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RESEARCH ARTICLE

Heterotic potential of partial male sterile-based hybrids in finger millet (*Eleusine corocona* L.): Implications to genetic improvement

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Abstract

Finger millet, a nutrient-rich and climate-resilient cereal, faces declining cultivation due to poor productivity, largely because of the lack of effective hybridization techniques. A set of 46 hybrids developed through partial male sterile line PS 1 was evaluated in summer and *kharif* seasons. Significant differences were observed among hybrids and parents for 16 traits, with key yield traits showing strong genotype × environment (G×E) interactions. Heterosis for grain yield ranged from -41.7% to 58.1% during summer and -38.5% to 48.4% in *kharif* over the check variety GPU 28. Notably, the hybrid PS1 × GE 4972 exhibited stable heterosis 23.4% and 48.4%), respectively across both the seasons, while PS1 × GE 4764 (58.1%), PS1 × GE 436 (31.9%) and PS1 x MR1 (26.6%) showed season-specific heterosis. These hybrids showed highest heterosis, reported thus far in finger millet and indicated the crop's potential for increased productivity. Promising heterotic hybrids were also identified for traits like fodder yield, ear head weight, and seed weight. High correlations between hybrid means and mid-parent values for traits like finger length, days to maturity, and seed weight suggested additive gene action. Genetic diversity analysis of 47 parents revealed substantial diversity and geographical clustering. However, no direct correlation was observed between heterosis and parental divergence based on morphological or SSR polymorphism. The present study is the first extensive heterosis investigation in finger millet demonstrating the potential of partial male sterility for improved hybridization and exploring broader genetic pools. The promising hybrids and parental lines offer new opportunities for finger millet improvement.

Keywords: Partial male sterility, heterosis, finger millet, parental diversity

Introduction

Climate change poses a threat to global food security by diminishing crop yields owing to rising temperatures. The agricultural regions in India are experiencing a decline in yield (Daloz et al. 2021). Finger millet (*Eleusine corocona* L.) cultivated by small farmers across Asia and Africa is noteworthy (Gebreyohannes et al. 2024). This self-pollinating C4 cereal (AABB, 2n=4x=36) is rich in calcium (350 mg/100 g) and potassium (408 mg/100 g) (Puranik et al. 2017). Amylopectin-rich carbohydrates are beneficial for diabetics, and its protein is both gluten-free and high in methionine (Kaur et al. 2024). The FAO acknowledges it as a future smart food owing to its climate resilience and nutritional value (Li and Siddique 2018). Its resistance to storage pests allows extended preservation (Gupta et al. 2017). Although crossing Indian and African gene pools has doubled productivity (Sood et al. 2019), yields have plateaued (Wright and Devos 2024), necessitating further research.

The yield barrier in finger millet can be overcome by leveraging crop diversity (Gebreyohannes et al. 2024) and heterosis. A significant challenge is the lack of efficient hybridization tools. The inbreeding nature and small florets

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of the crop complicate emasculation, necessitating natural crossing. Morphological pigmentation in male parents helpsto identify hybrids, but this limits the exploitation of diversity. Limited studies on heterosis (Gupta and Kumar 2009; Shailaja et al. 2010; Parashuram et al. 2011), often based on few plants due to low hybrid recovery in fertile × fertile crosses (Manjappa et al. 2024), may not provide fully reliable conclusions. A versatile male-sterile system could address this hybridization challenge. Although genetically male-sterile (INFM 95001) plants are available, maintenance issues restrict their application (Gupta et al. 1997). The Project Coordinating Unit, ICAR, GKVK, Bengaluru, developed a partial male sterile mutant, ps1, from the GPU 28 line (Gowda et al. 2014). ps1 sets 10% seeds upon selfing, facilitating maintenance with 20% seed set under open pollination and 49% under controlled crossing (Nagaraja et al. 2023). ps1's ease of maintenance, potential for hybrid production, and superior background make it ideal for heterosis studies. The present study explored heterosis by crossing 46 genotypes with ps1 over two seasons and analyzed their relationship with genetic diversity.

Materials and methods

Plant materials

The Partial sterile mutant (ps1) expressing 10% seed set (Fig. 1a), derived from the variety GPU 28 (Fig. 1b), served as the female parent. The 46 male parents included 28 improved varieties from India (Supplementary Table S1) and 18 elite germplasms from Asia and Africa (Supplementary Table S2), chosen for their blast resistance, high yield, early maturity, dwarf stature, drought tolerance, and stay-green characteristics. Fig. 1 illustrates the morphological features of the ps1 ear head compared to GPU 28. Seeds from 46 genotypes and a partially sterile line (ps1) were sown in a 1:1 ratio with a spacing of 10×30 cm, and 45 cm between crossing pairs, at GKVK, Bengaluru (12° 58′ N, 77° 35′ E, 930m MSL). Employing a modified contact method, ear heads of both parents that had just begun to bloom were selected after the flowered spikelets were removed. The fingers were then tied together and enclosed in butter paper to prevent pollen contamination (Fig. 2a). This paper was removed once seed filling commenced (Fig. 2b); ps1 seeds were harvested for heterosis assessment over two seasons.

Evaluation of hybrids

The hybrids, male parents, and check GPU 28 were assessed during the summer (February-May) and *kharif* (June-September) seasons using a Randomized Block Design with two replications. The lines were grown in three 3-meter rows with spacing of 10×22.5 cm, accommodating 90 competitive plants (Fig. 2c). Plants from crossed seeds exhibited a high proportion of fertile hybrids and a low occurrence of selfed, partially sterile ps1 plants. True hybrids were identified by

(a) (b)

Fig. 1. Morphological features of partial male sterile mutant ps1 (a) showing ~10% seed set compared to its wild type GPU 28 (b)

a complete seed set in ear during grain filling, whereas selfed plants showed only 10% seed set in ear (Fig. 2c). Observations were recorded on five randomly selected fertile plants, except for ear weight, fodder weight, and grain yield, which were recorded on ten plants. Eighteen traits were studied in the summer and 20 in *kharif,* including leaf and finger blast. Leaf blast severity was rated on a scale of 0-5.

Observations were recorded on nodal/ear head pigmentation, ear head shape, days to 50% flowering (DF), maturity (DM), productive tillers per plant (PT), plant height (PHT), peduncle length (PL), flag leaf length (FLL), width (FLW), finger length (FL), width (FW), fingers per ear head (FN), 1000 seed weight (TW), fodder weight (FOW), ear head weight (EW), grain yield (YLD), threshing percentage (TP), and harvest index (HI). At maturity, sun-dried panicles were threshed to determine the YLD and TP. Plants were cut at ground level and sun-dried for FOW.

Statistical analysis

Heterosis (hybrid vigor) was estimated by comparing hybrid performance with parents using three approaches: mid-parent heterosis (MPH), better parent heterosis (BPH), and standard heterosis (SH). MPH, BPH, and SH were calculated by comparing hybrid performance against the average of parents, better parent, and the standard check variety (GPU 28), respectively. Significance of heterosis was tested using the 't'-test. Correlation between mid-parent values and *per se* hybrid means was analyzed to understand the genetic nature of traits (Labroo et al. 2021). Individual and pooled ANOVA for randomized block design (RBD) trials were conducted using Microsoft Excel 2019.

Eighteen phenotypic traits, including pigmentation and ear shape, were used to assess parental diversity. Qualitative traits were numerically rated following IBPGR finger millet descriptors. Pairwise genetic dissimilarity was

Table 1. Pooled ANOVA of hybrids and parents for yield and its contributing traits, evaluated across Summer and *Kharif*

SV	d. f.	DF	DM	PT	PHT	PL	FLL	FLW	FL
Environment (E)	1	1424.69**	1564.97**	16.19**	95791.22**	14.38**	6420.89**	0.17**	1.68**
Replications/E	2	838594.14**	1946526.48**	1472.22**	2004538.40**	111755.98**	155016.19**	160.96**	7536.16**
Genotypes (G)	92	58.74**	112.37**	0.58**	576.93**	27.61**	44.46**	0.02**	6.89**
Parent (P)	46	96.58**	184.32**	0.61**	591.08**	28.21**	37.32**	0.03**	9.48**
Hybrids (H)	45	21.10**	41.16**	0.49**	166.12**	7.51*	8.42	0.01	3.59**
P vs H	1	11.92**	7.32	3.21**	18413.08**	904.69**	1994.26**	0.19**	36.03**
G x E (G x E)	92	12.39**	11.12**	0.34**	121.12**	9.63**	10.30*	0.01**	0.29
P x E	46	21.23**	16.35**	0.26	85.18	8.17**	9.74	0.02**	0.27
H x E	45	3.60**	5.73**	0.41**	43.64	7.12*	10.99*	0.01	0.31
P vs H x E	1	2.08	13.63*	0.24	5260.68**	189.46**	5.15	0.12**	0.00
Error	184	1.67	2.79	0.20	68.41	4.62	7.16	0.01	0.29
Total	371	22.31	36.23	0.37	465.23	11.56	34.44	0.01	1.93
CV (%)		1.92	1.63	16.08	7.97	8.77	9.27	9.71	8.53
SV	d. f.	FW	FN	TW	FOW	EW	YLD	TP	HI
Environment (E)	1	0.11**	256.28**	1.03**	10421.00**	179.76**	73.19**	157.34**	1751.85**
Replications/E	2	180.18**	8998.87**	1762.91**	182672.54**	45581.35**	28890.55**	1185633.6**	137197.63**
Genotypes (G)	92	0.01**	2.68**	0.41**	252.55**	60.18**	38.49**	56.46**	57.75**
Parent (P)	46	0.02**	2.24**	0.48**	173.23**	25.29**	14.37**	65.39**	83.44**
Hybrids (H)	45	0.00	1.03**	0.13**	144.82**	35.01**	20.95**	45.39**	30.87**
P vs H	1	0.00	96.80**	10.16**	8749.10**	2797.87**	1937.69**	144.51**	85.77**
G x E (G x E)	92	0.01**	0.98**	0.07**	77.74**	19.18**	10.94**	23.35**	30.49**
P x E	46	0.01**	1.03**	0.08**	62.21**	8.74**	5.79**	19.56**	33.52**
H x E	45	0.00	0.69	0.04**	94.91**	18.65**	9.56**	27.20**	15.72**
P vs H x E	1	0.01	11.64**	0.66**	19.63	523.45**	309.85**	23.99**	555.97**
Error	184	0.00	0.50	0.01	28.50	5.31	2.84	11.28	8.28
Total	371	0.01	1.85	0.13	124.13	22.80	13.86	25.81	30.71
CV (%)		5.63	10.22	3.84	17.04	14.72	13.52	4.21	10.60

*&** Significant at 0.05, 0.01 and 0.001 probability level; All values except CV are Mean Sum of Squares
DF = Days to 50% flowering; DM = Days to maturity; PT = Productive tiller number per plant; PHT = Plant height (cm); PL = Peduncle length (cm); FLL = Flag leaf length (cm); FLW = Flag leaf width (cm); FL = Finger length (cm); FW = Finger width (cm); FN = Fingers per ear head; FOW = Fodder weight per plant (g); EW = Ear head weight per plant (g); YLD = Grain yield per plant (g); TP = Threshing % and HI = Harvest index (%)

calculated using Gower's distance (Gower 1985) in SAS v.9.3, and principal coordinate analysiswas performed using DARwin v.6.0. A Neighbor-joining tree was constructed with weighted criteria and 10,000 bootstraps (Saitou & Nei, 1987). The relationship between heterosis and parental divergence was analyzed via correlation of Gower's genetic distance and mid-parent heterosis, with significance tested using Pearson's correlation and 't'-test. Additionally, heterosis was correlated with parental divergence based on 20 polymorphic SSR markers (Manjappa et al. 2018) using the Mantel test (Mantel 1967).

Results and discussion

Forty six hybrids were developed using the partially male sterile (ps1) as the female parent, while male parents were chosen irrespective of pigmentation differences. The material was planted in two replications with observations recorded from ten randomly selected plants per hybrid. These hybrids were assessed during the summer and *kharif* seasons to determine their seasonal specificity and stability. This study marks a pioneering effort in generating extensive hybrids in finger millet through male sterility, supported by a large sample size (Fig. 2c).

Pooled ANOVA over two seasons

Analysis of variance showed significant variation among genotypes (G), hybrids (H), and parents (P) for most traits, except for flag leaf length, width, and finger width in H.

Table 2. Relative contribution of G × E interaction variance to genotypic variance (%)

Type of G x E interaction	DF	DM	PT	PHT	PL	FLL	FLW	FL
G x E	21.1	9.9	58.1	21.0	34.9	23.2	60.1	4.2
P x E	22.0	8.9	43.2	14.4	29.0	26.1	52.3	2.8
H x E	17.0	13.9	84.5	26.3	94.9	130.6	93.5	8.7
P vs H x E	17.5	186.1	7.6	28.6	20.9	0.3	63.0	0.0
Type of G x E interaction	FW	FN	TW	FOW	EW	YLD	TP (%)	HI (%)
G x E	40.0	36.7	16.6	30.8	31.9	28.4	41.3	52.8
P x E	35.0	46.2	17.4	35.9	34.5	40.3	29.9	40.2
H x E	77.3	67.4	31.6	65.5	53.3	45.6	59.9	50.9
P vs H x E	0.0	12.0	6.5	0.2	18.7	16.0	16.6	648.2

Table 3. Mean and range of 46 hybrids for blast disease reaction, yield and its attributing traits evaluated during two seasons

Traits	Season	Mean	Range	Traits	Season	Mean	Range
LB	*Kharif*	1.6	0.5-2.5	FW	Summer	1.0	1.0-1.1
FB	*Kharif*	7.7	0-15.8		*Kharif*	1.0	0.8-1.0
DF	Summer	65.3	58.0-70.5	FN	Summer	6.8	5.4-8.7
	Kharif	69.4	64.0-75.0		*Kharif*	8.1	6.9-9.4
DM	Summer	100.1	90.0-108.0	TW	Summer	3.2	2.6-3.6
	Kharif	104.7	94.0-111.0		*Kharif*	3.3	2.8-3.8
PT	Summer	3.1	2.3-5.0	FOW	Summer	30.7	18.9-56.7
	Kharif	2.7	1.9-3.6		*Kharif*	41.8	19.6-59.5
PHT	Summer	91.7	74.2-105.1	EW	Summer	18.9	12.7-34.8
	Kharif	130.8	111.3-143.7		*Kharif*	17.9	11.3-29.9
PL	Summer	25.6	21.4-29.5	YLD	Summer	15.2	9.7-26.4
	Kharif	26.6	23.3-30.8		*Kharif*	14.3	9.4-22.6
FLL	Summer	27.2	21.2-31.5	TP	Summer	80.9	71.3-90.7
	Kharif	35.2	30.9-39.7		*Kharif*	80.1	66.9-88.9
FLW	Summer	0.9	0.8-1.0	HI	Summer	31.0	22.6-41.3
	Kharif	1.0	0.9-1.1		*Kharif*	24.2	16.3-33.7
FL	Summer	6.6	5.0-8.2				
	Kharif	6.7	5.2-8.7				

The P contributed more to genotypic variation than the H for all traits except ear weight and grain yield (Table 1), indicating rich parental diversity. P vs H was significant for all traits except for flag leaf dimensions and finger width. The environmental (E) component was significant for all traits, showing expression differences across seasons. While G and G × E interactions were significant (Table 2), the G × E contribution was only 4-10% for finger length and maturity, indicating a low environmental influence. However, the harvest index, productive tillers, flag leaf width, peduncle length, finger number, fodder weight, and ear head weight showed a higher E influence (30-60%). Similar trends were observed for the P × E and H × E interactions. Parents showed significant differences for leaf and finger blast resistance, whereas hybrids showed significance only for leaf blast, possibly due to resistance from the female parent ps1 (Supplementary Table S3).

Mean and range of hybrid performance and heterosis

Finger millet is mainly affected by blast disease caused by *Pyricularia grisea* (Cooke) causing leaf loss up to 50% in wet season and reaches up to 90% under congenial condition (Rajesh et al. 2025). Disease screening during the *kharif* season revealed a reduction in leaf and finger blast in the hybrids (leaf blast 1.6; finger blast 7.7) with low range, which

Table 4. Heterosis and mean performance of selected hybrids for blast disease reaction, yield and its attributing traits evaluated during summer and *kharif*

Traits	Hybrids with superior mean and heterosis	Heterosis % (Summer)			Heterosis % (*Kharif*)			Mean value (unit)	
		MPH	BPH	SH	MPH	BPH	SH	Summer	*Kharif*
LB	No. of desired hybrids	-	-	-	1	0	0	Scale	
	ps 1 x PRM 1	-	-	-	-47.8**	-	-	-	1.5
	GPU 28	-	-	-	-	-	-	-	1.3
FB	No. of desired hybrids	-	-	-	2	0	0	%	
	ps 1 x UduruMallige	-	-	-	-78.6**	-	-	-	4.6%
	ps 1 x GE 436	-	-	-	-50.3*	-	-	-	9.2%
	GPU 28	-	-	-		-	-	-	1.5%
DF	No. of desired hybrids	6	1	9	11	3	14	Days	
	ps 1 x VL 315	-3*		-8.57**	-	-	-12.8**	58	64
	ps 1 x UduruMallige	-	-	-5.71**	-	-	-9**	60.5	66
	ps 1x VL 149	-4.8**	-	-8.57**	-	-	-5.3**	63	64
	ps 1 x OEB 526	-	-		-4.5**	-	-12**	58.5	68
	ps 1 x GN 2	-	-	-6.43**	-	-	-5.3**	63	65.5
	ps 1 x BM 2	-	-	-3.57*	-	-	-6**	62.5	67.5
	ps 1 x KOPN 235	-	-	-	-7.8**	-	-	67.5	74
	GPU 28	-	-	-	-	-	-	66.5	70
DM	No. of desired hybrids	10	1	12	11	2	15	Days	
	ps 1 x VL 315	-4.3**	-	-10.9**	-3.6**	-	-11.7**	90	94
	ps 1 x UduruMallige	-2.6*	-	-7.4**	-	-	-9.4**	93.5	96.5
	ps 1x VL 149	-5.2**	-	-9.9**	-	-	-5.2**	91	101
	ps 1 x OEB 526	-	-	-3*	-3**	-	-9.4**	98	96.5
	PS 1 x GN 2	-	-	-4.5**	-	-	-6.6**	96.5	99.5
	PS 1 x BM 2	-	-	-3.5**	-	-	-7**	97.5	99
	PS 1 x KOPN 235	-	-	-	-7.6**	-	-	108	107
	GPU 28	-	-	-		-	-	101	106.5
PT	No. of desired hybrids	4	2	4	2	0	2	No's	
	ps 1 x VL 315	28*	-	-		-	-	3.6	3.0
	ps 1 x GE 3112	-	-	-	30.8*	-	37.3*	3.5	3.5
	ps 1 x GE 4764	81.8**	56.3**	56.3**	-	-	-	5.0	2.5
	ps 1 x GE 3666			32.8*	-	-	-	4.3	2.9
	ps 1 x A 404	22.3*		26.6*	29.7*		41.2*	4.1	3.6
	PS 1 x GE 4703	57.3**	38.3**	38.3**				4.4	2.7
	GPU 28							3.2	2.6
FL	No. of desired hybrids	2	0	5	12	5	15	cm	
	ps 1 x PRM 1	31.8**	-	-	53.8**	26.8**	26.8**	7	8.4
	ps 1 x GE 3666	-	-	20.7*	12.1*	-	23.3**	8.2	8.2
	ps 1 x GE 4693	-	-	18.5*	10.9*	-	25.3**	8	8.3
	ps 1 x GE 4798	-	-	-	12.2*	-	30.9**	7.5	8.7
	ps 1 x GE 4683	-	-	17*	13.6**	-	29.7**	7.9	8.6
	ps 1 x GE 1	-	-	-	22**	14.6*	30.6**	7.3	8.7
	ps 1 x KOPN 235	15*	-	19.3*	14.3**	-	21.5**	8.1	8.1
	GPU 28	-	-	-	-	-	-	6.8	6.6

Contd. .....

FN	No. of desired hybrids	22	7	8	30	13	36	No's	
	ps 1 x VL 315	40.5**	24.4*	24.4*				7.9	7.8
	ps 1 x OEB 526	-	-	-	-	-	35.3**	7.1	9.2
	ps 1 x GN 2	-	-	-	21.6**	-	36.8**	7.2	9.3
	ps 1 x Indaf 9	-	-	-	22.1**	-	38.2**	6.4	9.4
	ps 1 x GE 4972	-	23.8*	23.8*	25.4**	21.9**	-	7.9	8.775
	ps 1 x GE 5078	-	-	25.2*	-	-	-	8.0	7.5
	ps 1 x L 5	59.6**	37.8**	37.8**	-	-	-	8.7	8.525
	GPU 28	-	-	-	-	-	-	6.4	6.8
TW	No. of desired hybrids	14	1	4	24	3	5	g	
	ps 1 x GE 436	10**	-	-	9.46**	-	-	3.112	3.321
	PS 1 x GE 4693	-	-	13.8**	11.19**	-	9.1**	3.608	3.729
	ps 1 x GE 4687	8.6*	8*	8*	11.97*	-	-	3.425	3.540
	ps 1 x GE 4972	-	-	-	44.5**	30.6*	30.6*	31.9	59.2
	ps 1 x VR 762	47.1**	-	-	-	-	-	38.6	48.6
	GPU 28	-	-	-	-	-	-	33.6	45.3
EW	No. of desired hybrids	16	2	2	8	2	2	g	
	ps 1 x GE 4972	52.7**	23.6*	23.6*	56.6**	45.2**	45.2**	25.7	27.5
	ps 1 x GE 4764	119.7**	67.1**	67.1**	45.9**			34.8	20.7
	ps 1 x GE 436	-	-	-	91.4**	58.2**	58.2**	15.9	29.9
	ps 1 x TRY 1	41.8**	-	-	30.7*	-	-	21.9	21.0
	ps 1 x GE 4703	45.3**	-	-	52.5**	-	-	21.6	23.3
	ps 1 x HR 911	41.4**	-	-		-	-	21.8	17.1
	ps 1 x Indaf 7	39.4**	-	-	-	-	-	24.4	18.7
	ps 1 x GE 1130	47.9**	-	-	-	-	-	22.3	15.9
	GPU 28	-	-	-	-	-	-	20.8	18.9
YLD	No. of desired hybrids	21	2	2	9	3	3	g	
	ps 1 x GE 4972	53.9**	23.4*	23.4*	54.7**	48.4**	48.4**	20.6	22.6
	ps 1 x GE 4764	111.5**	58.1**	58.1**	54.9**	-	-	26.4	16.9
	ps 1 x GE 436	-	-	-	62.7**	31.9**	31.9**	13.4	20.1
	ps 1 x MR 1	-	-	-	34.4**	26.6*	26.6*	16.8	19.3
	ps 1 x TRY 1	40**	-	-	27*	-	-	17.5	16.4
	ps 1 x GE 4703	50.1**	-	-	40.5**	-	-	17.9	16.8
	ps 1 x HR 911	47.1**	-	-	-	-	-	18.1	13.6
	ps 1 x Indaf 7	33.1**	-	-	-	-	-	18.8	14.8
	ps 1 x GE 1130	53.2**	-	-	-	-	-	18.2	12.6
	GPU 28	-	-	-	-	-	-	16.7	15.2
HI	No. of desired hybrids	9	3	3	3	0	3	%	
	ps 1 x VL 315	34.3**	34.1**	34.1**	-	-	-	41.3	21.6
	ps 1 x UduruMallige	22.2*	-	-	30.4*	-	-	32.5	25.0
	ps 1 x BM 2	29.9**	27.6**	27.6**		-	-	39.3	26.9
	ps 1 x CO 13	15.7*	-	-	-	-	-	34.0	23.1
	ps 1 x CO 14	22*	-	-	-	-	-	31.9	23.7

Contd. .....

ps 1 x GE 436	-	-	-	-	-	26.5*	35.6	29.9
ps 1 x GPU 67	18.4*	-	-	26.4**		42.8**	33.1	33.7
ps 1 x GE 4972	19.2*	-	-	-	-	-	35.7	26.0
ps 1 x GE 4939	-	-	-	37.9**	-	-	30.8	27.7
ps 1 x PR 1044	18.8*	-	-	-	-	-	32.5	19.0
ps 1 x L 5	31.4**	20.1*	20.1*	-	-	-	37.0	27.6

Table 5. Correlation between mid-parent value and hybrid value

Traits	DF	DM	PT	PHT	PL	FLL	FLW	FL
Summer	0.732**	0.767**	0.349*	0.472**	0.409**	0.185	0.187	0.817**
Kharif	0.661**	0.776**	0.146	0.479**	0.423**	0.458**	-0.058	0.853**
Summer	FW	FN	TW	FOW	EW	YLD	TP	HI (%)
Kharif	-0.118	0.599**	-0.039	0.210	0.094	0.087	0.258	0.471**
Summer	0.119	-0.157	0.727**	0.178	0.103	-0.006	0.398**	0.141

*&** Significant at 0.05and 0.01 probability level

Table 6. Association and regression analysis between heterosis and parental distance for yield and its contributing traits evaluated during the summer and *kharif*

Traits	Summer					*Kharif*				
	r		b	SE	R2	r		b	SE	R2
	SSR	P				SSR	P			
DF	-0.043	-0.05				0.196	0.18			
DM	0.024	-0.01				0.096	0.08			
PT	-0.063	0.07				-0.151	-0.07			
PHT	0.208	0.29*	25.43	12.61	0.08	0.209	0.09			
PL	0.257	0.01				-0.116	0.41**	36.18	12.25	0.17
FLL	0.025	0.22				-0.037	0.42**	38.93	12.84	0.17
FLW	-0.083	0.35*	47.51	19.24	0.12	-0.084	0.31*	19.16	8.85	0.10
FL	0.043	0.11				0.160	0.17			
FW	0.248	0.27				-0.043	0.25			
FN	0.183	0.22				0.071	0.06			
TW	0.147	-0.16				0.127	0.33*	35.86	15.44	0.11
FOW	0.032	0.04				0.067	0.15			
EW	0.055	-0.004				0.175	-0.09			
YLD	0.047	0.04				0.171	-0.04			
TP (%)	-0.006	0.21				-0.050	0.10			
HI (%)	0.051	0.08				0.101	-0.17			

*&** Significant at 0.05and 0.01 probability level; r = Correlation between heterosis and parental divergence estimated based on SSR alleic data (SSR) and phenotypic data (P); b =Regression coefficient; SE = Standard error' R2, coefficient of determination

was attributed to the blast resistance of the female parent ps1. Fodder weight and grain yield varied in summer (18.9–56.7 g and 9.7–26.4 g) and *kharif* (19.6–59.5 g and 9.4–22.6 g), while ear head weight ranged from 12.7–34.8 g in Summer to 11.3–29.9 g in *Kharif* (Table 3). The hybrids matured earlier in the summer season (Table 4), influenced by higher temperatures (24.2°C) and longer sunshine duration (8.63 h) compared to the *Kharif* season (22.9°C, 5.13 h) (Jagadish et al. 2016). The hybrid ps1 × VL 315 matured the earliest in both summer (90 days) and *kharif* (94 days). In Summer, ps1 × GE 4764 exhibited the highest number of productive tillers (5), whereas ps1 × L 5 had the shortest peduncle length (21.4 cm)

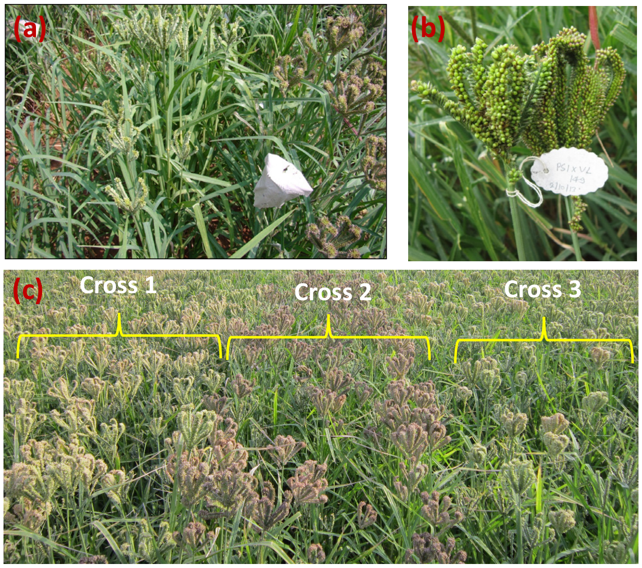

Fig. 2. Development of hybrids through contact method of crossing. **(a)Fertile genotypes used as male parents (right row) were planted alongside the PS1 line (left row), and crossing was performed by tying male and female ear heads together to facilitate outcrossing. The ear heads were then bagged to prevent pollen contamination. (b)During seed set, the PS1 ear head shows increased seed number due to outcrossing. (c) Crossed seeds from each cross were raised in three rows for field evaluation**

Better parent heterosis (BPH) and standard heterosis varied from -41.7% to 58.1% in summer and -38.5% to 48.4% in *kharif* (Table 4). For fodder weight, the MPH ranged from -36.5% to 106.6% in summer and -27.1% to 71.8% in *kharif*, whereas the BPH and SH ranged from -43.8% to 68.5% in summer and -56.9% to 31.3% in *kharif*. Productive tillers showed SH values between -28.9% and 56.3% in summer. The heterosis range indicates significant genetic diversity among the parents. High SH values for grain yield (58.1%) and fodder weight (68.5%) highlighted the potential for heterosis. Previous studies have reported lower SH values over GPU 28 (Shailaja et al. 2010). Heterosis mean and range for all the traits are available in Supplementary Table S4. The current high levels of heterosis reflect the genetic diversity potential for enhancing these traits.

Identification of heterotic hybrids

Significant heterosis was observed among the 46 hybrids compared with the standard check GPU 28 across the two seasons (Table 4). Seventeen hybrids demonstrated heterosis for maturity, with 12 exhibiting early maturity during summer. During the *kharif* season, 36 hybrids showed heterosis in terms of finger number. The hybrid ps1 × GE 4972 exhibited a high standard heterosis for grain yield,

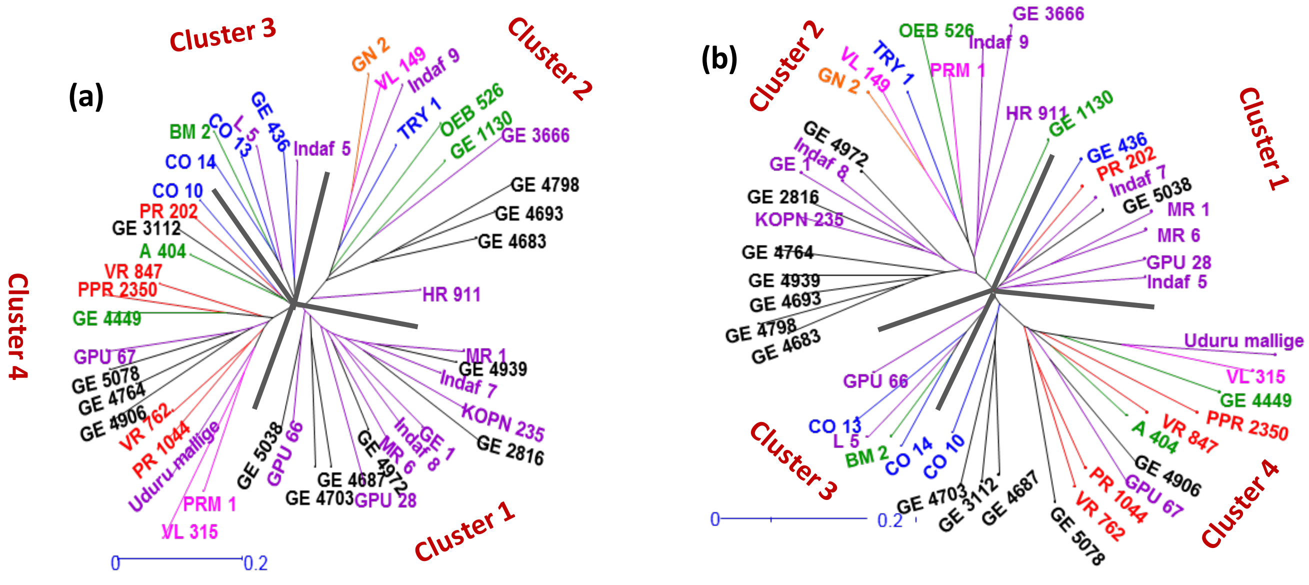

Fig. 3. Weighted neighbor-joining radial tree constructed from the dissimilarity matrix derived from Gower's genetic distance, calculated using 18 morphological traits evaluated during Summer (a) and *Kharif* (b). Genotypes showing clustering based on state of origin. Color legend: Blue, Tamil Nadu; Pink, Himachal Pradesh & Uttarakhand; Green, Jharkhand & Odisha; Orange, Gujrat; Red, Andhra Pradesh & Telangana State; Purple, Karnataka & Maharashtra; Black, African germplasm

contributing to lodging tolerance (Supplementary Table S4). During *Kharif*, ps1 × GE 1 and ps1 × GE 4798 demonstrated greater finger lengths (8.7 cm) (Table 4).

Mid-parent heterosis (MPH) for grain yield ranged from -27.4% to 111.5% in summer and -35.5% to 62.7% in *kharif*. with 23.4% in summer and 48.4% in *kharif*. ps1 × GE 4764 recorded 58.1% heterosis in summer, whereas ps1 × GE 436 (31.9%) and ps1 × MR 1 (26.6%) were observed in *kharif*. A higher standard heterosis was achieved in the present study than the previous studies using diverse parental

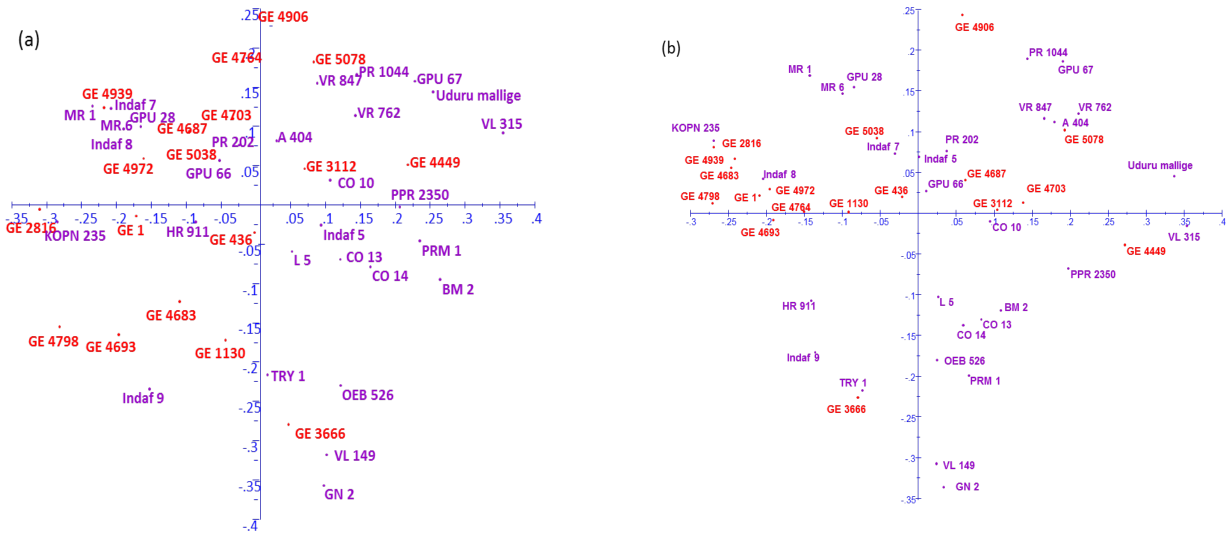

Fig. 4. Distribution of 47 parental lines used in heterosis study during Summer (a) and *Kharif* (b) based on Gower's dissimilarity matrix on axis (1/2) of PCoA scattered plot. Color legend: Red, later flowering; purple, medium flowering.

genotypes. The parents GE 4972, GE 4764, GE 436, and MR 1 possessed favourable yield alleles for future breeding. Besides nutritious grain for human, finger millet also forms nutritious fodder to the cattle in Asia and Africa (Kannababu et al. 2024). For fodder weight, ps1 × GE 4764 (68.5%) and ps1 × GE 4693 (27.7%) showed heterosis in summer, whereas ps1 × VR 847 (31.3%) and ps1 × GE 4972 (30.6%) performed well in *kharif*. Five hybrids exhibited negative standard heterosis for flowering days across seasons, producing yields higher than those of male parents but lower than those of GPU 28 (Supplementary Table S5). These hybrids are suitable for the development of short-duration rice varieties. Several hybrids surpassed GPU 28 for yield-contributing traits: ear head weight (ps1 × GE 4972, ps1 × GE 436), 1000 seed weight (ps1 × GE 4693, ps1 × GE 4798, ps1 × GE 4683, ps1 × GE 4687), finger number (ps1 × VL 315, ps1 × L 5, ps1 × GE 5078, ps1 × GE 4972), finger length (ps1 × GE 3666, ps1 × GE 4693, ps1 × GE 4683, ps1 × KOPN 235), and productive tillers (ps1 × GE 4764, ps1 × GE 4703, ps1 × GE 3112, ps1 × A 404). Heterotic hybrids for the other traits are listed in Supplementary Table S6.

Some hybrids exhibited heterosis for multiple traits (Supplementary Table S7). ps1 × VL 315 exhibited heterosis for traits such as flowering days, peduncle length, finger number, harvest index, and threshing percentage during summer. Meanwhile, ps1 × GE 4764 showed heterosis in tiller number, plant height, fodder weight, earhead weight, and grain yield. ps1 × GE 4972 demonstrated heterosis in grain yield, finger length, finger number, and ear head weight. In the *Kharif* season, ps1 × GE 436 displayed heterosis in flowering duration, flag leaf length, finger length, finger number, earhead weight, grain yield, and harvest index.

Previous studies have explored heterosis in traits, such as flowering time, tiller number, finger characteristics, seed weight, and harvest index (Shailaja et al. 2010; Divya et al. 2022). Gene banks preserve 40,182 finger millet accessions (Gebreyohannes et al. 2024), offering genetic resources for yield enhancement. Utilizing Ps1 facilitates multiple crosses to improve finger millet.

Gene action of traits revealed by correlation between mid-parent and per se hybrid value

The correlations between mid-parental values and hybrid performance were notably positive for finger length (r = 0.817 and 0.853), days to flowering (r = 0.732 and 0.661), and maturity (r = 0.767 and 0.776) across seasons (Table 5). Moderate positive correlations were observed for plant height (r = 0.472 & 0.479) and peduncle length (r = 0.409 & 0.423). Significant correlations were found for finger number (r = 0.599), harvest index (r = 0.471), and productive tiller number (r = 0.349) in Summer, while in *Kharif*, seed weight (r = 0.727), threshing percentage (r = 0.471), and flag leaf length (r = 0.458) showed significant correlations. The strong correlation between mid-parent values and hybrid means suggests additive gene action (Labroo et al. 2021), which is beneficial for population improvement in finger millet.

Parental diversity

The genetic diversity of the 47 parents was assessed using 18 morphological traits over the two seasons. The weighted neighbor-joining method categorizes parents into four clusters (Fig. 3). PCoA demonstrated significant diversity across all quadrants (Fig. 4). While the factorial analysis highlighted overall diversity, the tree method illuminated individual relationships. Tree clustering revealed no country-specific grouping of Indian and African parents. Among Indian parents, state-wise analysis showed distinct clustering for those from Tamil Nadu, Andhra Pradesh, Telangana, Himachal Pradesh, and Uttarakhand (Fig. 3), suggesting shared genetic traits due to regional gene flow. Parents from Karnataka clustered in the summer, but varied during the *Kharif* season.

Relationship between heterosis and parental divergence

This study initially explored the relationshipsbetween heterosis and parental divergence in finger millet. The genetic distance (GD) of parents showed a correlation with mid-parent heterosis for flag leaf width (r = 0.35) and plant height (r = 0.29) during the summer, as well as flag leaf length (r = 0.42), peduncle length (r = 0.41), 1000 seed weight (r = 0.33), and flag leaf width (r = 0.31) in the *Kharif* season (Table 6). No relationship was found between the grain yield and related traits. Linear regression indicated predictability for test weight ($H = -12.026 + 35.863 \times GD$) and flag leaf length ($H = -9.1528 + 38.929 \times GD$). For grain yield, significant heterosis resulted from the intermediate parental divergence. Similar associations between heterosis and divergence have been reported in chili (Krishnamurthy et al. 2013), pigeon pea (Praveen et al. 2015), and eggplant (Annepu et al. 2023). In chili and sesame, intermediate parental divergence led to more heterotic crosses. SSR-based parental divergence showed no significant correlation with heterosis (Table 6), possibly because of limited genome coverage. Similar findings have been reported for maize (Santos et al. 2013), sunflower (Gvozdenović, 2009), and sesame (Pandey et al. 2018). In rice, yield heterosis shows minimal correlation with parental distance (Zhang et al. 2010), whereas in eggplants, genetic distance predicts heterosis for fruit traits (Annepu et al. 2023).

Present study demonstrates the potential of the partial male sterile mutant Ps1 to enhance hybridization and yield improvement in finger millet. The promising hybrids identified in this study could be further explored for varietal development. These results underscore the utility of leveraging genetic diversity through male sterility to improve yield. Diversified partial male-sterile lines could facilitate rapid improvements tailored to specific regions. ps1 simplified the crossing process, enabling the efficient handling of more crosses. Further research is needed to explore its utility in population improvement and hybrid seed production. This study advances finger millet heterosis by employing a male-sterile line for hybrid development, conducting large-scale hybrid evaluations, selecting diverse parents without pigmentation markers, robustly evaluating across two seasons, and examining the relationship between heterosis and parental diversity. These findings offer valuable insights for accelerating crop improvement and hybrid development.

Supplementary material

Supplementary Tables S1 to S7 are available that can be accessed at www.isgpb.org

Authors' contribution

Conceptualization of research (M, MVC); Designing of the experiments (MVC); Contribution of experimental materials (M, MVC, SV); Execution of field experiments and data collection (M, MVC, SV); Analysis of data and interpretation (M, MVC, RS); Preparation of the manuscript (M, NC, MVC).

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Supplementary Table S1. List of finger millet varieties released from various Indian states, their pedigree and notable features utilized in hybrid development.

S. No.	Variety	Pedigree	State/Institute where developed	Special features
1	GPU 67	Selection from GE5331	UAS, Bengaluru	Profuse tillering
2	L 5	Malavi × Indaf 9	ARS Nagenahalli	Resistant to blast, pigmented, fist type ear
3	Indaf 7 (Hasta)	Annapurna × IE 927	VC Farm, Mandya	Cold tolerant
4	HR 911	UAS 1 × IE 927	UAS, Bengaluru	High yielding
5	Indaf 8	Hullubele × IE 929	UAS, Bengaluru	Late duration
6	Indaf 9	K 1 × IE 98 R	UAS, Bengaluru	Early maturity
7	TRY 1	Selection from HR 374	TNAU, Tiruchi	Dual purpose; grain and fodder; Salinity tolerant
8	CO 14	Malavi 1305 × CO 13	TNAU, Coimbatore	Moderately resistant to finger and neck blast
9	PRM 1	Selection from Ekeshwar of Pauri Garhwal region	GBPAU&T, Uttarakhand	Early and adapted to hilly region
10	VL 149	VL 204 × IE 882	VPKAS, Almora, Uttarakhand	Wide adaptation, earliness, resistance to leaf, finger and neck blast
11	VL 315	SDFM 69 × VL 231	Almora, Uttarakhand	Early duration, dwarf
12	A 404	Introduction from AP	BAU, Ranchi	Moderately resistant to blast, fairly drought tolerant, deep root system, non-lodging
13	GN 2 (NS 109)	Pure line from Gujarat local	GAU, Waghai, Gujarat	Moderately resistant to blast, highly drought tolerant, high finger number
14	OEB 526	SDFM × PE 244	OUA&T, Odisha	Moderately resistant to blast, non-lodging
15	VR 762	Pure line from VMEC134	Vizianagaram, AP	Moderately resistant to blast
16	PPR 2350 (Padmavati)	Pureline selection	ANGRAU, Perumalapalli, AP	Coastal AP
17	BM 2	Pureline selection	RAU, Ranchi	Tolerant to drought, moderately resistant to neck blast, slightly pigmented
18	PR 1044 (Ratnagiri)	Pureline selection from PM 629	ARS Peddapuram, AP	Moderately resistant to blast, drought tolerant, synchronous tillering & rich in protein
19	CO 10	Pureline selection from Maruaragi	TNAU, Coimbatore	Dwarf, more finger number, stay green, protein rich
20	MR 6	African white × RoH2	UAS, Bengaluru	High yielding, drought tolerant
21	MR1	Hamsa × IE 927	UAS, Bengaluru	Long duration, for early sowing
22	GPU 66	PR 202 × GPU 28	UAS, Bengaluru	Green plant parts with narrow leaves
23	KOPN 235	Selection from local germplasm	MPKVV, Rahuri	Suitable for sub mountain and Ghats zone
24	Co 13	Co 7 × TAH 107	TNAU, Coimbatore	Moderately resistant to blast, non-lodging
25	VR 847 (Srichaitanya)	GPU 26 × L 5	ANGRAU, Vizianagaram	Moderately resistant to blast
26	Indaf 5		UAS, Bengaluru	High yielding

Supplementary Table S2. **List of Elite finger millet germplasm used for hybrid development along with their origin and notable traits**

S. No.	Accession No.	Geographical origin	Special features
1	GE 4972	Zambia	More productive tillers and grain yield
2	GE 5038	Zimbabwe	High yield and ear weight
3	GE 4687	Uganda	More productive tillers
4	GE 4703	Ethiopia	More productive tillers
5	GE 5078	Zimbabwe	More finger numbers
6	GE 4798	Kenya	High yielding and high biomass
7	GE 4693	Uganda	High test weight and grain yield
8	GE 1130	India (UP)	High harvest Index and grain yield
9	GE 3112	Malawi	High Ca content (411.8 mg/g), protein (9.07 %)
10	GE 4449	India	Blast resistant
11	GE 4683	Uganda	High biomass content
12	GE 4764	Kenya	High biomass content
13	GE 436	India (TN)	Drought tolerant, blast resistant
14	GE 4906	Africa	Small glumes, naked seeds
15	GE 3666	India (MH)	More number of productive tillers
16	GE 4939	Zambia	High grain yield
17	GE 1	India (KA)	Virescent mutant of Indaf 8, High yielding, high finger number and finger width
18	GE 2816	Kenya	Highly heat tolerant

Supplementary Table S3. **Analysis of variance for hybrids and parents for blast disease reaction evaluated during Kharif.**

Source	d. f.	Leaf blast	Finger blast
Replication	1	0.30	166.61**
Entries	92	0.96**	120.46**
Parent	46	1.20**	204.17**
Hybrids	45	0.66**	23.85
Parents *vs* Hybrids	1	3.90**	725.00**
Error	92	0.28	26.42
CV (%)		29.59	51.76

**Significant at 0.01 probability level; All values except CV are Mean Sum of Squares

Supplementary Table S4. Mean and range of heterosis (%) in 46 hybrids for blast disease reaction, yield and its attributing traits evaluated during two seasons.

Trait	Season	Heterosis type	Mean heterosis value (%)	Range of heterosis (%)		Trait	Season	Heterosis type	Mean heterosis value (%)	Range of heterosis (%)	
				Minimum	Maximum					Minimum	Maximum
LB.	*Kharif*	MPH	37.2	-47.8	122.2	PL	Summer	MPH	-17.7	-21.3	-14.2
		BPH	108.3	100	150			BPH	24.4	-16.7	45.1
		SH	100.0	100	100			SH	-19.8	-25.4	-16.4
FB	*Kharif*	MPH	149.9	-78.6	424.3		*Kharif*	MPH	18.7	12.9	28.5
		BPH	759.4	682.2	926.6			BPH	27.8	16.5	57.2
		SH	718.7	644.46	926.62			SH	12.6	11.9	13.2
DF	Summer	MPH	0.0	-7	5.7	FLL	Summer	MPH	27.9	20.6	41.4
		BPH	5.6	-5	12			BPH	21.6	18.9	24.8
		SH	-2.8	-8.57	7.14			SH	22.7	20.2	24.8
	Kharif	MPH	-1.1	-7.8	10.3		*Kharif*	MPH	18.8	13.2	28
		BPH	7.0	-8	21.8			BPH	18.1	17.3	18.9
		SH	-3.9	-12.8	6			SH	13.7	10.4	19.4
DM	Summer	MPH	-0.9	-5.2	6.1	FLW	Summer	MPH	12.6	-18.1	31
		BPH	4.8	-3	14.1			BPH	-22.0	-25.9	-18.8
		SH	-2.0	-10.9	6.9			SH	-	-	-
	Kharif	MPH	-1.3	-7.6	7.3		*Kharif*	MPH	14.2	10.4	22.5
		BPH	5.3	-2.8	15.8			BPH	13.5	13.5	13.5
		SH	-4.4	-11.7	4.2			SH	13.5	13.5	13.5
PT	Summer	MPH	33.6	-21.5	81.8	FL	Summer	MPH	23.4	15	31.8
		BPH	9.8	-28.9	56.3			BPH	-20.5	-26.7	-13.5
		SH	25.0	-28.9	56.3			SH	-4.7	-26.7	20.7
	Kharif	MPH	30.3	29.7	30.8		*Kharif*	MPH	18.2	10.9	53.8
		BPH	-25.6	-25.6	-25.6			BPH	-8.0	-22.3	26.8
		SH	39.3	37.3	41.2			SH	3.8	-22.3	30.9
PHT	Summer	MPH	17.7	16	20.3	FW	Summer	MPH	-5.1	-21.6	16.3
		BPH	25.1	17.5	37			BPH	-16.0	-31	-10.9
		SH	19.1	17.5	20.5			SH	-12.3	-13.6	-10.9
	Kharif	MPH	18.9	12.2	29.2		*Kharif*	MPH	-13.5	-23.5	-9.1
		BPH	26.8	13.9	50.3			BPH	-15.1	-28.4	-9.9
		SH	18.3	13.9	23.1			SH	-12.8	-17.8	-9.9

FN	Summer	MPH	29.9	19.9	59.6	YLD	Summer	MPH	36.9	-27.4	111.5
		BPH	25.5	21.7	37.8			BPH	-16.5	-41.7	58.1
		SH	25.6	22.8	37.8			SH	-16.5	-41.7	58.1
	Kharif	MPH	17.8	11.3	36.9		*Kharif*	MPH	23.1	-35.5	62.7
		BPH	11.7	-16.7	30.9			BPH	-13.8	-38.5	48.4
		SH	22.1	14.7	38.2			SH	-12.9	-38.5	48.4
TW	Summer	MPH	9.4	7.1	12.3	TP	Summer	MPH	2.7	-11.1	11.9
		BPH	-7.3	-18.5	8			BPH	-4.2	-11.3	11.1
		SH	0.9	-18.5	13.8			SH	0.6	-11.3	12.8
	Kharif	MPH	10.4	-11.66	30.8		*Kharif*	MPH	2.9	-14.4	11.7
		BPH	-6.6	-18.1	11.2			BPH	-5	-16.7	9.7
		SH	-4.8	-18.1	11.2			SH	-2.8	-16.7	10.6
FOW	Summer	MPH	28.6	-36.5	106.6	HI	Summer	MPH	11.9	-34	34.3
		BPH	-20.6	-43.8	68.5			BPH	-5.4	-40.2	34.1
		SH	-20.6	-43.8	68.5			SH	6.8	-26.5	34.1
	Kharif	MPH	38.6	-27.1	71.8		*Kharif*	MPH	8.3	-29.4	37.9
		BPH	-21.1	-56.9	31.3			BPH	-28.9	-38.5	-21.4
		SH	-20.6	-56.9	31.3			SH	9.5	-31.1	42.8
EW	Summer	MPH	39.6	-25.5	119.7						
		BPH	-14.7	-38.9	67.1						
		SH	-14.7	-38.9	67.1						
	Kharif	MPH	31.5	-36	91.4						
		BPH	-5.6	-40.2	58.2						
		SH	-0.7	-40.2	58.2						

MPH: Mid parent heterosis, BPH: Better parent heterosis, SH: Standard heterosis, LB: Leaf blast, FB: Finger blast, DF: Days to 50% flowering, DM: Days to maturity, PT: Productive tillers per plant, PHT: Plant height (cm), PL: Peduncle length (cm), FLL: Flag leaf length (cm), FLW: Flag leaf width (cm), FL: Finger length (cm), FW: Finger width (cm), FN: Finger number per ear head, TW: 1000 seed weight (g), FOW: Fodder weight per plant (g), EW: Ear head weight per plant (g), YLD: Grain yield per plant (g), TP: Threshing percentage (%), and HI: Harvest index (%).

Supplementary Table S5. Performance of early duration hybrids and corresponding parents for days to maturity and grain yield per plant evaluated during Summer and Kharif.

Hybrids	Days to Maturity		Grain yield per plant (g)		Parents	Days to Maturity		Grain yield per plant (g)	
Season	Summer	*Kharif*	Summer	*Kharif*		Summer	*Kharif*	Summer	*Kharif*
ps 1 X VL 315	90	93	16.2	13.7	VL 315	87	89	10.5	10.0
ps 1 X Uduru Mallige	95	97	14.9	12.9	Uduru Mallige	91	88	12.9	6.0
ps 1 X VL 149	91	102	11.9	12.0	VL 149	91	92	8.3	12.2
ps 1 X GN 2	97	100	13.3	13.3	GN 2	93	92	12.6	11.5
ps 1 X BM 2	98	99	15.5	12.5	BM 2	94	96	7.1	12.5
					GPU28	101	110	16.7	15.2

Supplementary Table S6. Heterosis and mean performance of selected hybrids for yield attributing traits evaluated during Summer and kharif.

Traits	Hybrid with superior mean and heterosis	Heterosis (Summer)			Heterosis (Kharif)			Mean value	
		MPH	BPH	SH	MPH	BPH	SH	Summer	Kharif
PL	No. of desired hybrids	4	1	12	0	0	0	0	0
	ps 1 x VL 315	-	-	-25.1**	-	-	-	21.5	24.9
	ps 1x VL 149	-	-	-23.3**	-	-	-	22	28.5
	ps 1 x OEB 526	-	-	-18.8*	-	-	-	23.3	28.3
	ps 1 x L 5	-21.3**	-16.7**	-25.4**	-	-	-	21.4	25
	GPU 28	-	-	-	-	-	-	28.7	26.3
FLL	No. of desired hybrids	13	4	6	15	2	12		
	ps 1 x PRM 1	33.2**			28**	17.3*	17.3**	27.5	39
	ps 1 x CO 10	41.4**	22.6*	22.6*	15.8*	-	-	30.9	35.7
	ps 1 x PPR 2350	29.8**	-	-	19.1**	18.9*	19.4**	29	39.7
	ps 1 x GE 4693	21.7**	18.9*	24.6*	-	-	-	31.4	35.6
	ps 1 x GE 4683	32.3**	-	22.6*	-	-	-	30.9	34.1
	ps 1 x GE 5078	28.5**	24.8*	24.8*	-	-	-	31.5	31.8
	GPU 28	-	-	-	-	-	-	25.2	33.3
FLW	No. of desired hybrids	5	0	0	8	1	1		
	ps 1x VL 149	-	-	-	17.4**	-	-	0.9	1.01
	ps 1 x CO 10	31**	-	-	-	-	-	1.02	0.98
	ps 1 x GE 3666	28.7**	-	-	-	-	-	0.95	0.93
	ps 1 x L 5	-	-	-	22.5*	13.5*	13.5*	0.98	1.09
	GPU 28	-	-	-	-	-	-	0.89	0.96
FW	No. of desired hybrids	1	0	0	0	0	0		
	ps 1 x GE 3666	16.3**	-	-	-	-	-	1	0.92
	GPU 28							1.1	1.01
TP	No. of desired hybrids	5	2	4	7	2	2		
	ps 1 x VL 315	11.9**	11.1**	12.8**	-	-	-	90.7	80.8
	ps 1 x Uduru Mallige	7.9*	-	10.7*	9.4*	-	-	89.0	84.8
	ps 1x VL 149	9.2*	-	10.8**	-	-	-	89.0	86.1
	ps 1 x GE 4764	-	-	-	8.8*	-	-	76.0	81.7

	ps 1 x PR 202	-	-	-	10.2**	9.7*	10.6*	81.1	88.9
	ps 1 x Indaf 5	10.1**	9.4*	9.4*	-	-	-	87.9	82.7
	ps 1 x A 404	-	-	-	9.1*	8*	10.1*	85.5	88.5
	ps 1 x GE 4798	9*	-	-	11.7**	-	-	82.1	80.0
	ps 1 x L 5	-	-	-	8.8*	-	-	71.3	84.8
	GPU 28	-	-	-	-	-	-	80.4	80.4
HI	No. of desired hybrids	9	3	3	3	0	3		
	ps 1 x VL 315	34.3**	34.1**	34.1**	-	-	-	41.3	21.6
	ps 1 x Uduru Mallige	22.2*	-	-	30.4*	-	-	32.5	25.0
	ps 1 x BM 2	29.9**	27.6**	27.6**		-	-	39.3	26.9
	ps 1 x CO 13	15.7*	-	-	-	-	-	34.0	23.1
	ps 1 x CO 14	22*	-	-	-	-	-	31.9	23.7
	ps 1 x GE 436	-	-	-	-	-	26.5*	35.6	29.9
	ps 1 x GPU 67	18.4*	-	-	26.4**		42.8**	33.1	33.7
	ps 1 x GE 4972	19.2*	-	-	-	-	-	35.7	26.0
	ps 1 x GE 4939	-	-	-	37.9**	-	-	30.8	27.7
	ps 1 x PR 1044	18.8*	-	-	-	-	-	32.5	19.0
	ps 1 x L 5	31.4**	20.1*	20.1*	-	-	-	37.0	27.6
	GPU 28	-	-	-	-	-	-	30.8	23.6

*, ** significant at 0.05 and 0.01 level. MPH = Mid parent heterosis; BPH= Better parent heterosis, SH: =Sandard heterosis; PL= Peduncle length (cm); FLL = Flag leaf length (cm); FLW = Flag leaf width (cm); FW = Finger width (cm); TP = Threshing % and HI = Harvest index (%).

Supplementary Table S7. Heterotic hybrids showing heterosis for more number of traits during Summer and *Kharif*

								Summer							
Hybrids	DF	DM	PT	PHT	PL	FLL	FL	FN	TW	FOW	EW	YLD	TP	HI	Heterotic for number of traits
ps 1 x VL 315	-8.57	-10.9			-25.1			24.4					12.8	34.1	6
ps 1 x GE 4764			56.3	20.5						68.5	67.1	58.1			5
ps 1 x GE 4972							17.8	23.8			23.6	23.4			4
ps 1x VL 149	-8.57	-9.9			-23.3								10.8		4
ps 1 x GE 4693						24.6	18.5		13.8	25.7					4
ps 1 x L 5					-25.4	20.2		37.8						20.1	4
	Kharif														
ps 1 x GE 436	-6	-2.3				12.8	21.5	17.6			58.2	31.9		26.5	8
ps 1 x GE 4972							13.7	29		30.6	45.2	48.4			5
ps 1 x OEB 526	-12	-9.4				12.5		35.3						28.9	5
ps 1 x BM 2	-6	-7		14.7				23.5	8.1						5
ps 1 x GPU 67	-3.8	-2.3				12.2		14.7						42.8	5

Abbreviations: DF, days to 50% flowering; DM, days to maturity; PT, productive tiller number per plant; PHT, plant height (cm); PL, peduncle length (cm); FLL, flag leaf length (cm); FLW, flag leaf width (cm); FL, finger length (cm); FW, finger width (cm); FN, fingers per ear head; FOW, fodder weight per plant (g); EW, ear head weight per plant (g); YLD, grain yield per plant (g), TP, threshing %; HI, harvest index (%)