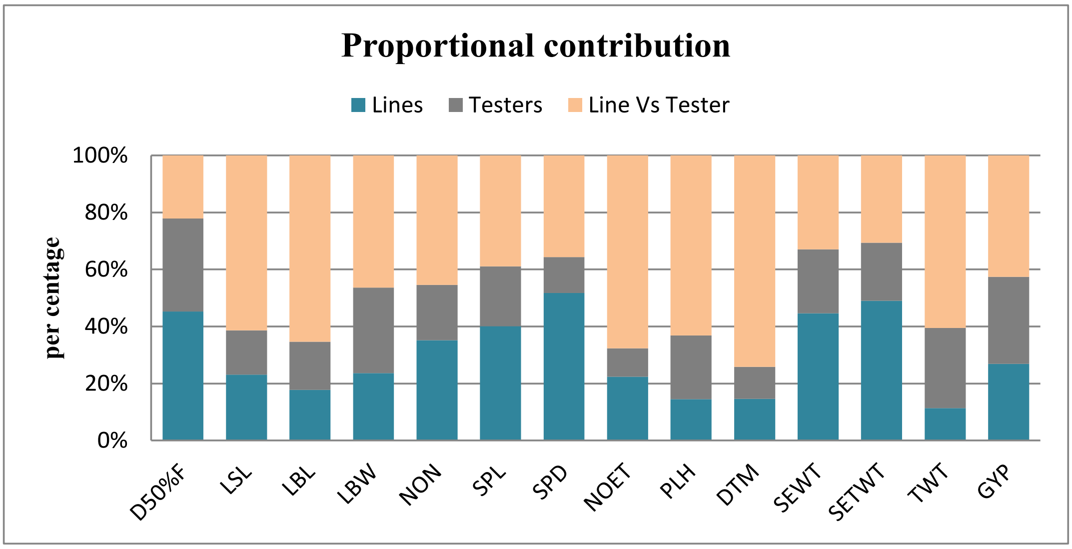

Fig. 1. Proportional contribution of lines and testers for different traits

D50%F – days to 50 per cent flowering, LSL- leaf sheath length, LBL – leaf blade length, LSW- leaf blade width, NON – Number of Nodes, SPL – spike length, SPD – spike diameter, NOET- number of economic tillers/plant, DTM – Days to Maturity,PLH- plant height,SEWT – Single Earhead Weight, SETWT - Single Earhead Threshed Weight , TWT – 1000 grain weight, GYP- Grain yield/ Plant

significant *gca* effects for grain yield, spike length, spike girth, single ear head weight, single earhead threshed weight and test weight. The parents *viz.,* ICMB 89111, ICMB 94333, ICMB 99666, PT 6029 were exhibited negative significant *gca* effects for days to 50 % flowering and days to maturity with significant grain yield. Surendhar *et al.* (2023), Yadav *et al*. (2022) and Solanki *et al.* (2017) were reported similar findings of *gca* effects in testers. ICMB 02777, ICMB 02444 and ICMB 93222 from lines and PT 6679, PT 6029, PT 6067, GMR 58, DMR purple and Shoolagiri local could be utilized as parents for hybrid development program. Surendar *et al.* (2023), Solanki *et al.* (2017) were reported similar trend in pearl millet hybrids. This parental line provides good opportunity for synthesizing improved hybrids with enhanced grain yield. Additionally, these lines exhibiting strong general combining ability for specific traits can be strategically employed in targeted component breeding programs to enhance particular desirable characteristics.

The parents were evaluated based on their mean performance combined with general combining ability effect which provides greater value in heterosis breeding programme (**Table 3**). ICMB 02777 and PT 6679 were the elite parents for grain yield and other yield related traits *viz.,* spike length, spike girth and test weight. ICMB 02444, ICMB 02111, ICMB 93222, PT 6029, PT 6067, PT 6300, PT 6476, and GMR 58 were best performing parents for yield attributing traits. Based on the above result, the elite parents are not necessarily to perform well in all the traits. Instead their inherent ability to transfer favorable gene to their offspring to develop superior hybrids is utilized in a heterosis breeding program. Hence these parental lines are considered as good combiners for hybrid development program.

Estimates of specific combining ability effects: Estimates of *sca* along with mean performance will yield a better result for hybrid selection program. **Table 5** presents the estimates of specific combining ability for the traits studied. The *sca* effects observed varied in both positive and negative directions. In general, crosses that exhibited high *sca* effects also demonstrated high mean performance values. This trend was consistent with the findings from the previous worker Patel *et al.* (2018) in pearl millet.

Among the 96 hybrids, 15 displayed positive significant *sca* effect for grain yield per plant. The cross ICMB 02777 × PT 6679 was the best performing hybrid and it had significant *sca* effect with high mean performance for grain yield per plant and other yield contributing traits *viz.,* spike length, single ear head weight, single earhead threshed weight and test weight. followed by ICMB 93222 × PT 6679, ICMB 02444 × PT 6679 and ICMB 93222 × PT 6476 that exhibited significant *sca* effect for grain yield per plant, spike girth, single ear head threshed weight and test weight. Both parents involved in these crosses were showed significant positive *gca* effect and it is due to additive gene action. Similar finding was reported by Choudhary *et al.* (2023) and Surendar *et al.* (2023). Parents involved in above cross combination are good x good combiner and similar result was reported by Warrier *et al.* (2020) and Siddique *et al.* (2019). **Table 5** presents the top-performing crosses along with their *sca* effects and mean performance. In addition to these, some

Table 2. General combining ability effect of lines and testers for 14 quantitative traits in Pearl millet

Lines/Tester	D50%F	LSL	LBL	LBW	NON	SPL	SPD	NOET	PLH	DTM	SEWT	SETWT	TWT	GYP	Combining ability / status
ICMB 89111	-1.23**	-0.78	-1.80**	0.14**	0.68**	-0.25	-1.39**	0.51**	4.40**	-0.55**	-2.37**	0.09	-0.02	2.42**	H
ICMB 93222	0.31	0.48	0.40	0.12**	0.38**	-0.20	-0.16**	-0.15**	5.41**	-0.22	3.53**	2.44**	0.64**	4.07**	H
ICMB 94333	-1.78**	0.27	-0.20	-0.10**	-0.56**	-0.70	-0.74**	-0.32**	-2.07**	-0.76**	-0.62	-12.51**	-1.12**	-28.55**	L
ICMB 95222	-0.03	0.49	-0.60**	0.35**	0.17**	-0.25	-0.59**	0.64**	1.40**	-0.68**	-0.73	-1.07	0.27**	-10.45**	L
ICMB 99666	0.35**	0.46	0.41	-0.12**	-0.26**	0.14	1.14**	0.33**	-4.99**	0.91**	-0.75**	-0.17	-0.04	9.96**	H
ICMB 02111	-1.40**	-0.28	-3.89**	-0.50**	-0.14**	-0.72**	0.37**	-0.62**	-3.78**	-0.01	2.31**	2.51**	1.40**	-0.82	L
ICMB 02444	-0.23	-0.23	2.89**	0.07*	-0.18	-0.08	0.68**	-0.22**	-5.47**	-0.26**	10.01**	8.35**	0.06	8.90**	H
ICMB 02777	4.02**	-0.41	2.79**	0.02	-0.09	3.86**	0.68**	-0.18**	5.11**	1.57**	6.72**	4.34**	-0.60**	14.48**	H
PT 6029	-2.17**	0.28	-2.62**	-0.21**	-0.20	-0.36	0.02	-0.30*	0.91	-1.16*	-2.77**	-2.64**	-0.77**	-10.88**	L
PT 6067	-1.98**	0.26	-1.39*	-0.05	-0.16	0.38	-0.19*	-0.27*	-1.82	-0.16	3.68**	1.55**	2.03**	6.97**	H
PT 6300	-1.42**	0.13	-2.73**	-0.18*	-0.15	-0.02	0.41**	-0.36**	-5.95**	-0.22	-2.33**	-0.69	0.18	-4.23*	L
PT 6303	2.20**	0.12	0.21	-0.17*	0.37**	0.44	0.41**	0.43**	4.71**	0.22	1.50*	1.65**	-0.22	3.23	H
PT 6476	1.45**	-0.41	-1.26**	0.38**	-0.06	0.25	0.55**	0.13	-2.40*	0.78	-0.13	0.91	1.08**	12.88**	H
PT 6679	1.20**	0.57	4.01**	0.56**	-0.35**	2.16**	0.67**	0.26*	-1.10	-0.72	9.88**	6.90**	2.22**	38.83**	H
PT 6946	0.51	-0.37	0.79	0.21*	-0.30**	-0.74	-0.19*	-0.02	-3.86**	0.09	0.99	0.89	-0.17	-7.38**	L
PT 7068	-0.92**	-0.40	0.64	-0.03	-0.11	-0.74	-0.21**	0.44**	-9.48**	0.72	-2.12**	0.56	-1.84**	-6.32**	L
GMR 58	-0.98**	-0.73	-2.33**	-0.43**	0.09	-1.88**	-0.46**	-0.08	-2.27*	-0.41	-2.96**	-2.08**	-0.48**	-5.51**	L
GMR 250	1.52**	-0.05	2.94**	-0.09	0.64**	0.14	-0.17*	-0.22	8.75**	0.66	0.87	-0.71	-0.11	-6.00**	L
DMR PURPLE	-0.48	0.36	1.00	0.08	0.13	-1.43**	-0.63**	0.22	8.91**	1.03*	-11.04**	-9.86**	-1.17**	-12.60**	L
SHOOLAGIRI	1.08**	0.25	0.75	-0.08	0.09	1.82**	-0.22**	-0.23	3.61**	-0.84	4.44**	3.50**	-0.76**	-8.98**	L
SE(g_i)	0.34	0.12	0.44	0.06	0.08	0.32	0.06	0.10	0.83	0.37	0.52	0.45	0.09	1.22	-
SE(g_j)	0.42	0.15	0.54	0.08	0.11	0.39	0.07	0.12	1.02	0.46	0.64	0.56	0.12	1.56	-

*significant at 5 % level ** significant at 1% level

D50%F – days to 50 per cent flowering, LSL- leaf sheath length, LBL – leaf blade length, LSW- leaf blade width, NON – Number of Nodes, SPL – spike length, SPD – spike diameter ,NOET- number of economic tillers/plant, DTM – Days to Maturity,PLH- plant height,SEWT – Single Earhead Weight, SETWT - Single Earhead Threshed Weight , TWT – 1000 grain weight, GYP- Grain yield/Plant

Table 3 Comparison of *gca* effect and mean performance (*per se* performance) of lines and tester for yield contributing traits

Traits	*Per se*	*gca* effect	Parents with significant *gca* effect and *per se*
SPL	ICMB 89111, ICMB 02444 and ICMB 02777, PT 6303PT 6679, PT 7068 and Shoolagiri local	ICMB 89111, ICMB 94333, ICMB 95222, ICMB 02111 and ICMB 02777, PT 6679, GMR 58, DMR purple and Shoolagiri local	ICMB 89111, ICMB 02777, PT 6679 and Shoolagiri local
SPD	ICMB 93222, ICMB 99666, ICMB 02111, ICMB 02444 and ICMB 02777, PT 6300, PT 6679 and PT 7068	ICMB 89111,ICMB 93222, ICMB 94333, ICMB 95222,ICMB 99666, ICMB 02111, ICMB 02444, ICMB 02777, PT 6067, PT 6300,PT 6303,PT 6476, PT 6679, PT 7068,GMR 58, GMR 250 DMR PURPLE and Shoolagiri local	ICMB 93222,ICMB 99666, ICMB 02111, ICMB 02444 and ICMB 02777, PT 6300, PT 6679 and PT 7068
NOET	ICMB 89111, ICMB 99666, ICMB 02444, PT 6029, PT 6300, PT 6476, GMR 58, GMR 250, DMR purple	ICMB 89111,ICMB 93222, ICMB 94333, ICMB 95222,ICMB 99666, ICMB 02111, ICMB 02444, ICMB 02777, PT 6067, PT 6300,PT 6303, PT 6679, PT 7068	ICMB 89111,ICMB 99666, ICMB 02444, PT 6029, PT 6300
PHT	ICMB 89111, ICMB 94333, ICMB 95222, ICMB 02444, ICMB 02777PT 7068, GMR 58, GMR 250 DMR PURPLE and Shoolagiri local	ICMB 89111,ICMB 93222, ICMB 94333, ICMB 95222,ICMB 99666, ICMB 02444, ICMB 02777, PT 6300,PT 6476, PT 6946,PT 7068,GMR 58, GMR 250 DMR PURPLE and Shoolagiri local	ICMB 89111, ICMB 94333, ICMB 95222, ICMB 02444, ICMB 02777 PT 7068,GMR 58, GMR 250 DMR PURPLE and Shoolagiri local
SEWT	ICMB 89111, ICMB 94333, ICMB 99666, ICMB 02111, GMR 58, DMR PURPLE and Shoolagiri local	ICMB 89111,ICMB 93222, ICMB 94333, ICMB 95222,ICMB 99666, ICMB 02111, ICMB 02444, ICMB 02777,PT 6029, PT 6067, PT 6303, PT 6679, GMR 58, DMR PURPLE and Shoolagiri local	ICMB 89111, ICMB 94333, ICMB 99666, ICMB 02111, GMR 58, DMR PURPLE and Shoolagiri local
SETWT	ICMB 93222, ICMB 94333, ICMB 02777, PT 6029, PT, 6300, PT 6303, PT 7068, GMR 58, GMR 250	ICMB 93222, ICMB 94333, ICMB 95222, ICMB 02111, ICMB 02444, ICMB 02777, PT 6029, PT 606,PT 6303, PT 6679, ,GMR 58,DMR PURPLE and Shoolagiri local	ICMB 93222, ICMB 94333, ICMB 02777, PT 6029, PT 6303 and GMR 58
TW	ICMB 02111, ICMB 02777, PT 6029, PT 6067, PT 6476, PT 6679, PT 7068 and DMR PURPLE	ICMB 89111,ICMB 93222, ICMB 94333, ICMB 95222 , ICMB 02111, ICMB 02777, PT 6029, PT 6067,PT 6476, PT 6679, PT 7068,GMR 58, DMR PURPLE and Shoolagiri local	ICMB 02111, ICMB 02777, PT 6029, PT 6067,PT 6476, PT 6679, PT 7068 and , DMR PURPLE
SPY	ICMB 93222, ICMB 94333, ICMB 95222, ICMB 02777, PT 6679, PT 7068, GMR 58, GMR 250	ICMB 89111,ICMB 93222, ICMB 94333, ICMB 95222,ICMB 99666, ICMB 02444, ICMB 02777, PT 6029,PT 6067, PT 6300,PT 6476, PT 6679, PT 6946,PT 7068,GMR 58, GMR 250 DMR PURPLE and Shoolagiri local	ICMB 93222, ICMB 94333, ICMB 95222, ICMB 02777, PT 6679, ,PT 7068,GMR 58, GMR 250

SPL – spike length, SPD – spike diameter, NOET- number of economic tillers/plant, ,PLH- plant height,SEWT – Single Earhead Weight, SETWT - Single Earhead Threshed Weight , TWT – 1000 grain weight, GYP- Grain yield/Plant

crosses with high *sca* effect values for different traits were not produced by good combiner parents but rather by combinations of good x poor or poor × good combiners. Crosses like ICMB 95222 × DMR Purple, ICMB 89111 × PT 6029, ICMB 94333 × PT 6303 for the number of economic tillers per plant and ICMB 89111 × GMR 250, ICMB 95222 × GMR 58, ICMB 95222 × PT 6303, and ICMB 93222 × Shoolagiri local for plant height exhibited significant *sca* effects, indicating poor x good combiner interactions whereas ICMB 99666 x PT 6946 for the number of economic tillers per plant and ICMB 02777 × DMR Purple, ICMB 02777 × GMR 250 and ICMB 93222 × Shoolagiri local for plant height were displayed significant *sca* effect in good × poor combiner combination. This may

Table 4 Estimates of *sca, gca* and *per se* performance of hybrids and their parents of top performing hybrids for yield attributing traits

Traits	Range of *sca* effect	Range of hybrids for their mean performance	Top ranking crosses	Mean performance	*sca* effect of crosses	*gca* effect of parents	No of crosses showed significant *sca* effect combined with mean
D50%F	3.2 - 2.32	42 – 53					
LSL	-0.8 - 0.72	11.45 - 15.85	ICMB 93222x Shoolagiri local	15.85	1.31	G x P	1
LBL	-3.09 – 3	46.97 - 70.58	ICMB 02777x PT 6679	70.52	5.44	G x G	10
			ICMB 93222x PT 6946	70.58	11.11	G x P	
			ICMB 02444x GMR 250	69.31	5.20	G x P	
			ICMB 89111x PT 6476	68.18	12.96	G x G	
			ICMB 93222x PT 6679	66.27	3.57	G x G	
LBW	-0.49 - 0.44	3.23 - 6.02	ICMB 02444x PT 6679	65.2	0.66	G x G	1
NON	-0.92 - 0.61	5.3 - 8.3	ICMB 95222x GMR 58	8.3	1.19	P x P	3
			ICMB 89111x PT 6476	8.2	0.73	G x G	
			ICMB 93222x PT 6679	7.7	0.82	G x G	
SPL	-2.53 – 2.12	17.18 - 32.8	ICMB 02777x Shoolagiri local	32.8	2.73	G x P	4
			ICMB 02777x PT 6679	32.71	2.73	G x G	
			ICMB 02777x PT 6946	31.2	4.11	G x P	
			ICMB 02777x PT 6300	27.81	-2.78	G x G	
SPD	-0.68 – 0.56	6.76 - 12.48	ICMB 99666 X PT 6679	12.48	1.03	G x G	13
			ICMB 02444 X PT 6476	11.81	0.93	G x G	
			ICMB 02444 X PT 6303	11.52	0.77	G x G	
			ICMB 02444 X PT 6300	11.43	0.70	G x G	
			ICMB 99666 X PT 6300	11.28	-0.75	G x G	
NOET	-0.69 – 0.60	3.1 - 7.6	ICMB 95222 X DMR PURPLE	6.3	-0.59	P x P	5
			ICMB 89111 X PT 6029	6.0	1.35	G x P	
			ICMB 94333 X PT 6303	5.7	1.15	P x G	
			ICMB 99666 X PT 6946	5.7	0.96	G x P	
			ICMB 99666 X GMR 58	5.6	0.92	G x P	
PHT	-6.06 – 11.47	160.49 - 221.96	ICMB 02777 X DMR purple	221.96	-20.11	G x P	16
			ICMB 89111 X GMR 250	205.17	10.37	G x P	
			ICMB 95222 X GMR 58	203.58	23.16	P x P	
			ICMB 02777 X GMR 250	203.57	10.07	G x P	
			ICMB 95222 X PT 6303	203.00	15.56	P x G	
			ICMB 93222 X Shoolagiri		12.34	G x P	
DTM	-4.07 - 3.51	81.5 – 90	-	-	-	-	--
SEWT	-3.53 – 3.06-	16.85 - 66.5	ICMB 02777 X PT 6679	66.51	14.14	G x G	14
			ICMB 02444 X PT 6679	61.30	5.66	G x G	
			ICMB 93222 X PT 6946	56.32	15.77	G x P	
			ICMB 02111 X GMR 250	53.61	14.67	P x P	
			ICMB 93222 X PT 6476	50.11	11.14	G x G	
SETWT	2.94 – 3.04	10 - 46.6	ICMB 02777 X PT 6679	46.62	7.95	G x G	11
			ICMB 02444 X PT 6029	43.03	0.77	G x P	
			ICMB 89111 X 6679	41.74	7.30	G x G	
			ICMB 02777 X PT 6303	40.51	4.04	G x G	
			ICMB 02444 X PT 6300	38.82	3.89	G x G	
TW	-0.68 – 0.6	6.92 - 20.99	ICMB 99666 X PT 6679	20.94	0.82	G x G	20
			ICMB 93222 X PT 6679	17.83	2.73	G x G	
			ICMB 93222 X PT 6067	17.26	2.35	G x G	
			ICMB 02777 X PT 6679	16.79	2.92	G x G	
			ICMB 02111 X DMR purple	15.88	1.64	G x P	
GPY	-8.01 – 8.11	69.70 - 215.20	ICMB 02777 X PT 6679	215.21	52.04	G x G	15
			ICMB 02444 X PT 6679	197.72	39.77	G x G	
			ICMB 93222 X PT 6679	169.11	16.37	G x G	
			ICMB 93222 X PT 6067	158.11	37.22	G x G	
			ICMB 02111 X PT 6067	150.20	34.55	P x G	

D50%F – days to 50 per cent flowering, LSL- leaf sheath length, LBL – leaf blade length, LSW- leaf blade width, NON – Number of Nodes, SPL – spike length, SPD – spike diameter ,NOET- number of economic tillers/plant, DTM – Days to Maturity,PLH- plant height,SEWT – Single Earhead Weight, SETWT - Single Earhead Threshed Weight , TWT – 1000 grain weight, GYP- Grain yield/ Plant

Table 5. Comparison of *sca* effect, *per se* performance and standard heterosis of top performing hybrid over C0H 10 and 86M38 for yield contributing traits

Traits	*per se* performance	Crosses with significant *sca* effect	Standard Heterosis	
			C0H 10	86M 38
SPL	32.8*	ICMB 02777x Shoolagiri local	-4.06	16.90 *
	32.71*	ICMB 02777x PT 6679	-3.08	18.09 *
	31.2*	ICMB 02777x PT 6946	-7.56 *	12.64 *
	27.81*	ICMB 02777x PT 6300	-17.48 *	0.54*
SPD	12.48	ICMB 99666 x PT 6679	15.77**	4.09**
	11.81	ICMB 02444 x PT 6476	12.17**	-1.58ns
	11.52	ICMB 02444 x PT 6303	6.12**	-4.59ns
	11.43	ICMB 02444 x PT 6300	6.68**	-4.09ns
	11.28	ICMB 99666 x PT 6300	-3.15ns	12.93**
NOET	6.3	ICMB 95222 x DMR purple	53.66**	55.56**
	6.0	ICMB 89111 x PT 6029	46.34**	48.15**
	5.7	ICMB 94333 x PT 6303	39.02**	40.74**
	5.7	ICMB 99666 x PT 6946	39.02**	40.74**
	5.6	ICMB 99666 x GMR 58	36.59**	38.27**
PHT	221.96	ICMB 02777 x DMR purple	54.94**	18.16**
	205.17	ICMB 89111 x GMR 250	43.22**	9.22**
	203.58	ICMB 95222 x GMR 58	42.35**	8.56**
	203.57	ICMB 02777 x GMR 250	41.92**	8.23**
	203.00	ICMB 95222 x PT 6303	41.70**	8.06**
		ICMB 93222 x Shoolagiri		
SEWT	66.51	ICMB 02777 x PT 6679	35.16 **	76.86 **
	61.30	ICMB 02444 x PT 6679	25.59**	63.03**
	56.32	ICMB 93222 x PT 6946	13.92**	49.01**
	53.61	ICMB 02111 x GMR 250	8.94ns	42.55**
	50.11	ICMB 93222 x PT 6476	2.24ns	33.78**
SETWT	46.62	ICMB 02777 x PT 6679	16.94**	61.53**
	43.03	ICMB 02444 x PT 6029	-9.16ns	25.58**
	41.74	ICMB 89111 x 6679	4.64ns	44.54**
	40.51	ICMB 02777 x PT 6303	-14.81**	17.68**
	38.82	ICMB 02444 x PT 6300	-2.26**	35.01**
TW	20.94	ICMB 99666 x PT 6679	-4.71ns	17.92**
	17.83	ICMB 93222 x PT 6679	20.07**	48.58**
	17.26	ICMB 93222 x PT 6067	16.23**	43.83**
	16.79	ICMB 02777 x PT 6679	13.06*	39.92**
	15.88	ICMB 02111 x DMR purple	-4.98ns	17.58**
SPY	215.21	ICMB 02777 x PT 6679	60.06**	90.06 **
	197.72	ICMB 02444 x PT 6679	46.78**	84.70 **
	169.11	ICMB 93222 x PT 6679	25.79**	58.28**
	158.11	ICMB 93222 x PT 6067	17.60**	47.97**
	150.20	ICMB 02111 x PT 6067	11.57**	40.90**

SPL – spike length, SPD – spike diameter ,NOET- number of economic tillers/plant, ,PLH- plant height,SEWT – Single Earhead Weight, SETWT - Single Earhead Threshed Weight , TWT – 1000 grain weight, GYP- Grain yield/Plant

be attributed to the better complementation of desirable alleles present in the parental lines. This finding aligns with research by Madane *et al.* (2023), Patel *et al.* (2018), and Solanki *et al.* (2017). Hence, when choosing parents for a hybridization program, it is important to consider both average and poor combiners. Crosses that involve two good general combiner parents should be promoted to generate the desired transgressive segregants. This is because their heterotic effects may be attributed to pseudo-additive interallelic interactions.

According to current observations, it appears that specific combining ability (SCA) has a more pronounced impact on all traits compared to general combining ability (GCA). This implies that the influence of dominance gene action is substantial for these traits. Enhancing these characteristics can be achieved through hybrid breeding or by selecting segregants in subsequent generations.

Estimates of standard heterosis : Hybrids under heterosis breeding program need to meet two essential criteria, namely, mean performance and displaying significant standard heterosis. Consequently, the hybrids were evaluated based on each of these criteria and then collectively recommended for use in heterosis breeding programs. The standard heterosis over checks COH 10 and private hybrid 86M38 for yield contributing traits of top performing hybrids are presented in **table 6**. The range of standard heterosis of grain yield per plant was observed from -48.16 to 60.06 per cent to check COH 10 and from -34.77 to 90.06 per cent for check 86M38. The hybrid *viz.,* ICMB 02777 × PT 6679 (60.06%, 90.06%,), ICMB 02444 × PT 6679 (46.78%, 84.70 %), ICMB 93222 × PT 6679 (25.79%, 58.28%), ICMB 93222 × PT 6067 (17.60, 47.97%) and ICMB 02111 × PT 6067 (11.57%, 40.90%) were expressed positive significant standard heterosis over COH 10 and private hybrid 86M38 along with positive significant *sca* effect for grain yield per plant. The hybrid ICMB 02777 × PT 6679 showed positive significant *sca* effect combined with positive significant standard heterosis over both check for other yield contributing traits viz., test weight, single ear head weight and single earhead threshed weight. the hybrid ICMB 93222 x PT 6679 had significant positive standard heterosis for test weight along with yield and ICMB 02444 x PT 6679 showed positive standard heterosis for single earhead weight combined with grain yield. These superior hybrids may be commercially utilized to obtain benefits of heterosis for grain yield and yield contributing traits. Similar findings were reported by Surendar *et al.* (2023), Subbulakshmi *et al.* (2018) and Karvar *et al.* (2017). These crosses displayed notably favorable levels of both general combining ability (GCA) and specific combining ability (SCA) for grain yield and its component traits. This suggests that the exceptional performance of these crosses is influenced by both the overall genetic makeup and the specific interactions of the parent plants. The genetic characteristics of these crosses can be harnessed through hybridization and reciprocal recurrent selection in subsequent generations to enhance pearl millet yields.

Relationship between heterosis and combining ability: The study presented in **table 6** showed the simple correlation coefficients between heterosis and combining ability conducted based on Liu *et al.* (2021) for yield and yield-related traits, revealing a strong and significant correlation with nearly all traits. Specifically, standard heterosis for grain yield had a highly significant correlation with general combining ability for grain yield (r = 0.73) and traits related to yield, such as spike length (r = 0.77), spike girth (r = 0.80), single earhead weight (r = 0.72), single earhead threshed weight (r = 0.82), and test weight (r = 0.59). The strongest correlations for grain yield were observed between standard heterosis and general combining ability for spike girth and single earhead threshed weight. On the other hand, specific combining ability for all traits exhibited a similar trend of correlation with standard heterosis for grain yield (r = 0.65) and yield-related traits, including spike length (r = 0.62), spike girth (r = 0.60), single earhead weight (r = 0.57), single earhead threshed weight (r = 0.58), and test weight (r = 0.78).

Based on these correlation studies, it is evident that the relationship between the parental general combining ability (GCA) and the heterosis of the hybrid is generally stronger than that between specific combining ability (SCA) and heterosis. This implies that the sum of parental GCA values is a more reliable predictor of the observed heterosis in all traits compared to SCA. Although GCA values are stronger than SCA, it's important to note that SCA is influenced by dominance and nonallelic gene interactions, similarly heterosis also primarily driven by dominance and nonallelic interactions. Hence, heterosis primarily depends on the effects of SCA. Therefore, the strength of SCA in a given hybrid plays a crucial role in determining the extent of heterosis. In the current study, both GCA and SCA can be used as predictors of heterosis in synthesized hybrids. Similar findings were reported by Liu *et al.* (2021) regarding the correlation between combining ability and heterosis.

The current research, the GCA/SCA variance less than one reveals the prevalence of non-additive gene action in all traits and highlighting the potential of heterosis breeding to exploit hybrid vigor. Despite the significant influence of SCA on heterosis, the combined effect of parental GCA values has demonstrated its accuracy as a predictor of heterosis, making it a valuable tool in hybrid breeding. Lines *viz.,* ICMB 02777, ICMB 02444, and ICMB 93222, and among the testers namely PT 6679, PT 6067, PT 6300, PT 6476, and PT 6300, are considered outstanding parental lines and the resultant hybrid were high-yielding combinations. Based on assessments of *per se* performance and specific combining ability, the

Table 6. Correlation coefficient between standard heterosis and combining ability

	D50F	LSL	LBL	LBW	NON	SPL	SPG	NOET	PHT	DTM	SEWT	SETWT	TW	GYP
STH -G	0.88**	0.62**	0.57**	0.71**	0.75**	0.77**	0.80**	0.57**	0.61**	0.50**	0.72**	0.82**	0.59**	0.73**
STH - S	0.47**	0.78**	0.81**	0.68**	0.67**	0.62**	0.60**	0.82**	0.79**	0.86**	0.57**	0.55**	0.78**	0.65**

*significant at 5 % level ** significant at 1% level D50%F – days to 50 per cent flowering, LSL- leaf sheath length, LBL – leaf blade length, LSW- leaf blade width, NON – Number of Nodes, SPL – spike length, SPD – spike diameter ,NOET- number of economic tillers/ plant, DTM – Days to Maturity,PLH- plant height,SEWT – Single Earhead Weight, SETWT - Single Earhead Threshed Weight , TWT – 1000 grain weight, GYP- Grain yield/Plant, STH – Stnadard Heterosis, G – General combining ability, S- Specific combining ability hybrids ICMB 02777 x PT 6679, ICMB 02444 x PT 6679, ICMB 93222 x PT 6679, ICMB 93222 x PT 6067, and ICMB 02111 x PT 6067 exhibited significant positive specific combining ability effects along with substantial standard heterosis. These hybrid combinations are of significant practical importance and have the potential for commercial utilization. They should undergo further assessment in extensive multi-location testing trials to confirm their suitability and performance in various environmental conditions.

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