

Combining ability and hybrid breeding in pearl millet (*Pennisetum glaucum* [L.] R. Br.) for agronomic traits and resistance to *Striga hermonthica*

Armel Rouamba

armelrouamba@yahoo.fr

University of KwaZulu-Natal

Hussein Shimelis

University of KwaZulu-Natal

Inoussa Drabo

International Maize and Wheat Improvement Center (CIMMYT)

Emmanuel Mrema

Tanzania Agriculture Research Institute, Tumbi Center

Jacob Mashilo

University of KwaZulu-Natal

Learnmore Mwadzingeni

Seed Co Limited

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Abstract

Pearl millet (*Pennisetum glaucum* [L.] R. Br., $2n = 2x = 14$) is a nutrient-dense and climate-resilient crop widely cultivated in the dry regions of Africa and Asia. In Burkina Faso, the actual mean yield of the crop is < 1 ton/ha compared with a potential yield of 3 tons/ha. Several constraints, including cultivar susceptibility to the noxious weed *Striga hermonthica* (Del.) Benth (Sh) and severe and recurrent drought stress limit the potential productivity of the crop. Therefore, this study aimed to determine the combining ability effects and degree of heterosis for agronomic traits and resistance to Sh among complementary pearl millet genotypes to select promising parental lines and hybrids to develop and deploy farmer-preferred varieties. The narrow- and broad-sense heritability were relatively higher for Striga-resistance ($\geq 70\%$) and low ($\leq 23\%$) for grain yield. The general combining ability (GCA) and specific combining ability (SCA) ratios were less than unity for agronomic traits and Striga reaction indicating the predominance of non-additive gene action conditioning the assessed traits. The new experimental hybrids such as IP-11358 $\times$ ICMB177111, IP-11358 $\times$ IKMB18002, IP-10579 $\times$ ICMB177002 and IP-9242 $\times$ ICMB177002 are recommended for multi-environment evaluation and production in Sh-infested pearl millet cultivation agro-ecologies in Burkina Faso or similar agro-ecologies.

1. Introduction

Pearl millet (*Pennisetum glaucum* [L.] R. Br., $2n = 2x = 14$) is a multi-purpose grain crop of social and economic importance in dry regions globally. In sub-Saharan Africa (SSA), pearl millet grain is processed to prepare various foods, whereas the dry stover is used for livestock feed, fuelwood, and construction material (Drabo 2016; Burgarella et al. 2018). The grain is rich in protein (i.e., 11 to 12.5%), calcium, phosphorous, iron and zinc, with a relatively high amount of vitamins, including thiamine, riboflavin and niacin (Ghatak et al. 2016; Gupta et al. 2022). It has several health benefits, including alleviating anaemia, constipation, cancer, diabetes, celiac and diarrhoea (Gupta et al. 2022). In SSA, the crop is mainly grown in arid and semi-arid environments and thrives under low moisture, high temperatures, and nutrient-deficient soil conditions (Shivhare & Lata 2017). The high phenotypic and genotypic plasticity of the crop makes it a crop of choice in harsh agroecologies of SSA with the potential to contribute to the livelihoods and nutritional well-being of the population.

Pearl millet is the third largest cereal grain crop produced in SSA. The leading producers in the region are Niger (3.5 million tons per annum), Mali (1.9 million tons), Nigeria (1.9 million tons), Senegal (1.1 million tons) and Burkina Faso (0.9 million tons) (FAOSTAT 2022). In Burkina Faso, the crop's actual yield is 0.76 ton/ha (MARAH 2022), much lower than the potential yield of 3.00 ton/ha (ECOWAS-UEMOA-CILSS 2021). Several biotic and abiotic stresses are attributed to its low productivity. Among the biotic stresses, *Striga hermonthica* (Del.) Benth (Sh) infestation is the leading cause of yield losses of up to 90 to 100% (Kountche et al. 2016; Kanampiu et al. 2018; Rouamba et al. 2021). In Burkina Faso, Sh is reported to cause yield losses of about 80% in pearl millet (Rouamba et al. 2021). *Striga* infestation is manifested in degraded environments and low-input cropping systems, especially in cereal monocropping conditions (Parker 2009; Parker 2012). The yield gap is partly attributed to farmers' lack of improved Sh-resistant varieties and modern crop management and inputs. Breeding and deploying Striga-resistant and high-yielding varieties will enhance crop productivity under low-input farming systems commonly practiced by small-scale farmers in SSA, including Burkina Faso.

Various genetic designs are widely used to develop breeding populations and determine the combining ability effects of parents for applied breeding, including for Sh-resistance (Nduwumuremyi et al. 2013; Sharma & Singh 2019; Yehia & El-Hashash 2019; Zebire et al. 2021; Balami et al. 2022). The line $\times$ tester mating design proposed by Kempthorne (1957) is useful for identifying the best-performing genotypes for hybrid development and performance evolution. The procedure enables to estimate of the general combining ability (GCA) of parents and the specific combining ability (SCA) effects of progenies (Barathi et al. 2020) and corresponding breeding values (Yehia & El-Hashash 2019; Barathi et al. 2020). In pearl millet, positive GCA effects have been reported for the following agronomic traits: days to 50% flowering, plant height, panicle length, thousand-grain weight and grain yield, which aided the identification of useful parental genotypes for breeding (Santosh et al. 2018; Kumawat et al. 2019; Barathi et al. 2020; Balami et al. 2022). Also, negative GCA effects have been reported for Sh reaction in pearl millet, indicating the possibility of developing pearl millet genotypes with enhanced resistance to the highly noxious weed in cereal crop production (Karaya et al. 2014; Sangaré et al. 2018; Zebire et al. 2020; Balami et al. 2022; Lobulu et al. 2023). Positive SCA effects were reported for panicle length, plant height, thousand-grain weight, and grain yield in pearl millet, whereas negative SCA effects were reported for Striga traits, allowing the identification of the best crosses (Karaya et al. 2014; Sangaré et al. 2018; Balami et al. 2022; Lobulu et al. 2023).

In an attempt to develop pearl millet varieties with increased yield and *Sh*-resistance, the Burkina Faso pearl millet breeding programme introduced pearl millet inbred lines from the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT). Initially, 148 pearl millet inbred lines, including two other lines used in the breeding programme, were screened for *Striga*-resistance, which aided the identification of five promising *Sh*-resistant lines for breeding (Unpublished data). The identified genotypes are useful genetic resources for open-pollinated or hybrid pearl millet breeding with *Sh*-resistance and promising agronomic traits. Therefore, the objective of this study was to determine the combining ability effects and degree of heterosis for agronomic traits and resistance to *Sh* among complementary pearl millet genotypes to select promising parental lines and hybrids to develop and deploy farmer-preferred varieties.

2 Materials and methods

2.1 Plant materials

The study used two sets of parents consisting of three lines and five testers. The testers were selected from diverse pearl millet lines exhibiting *Sh*-resistance, while the lines are local genotypes used in the pearl millet breeding programme in Burkina Faso. The standard single cross hybrid Nafagnon and experimental *Sh*-resistant genotype IP-15857 and *Sh* susceptible line SOSAT-C88 were used as check varieties. The names, sources of origin and attributes of the lines, testers and checks are presented in Table 1.

Table 1
Names, sources of origin and genetic attributes of lines, testers and check varieties used in the study.

Names, sources of origin and genetic attributes of lines, testers and check varieties used in the study.			
Parents	Genotypes	Source	Attributes
Line	ICMB177002	INERA	B-line
	IKMB18002		
	ICMB177111		
Tester	IP-6112	ICRISAT	<i>Striga</i> -resistant
	IP-10579		
	IP-9242		
	IP-3098		
	IP-11358		
Checks			
	Nafagnon	INERA	Hybrid
	IP-15857	ICRISAT	<i>Striga</i> -resistant
	SOSAT-C88	ICRISAT	<i>Striga</i> -susceptible
INERA = Institute of Environment and Agricultural Research, ICRISAT = International Crop Research Institute for the Semi-Arid Tropics			

2.2 Crossing procedure

The lines and testers were crossed using a line-by-tester mating design under greenhouse conditions at the Institute of Environment and Agricultural Research (INERA) main research station (12°28/27 N; 1°33/31 W) during the 2020 offseason. A five-litre capacity plastic pots were filled with a mixture of clay and sandy soil, and organic manure in a ratio of 2:1:1. Each of the lines and testers was planted in two rows of 10 pots in the greenhouse in three successions of two-week intervals. The plants were thinned to one plant per pot and irrigated every two days. A compound fertilizer (N: P: K; 14:23:14) was supplied in microdose of 3g/pot two weeks after planting. Weeds were continuously removed from pots. Plants were allowed to grow until the heading stage and were covered with pollen-bag before anthesis. When the panicle had produced pollen, viable pollen grains were collected from each tester in a pollen bag. Thereafter, the panicles of the lines were pollinated by gently shaking the pollen bag and dusting the pollen grains from

testers onto the panicles to allow the transfer of pollen grains to the stigma. The pollinated panicles were bagged and labelled until the seed maturation. The seeds were harvested from successfully pollinated panicles and labelled and stored for later use.

2.3 Study sites

Fifteen experimental F₁ hybrids, their eight parents, and three checks (Table 1) were evaluated at three locations in Burkina Faso. The two locations include Gampela and Fada, where agronomic performances were evaluated. The third location is the INERA main research station at Ouagadougou, and the study was conducted under greenhouse conditions to evaluate *Sh*-resistance using artificial infestation. The studies were conducted during the 2021 growing season. The Gampela and Fada sites are the principal pearl millet evaluation sites in the country. Gampela and Fada are located at 12° 25'51" N; 1°22'18" W and 11°56'16" N, 0°17'48" E, respectively. The sites receive a total annual rainfall of 600 to 900 mm and 700 to 900 mm with erratic distribution. During the study period (June to October 2021), 940.8 mm and 731.56 mm of rainfall were recorded at Gampela and Fada, respectively.

2.4 Experimental design and trial management

The field experiments (at Gampela and Fada) were planted using a 4 × 6 alpha lattice design with two replications. Field plots consisted of one row of 4 m in length with a spacing of 0.80 m between rows and 0.40 m spacing between plants within a row. 15 days after sowing, plants were thinned to one plant per hill to achieve the desired plant density of 31250 /ha. The trials received soil fertilisers of 100 kg/ha of nitrogen, phosphorus and potassium (NPK: 14:23:14) fifteen days after planting and 50 kg/ha N in the form of urea at the booting stage at Gampela and Fada under rain-fed conditions. All other management practices followed the standard agronomic practices recommended for pearl millet production in Burkina Faso (INERA 2000). In the greenhouse, five-litre capacity plastic pots were filled with a soil media composed of clay and sand. The media was infested with a scoop of sand mixed with 0.05 g of 2-year-old *Sh* seed collected from farmers' fields in Burkina Faso and preconditioned for eleven days before planting. Hand weeding was routinely done to remove all other weeds except *Sh*.

2.5 Data collection

The following agronomic data were collected: days to 50% flowering (DTF) recorded as the number of days when 50% of the plants in each plot had intruded stigma, plant height (PH) measured from the base of the plant (expressed in cm) to the top of the panicle of the main tiller, the number of tillers (NT) were counted per plant, panicle length (PCL) measured in cm from the base to the top of the main tiller panicle, panicle diameter (PCD) measured in mm using a vernier calliper aiming the middle section of the panicle, panicle weight (PWT, g) recorded by weighing the harvested panicles for each entry after 14 days of sun-drying, and thousand-grain weight (TGW, g) determined by weighing a thousand grains. Grain weight per plant (GW, g) was determined by weighing the grains after threshing and dividing them by the number of harvested plants for each plot. Grain yield (GY) was computed as the grain weight per plant of the total plants per plot area and extrapolated to kg per hectare (kg/ha). Under the greenhouse environment, data on *Striga* parameters were collected, including the number of emerged *Sh* plants in each pot, estimated at 60 days (SN60) and 80 days (SN80) after sowing. The area under the *Striga* Number Progress Curve (ASNPC) was computed using the successive *Striga* counts according to Haussmann et al. (2000) as follows:

$$ASNPC = \sum_{i=0}^{n-1} \left[\frac{Y_i + Y_{(i+1)}}{2} \right] (t_{i+1} - t_i)$$

where n is the number of *Striga* assessment dates, Y_i is the *Striga* count at the i^{th} assessment date, $Y_{(i+1)}$ is the *Striga* count at the i^{th} plus 1 assessment date, t_i is the number of days after planting (DAP) at the i^{th} assessment date, $t_{(i+1)}$ is DAP at the i^{th} plus 1 assessment date.

2.6 Data analysis

2.6.1 Analysis of Variance

The collected data were assembled in Excel and subjected to the combined analysis of variance (ANOVA) in GenStat 20th Edition (VSN International, Hemphstead, UK) after performing tests for normality and homogeneity of variances. Differences between treatment means were determined using the least significant difference (LSD) test at 5% level of significance.

2.6.2 Combining ability estimates

The GCA and SCA effects were estimated using a line-by-tester genetic analysis using the agricolae package (de Mendiburu & de Mendiburu 2019) in R software version 4.1.2 (R Core Team 2021). The GCA and SCA effects were determined for each site. The genotypes were considered fixed effects, while replications were treated as random effects. The following linear model was used to determine the combining ability effects:

$$Y_{ijk} = \mu + r_k + g_i + g_j + s_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} is the observed performance of the cross between the i^{th} line and j^{th} tester; μ is the overall trial mean; r_k is the effect of replicate k ; g_i general combining ability of the lines; g_j is the general combining ability of the testers; s_{ij} is the specific combining ability of the cross between line i and tester j ; ε_{ijk} is the residual. The significance of the estimated GCA effects of the lines and testers and the SCA effects of experimental hybrids were tested using the t-test procedure at the 5% significance level (Divya et al. 2014).

2.6.3 Estimate of Heterosis

The mid-parent heterosis (MPH) and standard heterosis (SH) were calculated according to Falconer & Mackay (1996). These were computed as a percentage increase or decrease of the cross performances over the mid-parents and the best standard check, respectively, referring to the superiority of the F_1 over mid-parents (MP) and the check variety (Cv). Mid-parent and standard heterosis were estimated using the following formula (Falconer & Mackay 1996):

$$\text{MPH (\%)} = \frac{F_1 - \text{MP}}{\text{MP}} \times 100$$

$$\text{SH (\%)} = \frac{F_1 - \text{Cv}}{\text{Cv}} \times 100$$

2.6.4 The ratio of the general combining ability and the specific combining ability effects

The ratio of the general combining ability (GCA) and the specific combining ability (SCA) effects was determined using the general prediction ratio (GPR) according to Baker (1978) as follows:

$$\text{GCA/SCA} = 2\text{MSGCA}/(2\text{MSGCA} + \text{MSSCA})$$

where MSGCA and MSSCA are the mean squares of GCA and SCA effects, respectively.

A Bakers' ratio close to 1.00 indicates that the GCA effects were more important in conditioning the heritability of that trait, whereas a ratio close to zero would indicate that SCA effects would be more important in controlling trait heritability.

2.6.5 Estimate of heritability

The broad-sense heritability (H^2) and narrow-sense heritability (h^2) for each environment were determined using the Analysis of Genetic Designs with R (AGD-R) version 5.0 (Rodríguez et al. 2015) software according to Acquaah (2012) using the following formulae:

$$H^2 (\text{bs}) = V_G/V_P$$

$$h^2 (\text{ns}) = V_A/V_P$$

where V_G is the genetic variance, V_A is the additive genetic variance, and V_P is the total phenotypic variance.

3. Results

3.1 Analysis of variance for agronomic traits

Table 2 presented the assessed agronomic traits' mean squares and significant tests. The genotype effects showed significant differences ($P < 0.001$) for all assessed agronomic traits, while the locations showed a significant effect ($P < 0.01$) on DTF and GY. Genotype-by-test site interaction effect was significant ($P < 0.01$; $P < 0.001$) for DTF and GY (Table 2).

Table 2
Mean squares and significant tests from combined analysis of variance for agronomic traits of pearl millet genotypes across two environments in Burkina Faso.

SV	DF	DTF	PH	NT	PCL	PCD	TGW	GY
Replication	1	49.18**	118.40 ^{ns}	0.00 ^{ns}	0.12 ^{ns}	10.70 ^{ns}	3.61 ^{ns}	5957.00 ^{ns}
Block	5	17.37*	1301.30**	0.91 ^{ns}	23.03 ^{ns}	15.58*	2.77 ^{ns}	6267.00 ^{ns}
Genotype (Gen)	23	29.69***	2305.10***	2.01*	112.99.***	30.07***	4.42**	194967.00***
Environment (Env)	1	1235.23***	30451.20***	0.30 ^{ns}	151.15**	4.30 ^{ns}	9.01**	3950400.00**
Gen*Env	18	29.11***	790.60 ^{ns}	1.23 ^{ns}	16.16 ^{ns}	3.42 ^{ns}	2.58 ^{ns}	154173.00**
Error	30	6.58	447.80	1.05	17.39	6.10	1.59	64229.00
Trial statistics								
Mean		60.33	191.70	4.81	28.96	20.88	8.40	694.00
CV (%)		4.26	11.03	21.093	14.38	11.78	15.04	36.19
SED		2.57	21.16	1.02	4.17	2.47	1.26	253.40
LSD (5%)		1.22	9.66	0.48	1.90	1.16	0.58	126.00

SV = source of variation; DF = degree of freedom; DTF = day to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grain yield (kg/ha); CV = coefficient of variation; SED = standard error of the mean difference; LSD (5%) = Least significant difference at 5% probability value; * = denote significant differences at 0.05 probability level; ** = denote significant differences at 0.01 probability level; *** = denote significant differences at 0.001 probability level; ns = denote not significant.

3.2 Mean response of pearl millet genotypes for agronomic traits under field conditions

The mean values for crosses, lines, testers, and checks evaluated across *Sh*-non-infested environments in Burkina Faso are presented in Table 3. DTF varied from 56 to 64 for crosses. It ranged from 54 to 70 for testers and from 56 to 66 for lines. PH varied from 171 to 236 cm for crosses, while for lines and testers, it varied from 137 to 167 cm and 132 to 186 cm, respectively. The following crosses had longer plant height (> 200 cm) namely: IP-11358 × IKMB18002, IP-6112 × ICMB177002, IP-11358 × ICMB177002, IP-10579 × ICMB177111, IP-10579 × ICMB177002, IP-6112 × ICMB177111, IP-11358 × ICMB177111 and IP-6112 × IKMB18002. Also, 33.33% of crosses recorded PH exceeding their parental lines and testers. Cross IP-9242 × ICMB177111 presented the maximum NT (5 tillers per plant), whereas tester IP-6112 had the lowest NT (2 tillers per plant). IP-11358 × ICMB177002 had the highest PCL (38.64 cm) and IP-6112 × ICMB177111 had the lowest (18.26 cm). PCD ranged from 19 to 31 mm, 18 to 24 mm and 13 to 21 mm for crosses, lines and testers, respectively. Crosses IP-6112 × ICMB177111 and IP-6112 × IKMB18002 recorded PCD at 31.95 and 25.28 mm, in that order, higher than the lines and testers. Cross IP-11358 × ICMB177002 had the highest TGW (10.72 g), followed by IP-11358 × IKMB18002 (10.07 g), whereas IP-3098 × ICMB177002 had the lowest TGW (7.17 g). The crosses, except IP-3098 × ICMB177002, IP-6112 × ICMB177002 and IP-10579 × ICMB177002 recorded higher TGW (> 8 g) than lines and testers. Crosses had mean grain yields ranging from 455.20 to 1128.10 kg/ha. Crosses IP-11358 × ICMB177111 (1128.10 kg/ha), IP-11358 × IKMB18002 (938.60 kg/ha) and IP-6112 × IKMB18002 (890.30 kg/ha) were high performers for GY than their parental lines and testers. None of the families out-performed the check variety Nafagnon which had a mean grain yield of 1506.40 kg/ha. The mean grain yield ranged between 138.30 to 744.50 kg/ha for lines, while for testers, it ranged from 202.30 to 883.50 kg/ha.

Table 3
Mean values for agronomic traits among pearl millet lines, testers, crosses, and checks evaluated under two environments in field conditions in Burkina Faso.

Crosses	DTF	PH	NT	PCL	PCD	TGW	GY
IP-3098 × ICMB177002	59.91	172.90	3.22	33.92	20.08	7.17	455.20
IP-10579 × ICMB177111	60.36	216.90	4.83	23.50	20.05	8.74	537.30
IP-3098 × IKMB18002	56.54	185.30	3.54	28.09	20.00	8.20	617.50
IP-10579 × IKMB18002	60.72	219.60	4.28	28.48	20.79	8.48	658.60
IP-6112 × ICMB177002	57.29	213.00	3.71	29.68	21.47	7.47	725.60
IP-10579 × ICMB177002	62.41	216.00	3.84	36.50	21.71	7.46	740.90
IP-3098 × ICMB177111	55.65	195.40	4.59	26.09	20.59	8.76	741.90
IP-9242 × ICMB177111	56.58	171.30	5.05	24.69	22.34	8.76	760.80
IP-9242 × IKMB18002	57.00	186.20	4.88	31.02	19.53	8.67	770.70
IP-11358 × ICMB177002	63.44	217.60	3.47	38.64	18.92	10.72	773.40
IP-6112 × ICMB177111	60.63	214.40	4.71	18.26	31.95	9.56	801.30
IP-9242 × ICMB177002	58.79	171.20	4.30	35.44	20.76	8.56	825.50
IP-6112 × IKMB18002	63.23	207.30	4.30	26.50	25.28	9.61	890.30
IP-11358 × IKMB18002	62.80	235.90	4.59	33.23	21.69	10.07	938.60
IP-11358 × ICMB177111	59.60	213.20	4.79	30.13	19.75	9.26	1128.10
Lines							
ICMB177002	66.04	137.50	4.00	39.00	18.00	7.56	138.30
IKMB18002	55.68	156.40	4.51	22.46	20.88	6.89	189.50
ICMB177111	60.97	166.80	3.64	22.93	23.33	6.90	744.50
Testers							
IP-10579	61.02	185.60	4.05	22.18	13.50	6.78	202.30
IP-9242	58.13	132.50	4.28	22.04	20.95	6.97	388.90
IP-3098	53.98	180.00	4.53	21.52	14.04	7.00	465.90
IP-11358	70.04	214.80	4.38	30.00	17.52	7.38	883.50
IP-6112	60.00	160.00	2.00	31.00	19.00	-	-
Checks							
Nafagnon	58.87	204.70	5.91	33.86	23.61	9.55	1506.40

DTF = day to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grains yield (kg/ha); - = denote missing value due to poor seed set.

3.3 Mean response of pearl millet genotypes for *Striga* parameters under greenhouse conditions

Striga parameters evaluated under greenhouse conditions are presented in Table 4. SN60 varied from 0 for cross IP-10579 × ICMB177002 to 31.00 *Striga* plants per pot for cross IP-3098 × ICMB177111. The following crosses, namely: IP-10579 × ICMB177002, IP-9242 × ICMB177002, IP-11358 × ICMB177111, IP-11358 × IKMB18002, IP-10579 × ICMB177111 and IP-10579 ×

IKMB18002, had the lowest SN60 count (< 2). The crosses IP-3098 $\times$ ICMB177111, IP-6112 $\times$ IKMB18002, IP-3098 $\times$ IKMB18002, IP-6112 $\times$ ICMB177111 and IP-9242 $\times$ IKMB18002 had the highest *Striga* count (> 10) at SN60. For lines, ICMB177002 had the lowest count (1.20) at SN60, whereas tester IP-9242 had the lowest SN60 count (0.30). At SN80, the mean *Striga* count per pot varied from 0.20 for cross IP-10579 $\times$ ICMB177002 to 25.00 for cross IP-6112 $\times$ IKMB18002. Crosses IP-10579 $\times$ ICMB177002, IP-9242 $\times$ ICMB177002, IP-11358 $\times$ ICMB177111, IP-10579 $\times$ IKMB18002, IP-10579 $\times$ ICMB177111 and IP-11358 $\times$ IKMB18002 recorded the lowest *Striga* count (< 3) at SN80, whilst IP-6112 $\times$ IKMB18002, IP-3098 $\times$ ICMB177111, IP-6112 $\times$ ICMB177111, IP-3098 $\times$ IKMB18002 and IP-9242 $\times$ IKMB18002 recorded the highest values (> 10). SN60 for lines ranged from 1.20 to 5.00 and 1 to 5.30 for SN80, whereas SN60 and SN80 ranged from 0 to 10.20 and 0 to 8.20 for testers. ASNPC ranged from 1.80 for cross IP-10579 $\times$ ICMB177002 to 485.10 for cross IP-6112 $\times$ IKMB18002 and 21.80 for line ICMB177002 to 103.50 for line IKMB18002. ASNPC for testers ranged between 10.10 for IP-9242 to 183.50 for IP-3098. IP-15857, the *Sh*-resistant check, had low SN60 (0.80), whereas SOSAT-C88, the susceptible check, recorded high SN60 (8.00). For SN80, the *Sh*-resistant check had low count (2.50) and the susceptible check, SOSAT-C88 had high SN80 count (10.70). The ASNPC was low (33.50) and high (186.80) for *Sh*-resistant and susceptible checks, respectively.

Table 4
Mean values of *S. hermonthica* parameters when evaluating pearl millet lines, testers, crosses and checks under greenhouse conditions with artificial *Striga* infestation

Crosses	SN60	SN80	ASNPC
IP-10579 × ICMB177002	0.00	0.20	1.80
IP-3098 × IKMB18002	22.20	22.20	443.50
IP-11358 × ICMB177002	3.30	3.80	71.80
IP-3098 × ICMB177002	2.70	3.30	60.10
IP-6112 × IKMB18002	23.50	25.00	485.10
IP-6112 × ICMB177002	4.50	3.00	75.10
IP-9242 × ICMB177111	6.70	5.70	123.50
IP-3098 × ICMB177111	31.00	23.50	545.10
IP-9242 × ICMB177002	0.20	0.30	5.10
IP-10579 × ICMB177111	1.70	2.20	38.50
IP-9242 × IKMB18002	12.80	12.00	248.50
IP-10579 × IKMB18002	1.70	2.00	36.80
IP-6112 × ICMB177111	18.30	23.30	416.80
IP-11358 × IKMB18002	1.20	2.20	33.50
IP-11358 × ICMB177111	0.50	0.70	11.80
Lines			
ICMB177002	1.20	1.00	21.80
ICMB177111	3.00	3.30	63.50
IKMB18002	5.00	5.30	103.50
Testers			
IP-3098	10.20	8.20	183.50
IP-6112	0.80	0.50	25.00
IP-9242	0.30	0.70	10.10
IP-10579	1.50	1.10	26.00
IP-11358	2.30	2.30	45.10
Checks			
IP-15857	0.80	2.50	33.50
SOSAT-C88	8.00	10.70	186.80

SN60 = *Striga* count 60 days after planting; SN80 = *Striga* count 80 days after planting; ASNPC = area under the *Striga* number progress curve.

3.4 Combining ability analysis for agronomic traits and *Striga*-resistance

The analysis of variance for lines, testers and crosses for agronomic traits at Gampela, Fada and greenhouse conditions is presented in Tables 5 and 6. Parents differed significantly ($P \leq 0.05$) for all evaluated traits except TGW at the Gampela site,

whereas there were significant ($P \leq 0.05$) differences except PH and NT at Fada. Lines showed significant ($P \leq 0.01$; $P \leq 0.001$) differences for NT at Gampela and PCL at Fada. Testers showed significant ($P \leq 0.01$) differences for PH, PCL and TGW at Gampela and significant ($P \leq 0.05$; $P \leq 0.01$; $P \leq 0.001$) for PH, PCL and GY at Fada (Table 5). Line $\times$ tester showed a non-significant effect for all traits at Gampela but significant ($P \leq 0.05$) for DTF at Fada. DTF, PCD, and TGW had high narrow-sense heritability ($> 58\%$) at both Gampela and Fada. In that order, low narrow-sense heritability was observed for PH, NT, and GY at 4.87 to 8.17%, 3.00 to 13.95%, and 23.96 to 47.07% at both locations.

Table 6 presented mean squares and significant tests for lines, testers, and crosses under *Striga* infestation in the greenhouse. A significant ($P < 0.001$) difference was observed for genotypes, parents vs crosses, crosses, testers and line $\times$ tester, for *Striga* parameters. SN60, SN80 and ASNPC had high broad- and-narrow-sense heritability values of > 99 and $> 69\%$, in that order. Baker's ratio was less than unity (≤ 0.99) for all *Striga* parameters.

Table 5
Mean squares and significant tests for lines, testers and crosses evaluated at Gampela and Fada sites in Burkina Faso.

Gampela								
SV	DF	DTF	PH	NT	PCL	PCD	TGW	GY
Replication	1	2.73 ^{ns}	584.76 ^{ns}	1.90 ^{ns}	2.77 ^{ns}	19.93 ^{ns}	1.57 ^{ns}	172827.79 ^{ns}
Treatment	23	35.03 ^{***}	2070.75 ^{***}	2.30 ^{**}	64.35 ^{***}	27.92 ^{**}	2.38 [*]	132178.82 ^{**}
Parents (P)	8	66.61 ^{***}	2738.97 ^{***}	3.47 ^{**}	65.84 ^{***}	31.38 ^{**}	0.98 ^{ns}	190244.91 ^{**}
P vs Cr	1	82.14 ^{**}	10235.45 ^{***}	1.25 ^{ns}	32.34 ^{ns}	47.65 [*]	8.68 ^{**}	436951.52 ^{**}
Crosses (Cr)	14	13.62 [*]	1105.71 ^{**}	1.70 ^{ns}	65.78 ^{***}	24.53 [*]	36.80 [*]	81376.30 ^{ns}
Line (L)	2	10.13 ^{ns}	250.00 ^{ns}	7.23 ^{**}	336.43 ^{ns}	19.23 ^{ns}	2.30 ^{ns}	96225.40 ^{ns}
Tester (T)	4	25.67 ^{ns}	3184.58 ^{**}	1.22 ^{ns}	48.38 ^{**}	46.70 ^{ns}	6.00 ^{**}	88683.15 ^{ns}
L×T	8	8.47 ^{ns}	280.21 ^{ns}	0.57 ^{ns}	6.81 ^{ns}	14.78 ^{ns}	1.02 ^{ns}	74010.60 ^{ns}
Error	22	6.26	351.68	0.86	10.39	9.51	1.18	51231.14
Trial statistics								
SED (L)		0.79	5.93	0.29	1.02	0.98	0.34	71.58
SED (T)		1.02	7.66	0.38	1.32	1.26	0.44	92.40
SED (L×T)		1.77	13.26	0.65	2.28	2.18	0.77	160.05
H ² (%)		74.78	66.59	36.05	98.72	94.54	77.49	84.16
h ² (%)		69.65	8.17	13.95	94.74	68.95	77.49	47.07
GCA/SCA		0.89	0.96	0.97	0.99	0.90	0.94	0.83
Fada								
Replication	1	7.03 ^{ns}	37.52 ^{ns}	1.03 ^{ns}	14.75 ^{ns}	12.78 ^{ns}	2.23 ^{ns}	580613.29 ^{ns}
Treatment	19	120.44 ^{***}	1534.18 [*]	0.54 ^{ns}	64.25 ^{ns}	22.65 [*]	4.84 ^{ns}	284712.14 ^{ns}
Parents (P)	5	191.98 ^{***}	1455.48 ^{ns}	0.78 ^{ns}	114.48 [*]	35.02 ^{**}	8.26 [*]	1690716.65 ^{***}
P vs Cr								
Crosses (Cr)	14	97.96 ^{**}	1191.79 ^{ns}	0.42 ^{ns}	50.49 ^{ns}	18.79 [*]	2.34 ^{ns}	224252.63 ^{ns}
Line (L)	2	91.47 ^{ns}	144.78 ^{ns}	0.68 ^{ns}	152.21 ^{***}	11.14 ^{ns}	2.49 ^{ns}	238.49 ^{ns}
Tester (T)	4	155.86 ^{ns}	3031.90 ^{**}	0.28 ^{ns}	84.41 ^{***}	27.66 ^{ns}	1.88 ^{ns}	517614.28 [*]
L×T	8	70.63 [*]	533.49 ^{ns}	0.42 ^{ns}	8.09 ^{ns}	16.26 ^{ns}	2.53 ^{ns}	133575.34 ^{ns}
Error	13	21.34	621.32	0.38	30.19	6.71	2.12	135547.42
Trial statistics								
SED (L)		1.46	7.88	0.20	1.74	0.82	0.46	116.42
SED (T)		1.89	10.18	0.25	2.24	1.06	0.59	150.30
SED (L×T)		3.27	17.63	0.44	3.89	1.83	1.03	260.33

Gampela								
SV	DF	DTF	PH	NT	PCL	PCD	TGW	GY
H ² (%)		98.35	58.99	-	93.28	87.44	86.76	-
h ² (%)		58.93	4.87	3.00	12.44	58.57	62.19	23.96
GCA/SCA		0.88	0.92	0.82	0.98	0.83	0.78	0.89

SV = source of variation; DF = degree of freedom; DTF = days to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grain yield (kg/ha); P = parents; Cr = crosses; L = line; T = tester; L×T = line × tester; SED = standard error of the mean difference; H² (%) = broad sense heritability; h² (%) = narrow sense heritability; GCA = general combining ability; SCA = specific combining ability; * = denote significant at the 0.05 probability level; ** = denote significant at the 0.01 probability level; *** = denote significant differences at 0.001 probability level; ns = denote not significant.

Table 6
Mean squares and significant tests for lines, testers, and crosses when evaluating 24 pearl millet genotypes with *Striga* infestation.

SV	DF	SN60	SN80	ASNPC
Replication	1	22.04 ^{ns}	1.07 ^{ns}	1349.92 ^{ns}
Treatment	23	149.27***	135.04***	55936.44***
Parents (P)	8	19.12 ^{ns}	18.85 ^{ns}	7248.96 ^{ns}
P vs Cr	1	347.55***	306.84***	131017.92***
Crosses (Cr)	14	209.47***	189.16***	78394.89***
Line (L)	2	322.47 ^{ns}	321.98 ^{ns}	128643.12 ^{ns}
Tester (T)	4	382.78*	346.94*	144557.35*
L×T	8	94.58***	77.07***	32751.60***
Error	22	8.99	10.02	3320.78
Trial statistics				
SED (L)		0.95	1.00	18.22
SED (T)		1.22	1.29	23.53
SED (L×T)		2.12	2.24	40.75
H ² (%)		99.24	99.02	99.26
h ² (%)		69.52	71.99	71.23
GCA/SCA		0.94	0.95	0.94

SV = source of variation; DF = degree of freedom; SN60 = *Striga* count 60 days after planting; SN80 = *Striga* count 80 days after planting; ASNPC = area under the *Striga* number progress curve; P = parents; Cr = crosses; L = line; T = tester; L×T = line × tester; SED = standard error of the mean difference; H² (%) = broad sense heritability; h² (%) = narrow sense heritability; GCA = general combining ability; SCA = specific combining ability; * = denote significant differences at 0.05 probability level; *** = denote significant differences at 0.001 probability level; ns = denote not significant.

3.4.1 General combining ability effects for agronomic and *Striga* parameters

GCA effects for agronomic traits and *Sh* parameters are presented in Tables 7 and 8, respectively. The line ICMB177002 recorded positive GCA effects for DTF (0.43), PH (2.26) and PCL (6.33). The testers IP-11358 and IP-6112 and line ICMB177111 had high positive GCA effects for GY at 158.99, 69.61 and 86.67 across locations. Negative GCA effects were computed for *Sh* parameters in a desirable direction. Testers IP-10579 and IP-11358 and line ICMB177002 had negative GCA effects for *Sh* parameters, SN60 (-7.58, -6.99, -6.55), SN80 (-7.18, -6.40, -6.49) and ASNPC (-147.45, -134.08, -130.33), whereas testers IP-6112 and IP-3098 and lines IKMB18002 and ICMB177111 had positive GCA effects for SN60 at 6.77, 9.92, 3.59 and 2.95, SN80 at 8.50, 7.72, 4.04 and 2.44 and ASNPC at 152.55, 176.43, 76.34 and 53.99 respectively.

Table 7
General combining ability (GCA) effects of the pearl millet lines and testers evaluated in two environments in Burkina Faso.

Genotypes	DTF	PH	NT	PCL	PCD	TGW	GY
ICMB177002	0.43 ^{ns}	2.26 ^{ns}	-0.24 ^{ns}	6.33 ^{**}	-0.07 ^{ns}	-0.06 ^{ns}	-24.98 ^{ns}
ICMB177111	-0.30 ^{ns}	6.36 ^{ns}	0.32 ^{ns}	-3.50 ^{ns}	2.38 ^{ns}	0.21 ^{ns}	86.67 ^{ns}
IKMB18002	-1.67 ^{ns}	11.22 ^{ns}	0.14 ^{ns}	0.05 ^{ns}	0.92 ^{ns}	0.26 ^{ns}	22.15 ^{ns}
IP-3098	-2.76 ^{ns}	-0.38 ^{ns}	0.01 ^{ns}	-0.11 ^{ns}	-0.88 ^{ns}	-0.02 ^{ns}	-24.89 ^{ns}
IP-6112	-0.87 ^{ns}	6.24 ^{ns}	-0.16 ^{ns}	-0.17 ^{ns}	1.93 ^{ns}	0.04 ^{ns}	69.61 ^{ns}
IP-9242	-0.71 ^{ns}	-14.72 ^{ns}	0.17 ^{ns}	0.02 ^{ns}	0.21 ^{ns}	0.07 ^{ns}	9.70 ^{ns}
IP-10579	1.87 ^{ns}	23.32 ^{ns}	0.02 ^{ns}	0.05 ^{ns}	-0.42 ^{ns}	0.00 ^{ns}	6.51 ^{ns}
IP-11358	2.44 ^{ns}	20.96 ^{ns}	-0.01 ^{ns}	0.31 [*]	-0.45 ^{ns}	0.18 ^{ns}	158.99 ^{ns}

DTF = days to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grain yield (kg/ha); * = denote significant differences at 0.05 probability level; ** = denote significant differences at 0.01 probability level; *** = denote significant differences at 0.001 probability level; ns = denote not significant.

Table 8
General combining ability (GCA) effects of the pearl millet lines and testers evaluated in a greenhouse condition under *Striga* infestation

Genotypes	SN60	SN80	ASNPC
ICMB177002	-6.55 ^{***}	-6.49 ^{***}	-130.33 ^{***}
ICMB177111	2.95 ^{**}	2.44 [*]	53.99 ^{**}
IKMB18002	3.59 ^{***}	4.04 ^{***}	76.34 ^{***}
IP-3098	9.92 ^{***}	7.72 ^{***}	176.43 ^{***}
IP-6112	6.77 ^{***}	8.50 ^{***}	152.55 ^{***}
IP-9242	-2.13 ^{ns}	-2.63 ^{ns}	-47.45 ^{ns}
IP-10579	-7.58 ^{***}	-7.18 ^{***}	-147.45 ^{***}
IP-11358	-6.99 ^{***}	-6.40 ^{***}	-134.08 ^{***}

SN60 = *Striga* count 60 days after planting; SN80 = *Striga* count 80 days after planting; ASNPC = area under the *Striga* number progress curve; * = denote significant differences at 0.05 probability level; ** = denote significant differences at 0.01 probability level; *** = denote significant differences at 0.001 probability level; ns = denote not significant.

3.4.2 Specific combining ability effects for agronomic and *Striga* parameters

SCA effects of agronomic traits for crosses evaluated across two environments in Burkina Faso are presented in Table 9. Crosses IP-9242 × ICMB177002, IP-3098 × IKMB18002, IP-10579 × IKMB18002, IP-11358 × ICMB177111 and IP-6112 × ICMB177002 had high positive SCA effects for GY at 65.33, 58.07, 39.62, 23.62 and 23.15 in that order. The hybrids IP-11358 × ICMB177002 had positive SCA effects for PCL (2.03), TGW (1.11) and GY (7.88).

Table 10 presented the SCA effects for crosses evaluated in the greenhouse under *Sh*-infestation. Crosses IP-3098 × ICMB177002, IP-6112 × ICMB177002 and IP-11358 × ICMB177111 had high and negative SCA for *Sh* parameters SN60 at -9.40, -4.40 and - 4.14, SN80 at -6.50, -7.63 and - 4.01 and ASNPC at -159.10, -120.22 and - 81.21 in that order. Crosses IP-3098 × ICMB177111, IP-11358 × ICMB177002 and IP-10579 × ICMB177002 had large and positive SCA effects for SN60 (9.45, 8.21 and 5.45), SN80 (4.72, 8.12 and 5.20) and ASNPC (141.58, 163.11 and 106.43).

Table 9
Specific combining ability (SCA) effects for agronomic traits among pearl millet crosses evaluated across two environments in Burkina Faso.

Hybrids	DTF	PH	NT	PCL	PCD	TGW	GY
IP-3098 × ICMB177002	0.95 ^{ns}	-2.28E-13 ^{ns}	-0.26 ^{ns}	-0.65 ^{ns}	0.36 ^{ns}	-0.50 ^{ns}	-63.77 ^{ns}
IP-6112 × ICMB177002	1.25 ^{ns}	2.49E-13 ^{ns}	0.04 ^{ns}	-2.93 ^{ns}	-0.33 ^{ns}	-0.51 ^{ns}	23.15 ^{ns}
IP-9242 × ICMB177002	-0.87 ^{ns}	1.13E-14 ^{ns}	0.07 ^{ns}	0.46 ^{ns}	0.30 ^{ns}	0.18 ^{ns}	65.33 ^{ns}
IP-10579 × ICMB177002	-0.74 ^{ns}	4.79E-14 ^{ns}	-0.06 ^{ns}	0.90 ^{ns}	1.28 ^{ns}	-0.34 ^{ns}	21.10 ^{ns}
IP-11358 × ICMB177002	-1.08 ^{ns}	1.35E-13 ^{ns}	-0.14 ^{ns}	2.03 ^{ns}	-0.47 ^{ns}	1.11*	7.88 ^{ns}
IP-3098 × ICMB177111	-1.20 ^{ns}	4.64E-14 ^{ns}	0.27 ^{ns}	0.80 ^{ns}	-0.71 ^{ns}	0.21 ^{ns}	16.81 ^{ns}
IP-6112 × ICMB177111	-0.06 ^{ns}	6.37E-14 ^{ns}	0.11 ^{ns}	-3.20 ^{ns}	3.56**	0.32 ^{ns}	-2.15 ^{ns}
IP-9242 × ICMB177111	0.79 ^{ns}	9.86E-15 ^{ns}	0.13 ^{ns}	0.51 ^{ns}	-1.06 ^{ns}	0.28 ^{ns}	-31.00 ^{ns}
IP-10579 × ICMB177111	-0.51 ^{ns}	1.42E-13 ^{ns}	0.21 ^{ns}	0.95 ^{ns}	0.15 ^{ns}	0.40 ^{ns}	-55.24 ^{ns}
IP-11358 × ICMB177111	-0.49 ^{ns}	-1.95E-13 ^{ns}	-0.08 ^{ns}	0.67 ^{ns}	-1.13 ^{ns}	-0.32 ^{ns}	23.62 ^{ns}
IP-3098 × IKMB18002	-0.07 ^{ns}	-5.06E-14 ^{ns}	-0.22 ^{ns}	0.17 ^{ns}	0.01 ^{ns}	0.03 ^{ns}	58.07 ^{ns}
IP-6112 × IKMB18002	-0.96 ^{ns}	-1.21E-13 ^{ns}	-0.02 ^{ns}	-1.36 ^{ns}	0.58 ^{ns}	0.34 ^{ns}	14.82 ^{ns}
IP-9242 × IKMB18002	0.13 ^{ns}	1.42E-13 ^{ns}	0.21 ^{ns}	1.10 ^{ns}	-0.81 ^{ns}	-0.16 ^{ns}	20.71 ^{ns}
IP-10579 × IKMB18002	-0.45 ^{ns}	2.25E-13 ^{ns}	-0.02 ^{ns}	2.16 ^{ns}	0.93 ^{ns}	0.14 ^{ns}	39.62 ^{ns}
IP-11358 × IKMB18002	-0.55 ^{ns}	9.66E-14 ^{ns}	0.11 ^{ns}	2.35 ^{ns}	-0.11 ^{ns}	0.48 ^{ns}	-28.89 ^{ns}

DTF = days to 50% flowering; PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grain yield (kg/ha); * = denote significant differences at 0.05 probability level; ** = denote significant differences at 0.01 probability level; ns = denote not significant.

Table 10
Specific combining ability (SCA) effects for *Striga* parameters
among pearl millet crosses evaluated under *Striga*-infestation

Hybrids	SN60	SN80	ASNPC
IP-3098 × ICMB177002	-9.40**	-6.50*	-159.10**
IP-6112 × ICMB177002	-4.40 ^{ns}	-7.63**	-120.22*
IP-9242 × ICMB177002	0.14 ^{ns}	0.80 ^{ns}	9.78 ^{ns}
IP-10579 × ICMB177002	5.45*	5.20*	106.43*
IP-11358 × ICMB177002	8.21**	8.12**	163.11**
IP-3098 × ICMB177111	9.45**	4.72 ^{ns}	141.58**
IP-6112 × ICMB177111	-0.05 ^{ns}	3.79 ^{ns}	37.11 ^{ns}
IP-9242 × ICMB177111	-2.85 ^{ns}	-2.78 ^{ns}	-56.24 ^{ns}
IP-10579 × ICMB177111	-2.40 ^{ns}	-1.70 ^{ns}	-41.24 ^{ns}
IP-11358 × ICMB177111	-4.14 ^{ns}	-4.01 ^{ns}	-81.21 ^{ns}
IP-3098 × IKMB18002	-0.04 ^{ns}	1.77 ^{ns}	17.53 ^{ns}
IP-6112 × IKMB18002	4.45 ^{ns}	3.84 ^{ns}	83.11 ^{ns}
IP-9242 × IKMB18002	2.71 ^{ns}	1.97 ^{ns}	46.46 ^{ns}
IP-10579 × IKMB18002	-3.04 ^{ns}	-3.48 ^{ns}	-65.19 ^{ns}
IP-11358 × IKMB18002	-4.07 ^{ns}	-4.11 ^{ns}	-81.91 ^{ns}

SN60 = *Striga* count 60 days after planting; SN80 = *Striga* count 80 days after planting; ASNPC = area under the *Striga* number progress curve; * = denote significant differences at 0.05 probability level; ** = denote significant differences at 0.01 probability level; ns = denote not significant.

3.5 Heterosis for agronomic traits

Mid-parent and standard heterosis for pearl millet crosses for agronomic traits evaluated across two environments in Burkina Faso are presented in Table 11. MPH for PH were positive and varied from 2 to 30%. The MPH for NT was positive for 53.33% of the crosses. The MPH for PCL was positive in 86.67% of crosses, such as in IP-10579 × ICMB177002, IP-3098 × IKMB18002, IP-9242 × ICMB177002 and IP-6112 × IKMB18002 at 46.58, 28.07, 25.43 and 21.98%, in that order. For PCD, high and positive MPH was observed for IP-10579 × ICMB177002 and IP-6112 × IKMB18002 at 64.67 and 15.96%, in that order. High MPH for TGW was recorded for IP-11358 × ICMB177002 (91.25%), IP-6112 × ICMB177111 (46.70%), IP-6112 × IKMB18002 (39.81%), IP-3098 × ICMB177111 (33.72%) and IP-10579 × ICMB177002 (25.20%). For GY, MPH was high and positive for IP-6112 × ICMB177002, IP-6112 × IKMB18002, IP-10579 × IKMB18002 and IP-9242 × IKMB18002 at 160.71, 89.98 38.02 and 21.07%, in that order.

The SH for PH was positive for 40% of crosses. All crosses recorded negative SH for NT and GY. For PCL, high and positive SH was observed for IP-11358 × ICMB177002 (17.33%), IP-10579 × ICMB177002 (11.70%) and IP-9242 × ICMB177002 (8.69%). Positive SH were recorded for 6.67% of crosses for PCD, whereas 53.33% had positive SH for TGW.

Table 11

Mid-parent and standard heterosis for agronomic traits among pearl millet crosses evaluated across two environments in Burkina Faso.

Hybrid	Mid-parent heterosis						Standard heterosis					
	PH	NT	PCL	PCD	TGW	GY	PH	NT	PCL	PCD	TGW	GY
IP-10579 × ICMB177002	29.75	-5.88	46.58	64.67	25.20	8.06	4.23	-49.94	11.70	-12.35	-14.55	-68.12
IP-3098 × ICMB177002	6.94	-3.68	2.38	2.49	-1.33	7.72	-17.75	-49.94	4.83	-19.94	-18.14	-67.45
IP-3098 × IKMB18002	28.74	-22.75	28.07	4.40	17.84	3.03	-9.87	-46.61	-14.09	-19.28	-7.85	-54.45
IP-10579 × ICMB177111	8.29	7.11	1.47	3.14	9.42	4.25	4.47	-23.27	-28.98	-20.42	0.07	-53.72
IP-11358 × ICMB177002	21.66	32.47	16.43	2.51	91.25	-1.57	6.35	-39.94	17.33	-23.65	22.99	-46.02
IP-6112 × ICMB177002	19.97	-6.25	-2.50	1.35	0.99	160.71	-1.09	-36.61	-9.09	-13.23	-13.79	-43.24
IP-10579 × IKMB18002	10.83	1.02	9.39	7.57	6.71	38.02	6.95	-29.94	-13.01	-16.16	-2.03	-41.89
IP-9242 × ICMB177111	2.57	5.96	1.65	0.60	7.74	1.33	-16.38	-13.27	-24.77	-10.52	0.41	-41.89
IP-3098 × ICMB177111	15.71	20.76	8.47	-4.10	33.72	0.47	-5.87	-6.35	-20.45	-17.08	0.19	-41.58
IP-9242 × IKMB18002	7.00	0.62	9.77	-1.03	6.71	21.07	-10.55	-23.27	-4.83	-21.55	-0.27	-38.16
IP-9242 × ICMB177002	19.98	-13.28	25.43	7.79	22.01	20.70	-9.68	-29.94	8.69	-16.08	-1.64	-37.53
IP-6112 × IKMB18002	25.82	-9.99	21.98	15.96	39.81	89.98	-1.54	-29.94	-18.98	1.06	8.98	-35.42
IP-6112 × ICMB177111	19.48	-1.74	-14.67	8.97	46.70	8.17	-1.09	-46.35	-43.86	-34.67	9.90	-35.31
IP-11358 × IKMB18002	11.85	1.68	7.05	3.25	14.18	7.63	15.22	-26.61	1.93	-12.05	15.86	-24.96
IP-11358 × ICMB177111	6.65	8.35	3.11	2.11	12.49	3.88	3.71	-16.61	-8.98	-9.74	6.73	-3.08

PH = plant height at maturity (cm); NT = number of tillers per plant; PCL = panicle length (cm); PCD = panicle diameter (mm); TGW = thousand grains weight (g); GY = grains yield (kg/ha).

4 Discussion

Striga, commonly called witchweed, is a noxious parasitic weed that causes significant yield losses in cereal crops, including pearl millet. Due to *Striga* parasitism, yield losses varying from 80 to 100% have been reported in pearl millet (Kountche et al. 2016; Kanampiu et al. 2018; Rouamba et al. 2021). In Burkina Faso, the weed poses a major constraint to pearl millet production, especially under low-input production systems (Boussim et al. 2011; Drabo et al. 2018; Rouamba et al. 2021). The currently cultivated varieties are susceptible to *Striga*, and there are modest previous breeding efforts, but *Striga*-resistant pearl millet varieties are yet to be developed. There is a need to develop high-yielding and *Sh*-resistant pearl millet varieties with farmers' preferred traits. The current study determined the combining ability and heterosis for agronomic traits and *Sh*-resistance in pearl millet to select

promising parental lines and testers for breeding and selection of *Sh*-resistant hybrids with farmer-preferred traits for genetic advancement and cultivar release.

The significant difference observed among the studied pearl millet genotypes for most agronomic traits suggests the presence of adequate genetic variation for breeding (Table 2). Significant interaction effects existed between lines, testers and crosses and the test environments for most traits. The differential response indicated that lines, testers and crosses allow the selection of the best candidates based on the target production environments. For example, crosses IP-11358 × ICMB177111, IP-11358 × IKMB18002, IP-6112 × ICMB177111 and IP-9242 × ICMB177002 with grain yields of 1128.10, 938.60, 890.30 and 825.50 kg/ha, in that order, were the top-yielders across the test locations (Table 3). Therefore, they are suitable for production in the major pearl millet production zones of Burkina Faso and similar environments of SSA. The study identified crosses IP-10579 × ICMB177002, IP-9242 × ICMB177002 and IP-11358 × ICMB177111 with low levels of *Striga* damage and possessing candidate *Sh*-resistant genes as compared to the resistant check (Table 4). These suggest the possibility to develop *Sh*-resistant pearl millet genotypes. Also, the testers IP-9242, IP-6112, and IP-10579 were *Striga*-resistant and valuable germplasm to augment this trait into elite pearl millet genotypes (Table 4).

Combining ability analysis allows the selection of parents for breeding, new progenies for selection, genetic advancement and new variety release. The present study revealed that most agronomic and *Striga* parameters were conditioned by non-additive gene effects (Table 5), in agreement with Sanghera & Hussain (2012), Barathi et al. (2020), and Balami et al. (2022). The preponderance of non-additive gene action in the expression of pearl millet traits indicates that hybrid breeding is possible using the current gene pool to exploit heterosis. Narrow-sense heritability varied from high (94.74%) to low (3.00%) for agronomic traits and high (69.52%) for *Striga* traits suggesting the involvement of additive and non-additive gene effects controlling their expression. Reportedly, non-additive genetic effects were found to govern the inheritance of plant height, the number of tillers per plant, and grain yield in pearl millet in India (Rattunde 1988; Jeeterwal et al. 2018).

The tester parent IP-11358 had high positive GCA effects for grain yield and negative GCA effects for the number of emerged *Sh* plants estimated at 60 days and 80 days after sowing and the area under the *Striga* number progress curve. Positive effects for grain yield and negative effects for the number of *Sh* counts are desirable traits when breeding for high-yielding and *Striga*-resistant varieties (Lobulu et al. 2023). In contrast, negative effects for days to 50% flowering and the number of *Sh* count are desirable for early maturity and *Striga*-resistance (Balami et al. 2022). As a result, the tester parent IP-11358 was identified as a good combiner for grain yield and *Sh*-resistance for future breeding. High positive SCA effects for grain yield and negative SCA effects for the number of *Sh* recorded for IP-6112 × ICMB177002 and IP-11358 × ICMB177111 indicated that their parents have greater genetic distance and combine well to produce *Sh*-resistant high-yielding progenies. High SCA effects for panicle length, thousand-grain weight, and grain yield for IP-11358 × ICMB177002 indicated the ability to develop new pearl millet varieties which combined desirable and yield-improving agronomic traits. Significant SCA effects for yield and yield components and low SCA for *Striga* tolerance were reported by Balami et al. (2022) in pearl millet. Host-plant resistance has been widely recognised as the most economical and sustainable method for the long-term control of *Striga* in farmers' fields (Yoder & Scholes 2010).

Negative and positive standard heterosis observed for the number of tillers and thousand-grain weight is in line with findings by Sumit & Wali (2016), Sumathi & Revathi (2017), Acharya et al. (2017), and Dawud (2018) in pearl millet. High standard heterosis for the grain yield was observed for some evaluated pearl millet crosses, such as IP-11358 × ICMB177111, IP-11358 × IKMB18002 and IP-6112 × ICMB177111, suggesting successful development and delivery of high-yielding pearl millet hybrids. This is in line with the findings by Chittora & Patel (2017) and Sumathi & Revathi (2017), who reported higher hybrid vigour in pearl millet. The newly bred experimental hybrids are recommended for genetic advancement and further selection to recommend for high-yielding and *Striga*-resistant pearl millet varieties.

5 Conclusion

The present study estimated the combining ability of selected lines and testers and the hybrid performance of their crosses for agronomic traits and resistance to *Striga* for variety development in pearl millet. The testers IP-10579, IP-6112 and IP-11358 were identified as promising genetic stocks for grain yield and *Striga*-resistance breeding. Lines such as ICMB177111 and IKMB18002 were identified as valuable sources of genes for breeding for high-yield potential. The experimental hybrids IP-11358 × ICMB177111,

IP-10579 × IKMB18002 and IP-6112 × ICMB177002 with high grain yield potential and *Striga*-resistance were identified for multi-environment evaluation, genetic advancement and production in Burkina Faso.

Declarations

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Authors' contributions

A.R.: Methodology, data collection, data analysis, and Writing of the manuscript draft. H.S.: Supervision, writing conceptualization, review, and editing. I.D.: Guided experiment designing, writing, reviewing and editing. E.M.: Reviewing and editing. J.M.: Reviewing and editing. L.M.: Reviewing and editing.

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