

Combining Ability and Heterosis for Grain Yield and Rust Resistance in Pearl Millet

G. Lubadde¹, P. Tongoona², J. Derera² & J. Sibiya²

¹ National Semi-Arid Resources Research Institute, Soroti, Uganda

² College of Agriculture, Engineering and Science, University of Kwazulu Natal, Scottsville, South Africa

Correspondence: G. Lubadde, National Semi-Arid Resources Research Institute, P.O. Box Private Bag, Soroti, Uganda. Tel: 256-772-965-752. E-mail: glubadde@gmail.com

Received: January 5, 2015 Accepted: April 3, 2015 Online Published: June 15, 2016

doi:10.5539/jas.v8n7p80

URL: <http://dx.doi.org/10.5539/jas.v8n7p80>

Abstract

Pearl millet is a dual-purpose crop in semi-arid zones of Uganda. However, no studies have been conducted to determine the gene effects for yield and yield-related traits and rust resistance in these environments; yet this knowledge is important in improving grain yield and rust resistance. A North Carolina II mating design was adopted to study the genetic effects for rust resistance and yield-related traits of improved pearl millet genotypes. The experimental design to study the objectives was alpha in two [locations, seasons and replications]. A higher proportion of general combining ability (GCA) effect was observed for grain yield, days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, plant height, total tiller number, number of productive tillers, percentage of productive tillers, panicle area, leaf area, 1000-grain weight, biological yield and harvest index. The specific combining ability (SCA) effect was predominant for area under disease progress curve. Eleven hybrids performed better than the best male parent and five crosses performed better than the best female parent for grain yield while all the fifteen selected best crosses performed better than all parents for area under disease progress curve. Ten crosses were more resistant to rust than the best male parent and all the crosses were more resistant to rust than the female parents. The additive gene action was predominant for grain yield, rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, total tiller number, percentage of productive tillers, panicle area, 1000-grain weight, biological yield, harvest index and leaf area. High better-parent heterosis was also observed for most traits including grain yield and rust resistance. The traits were also characterized by relatively low levels of narrow sense heritability.

Keywords: combining ability, gene action, heritability, heterosis, rust

1. Introduction

Pearl millet is a staple crop in the crop-livestock production systems of the drought-prone zones (Sharma & Pareek, 1993). The crop is grown worldwide mainly for food and forage (Girgi et al., 2006). It performs well under stressful conditions of drought and acidic soils (FAO, 2004); though it also does competitively well in favorable environments (Bhatnagar et al., 1998; Christinck, 2002). In the stressful environments, farmers grow low yielding landraces characterized by yield stability rather than high grain yield per se; implying that minimizing risk to crop failure is a major priority than high grain yield (Kelley et al., 1996; Van Oosterom et al., 1996). However, stress-adapted varieties with high grain yield have been developed through hybrid breeding (Van Oosterom et al., 1996) but are not available in Uganda; a reason why low yielding rust susceptible genotypes (Lubadde et al., 2014) are perpetually grown. The disease causes high grain and forage loss (Wilson, 2000); hence the need to develop and provide improved pearl millet varieties with high grain yield and resistance to rust. However, to develop high yielding varieties, knowledge about genetic factors responsible for the inheritance of important traits is essential. This is achieved through identifying the predominant genetic components (Vengadessan, 2008) and establishing the magnitude of their effects on trait expression. The genetic analysis helps to elucidate the combining ability which leads to identification of the best parent combinations that result in superior performing hybrids (Banziger & Cooper, 2001). The combining ability of inbred lines also helps to determine the potential value of the variety development programme (Legesse et al., 2009). Through combining ability analysis the nature of gene action involved in expression of traits is also established. The additive gene action is related to general combining ability while specific combining ability is associated with

non-additive genetic effects (Falconer, 1989). To assess combining ability an appropriate crossing design should be adopted. Commonly used designs (Hallauer & Miranda, 1988) in pearl millet breeding include; diallel, line x tester, generation mean analysis, triple test cross and North Carolina mating designs. The diallel design has been widely used in pearl millet breeding to assess type of gene action for grain yield (Bhadalia et al., 2012, 2014), 1000-grain weight (Izge et al., 2007), phytate acid content (Satija & Thukral., 1985; Shanmuganathan et al., 2006), zinc and iron content (Rai et al., 2013; Velu et al., 2011), salt tolerance (Ali et al., 2006; Venkata et al., 2012) and assessing gene action for Napier grass × pearl millet crosses (Pereira et al., 2006). The line × tester has been adopted to assess the combining ability of inbred parents (Arulselvi et al., 2009) in order to establish their potential to develop superior hybrids for grain quality traits (Parmar et al., 2013). It has also been used to assess gene action and heterosis for micronutrients like zinc and iron content (Govindaraj et al., 2013), heterosis for early maturity (Kumhar, 2007), combining ability for dry fodder yield (Chaudhary et al., 2012) and male sterile lines (Rasal & Patil, 2003). Generation mean analysis and triple test cross designs have been used to assess nature of gene action for grain sink size (Vengadessan, 2008) and physiological traits in pearl millet (Singh et al., 1991) while the North Carolina II mating design has been widely used in genetic assessment to identify the best parents for hybrid development and identify superior hybrids for specific traits (Hallauer & Miranda, 1988). The design has been used to assess gene action for downy mildew (Angarawai et al., 2008) while in this study it was used to assess the nature of gene action predominantly governing the expression of the traits. The objectives were to establish i) the combining ability effects, ii) nature of gene action and iii) levels of heterosis for grain yield, rust resistance and selected yield-related traits.

2. Materials and Methods

2.1 Experimental Materials

Sixteen improved varieties (Table 1) were used as parents and crossed in a North Carolina II design. Six rust resistant male parents were crossed with ten susceptible female parents resulting in 60 F₁ crosses. To avoid undesirable pollination the plant heads were covered at boot stage. To minimise selfing which occurs due to stigmas that may emerge later after the crossing, the lower quarter and upper quarter of the panicle were cut off before threshing. In addition, uprooting off-types was done during evaluation.

Table 1. The parental materials used to make crosses

Experimental materials	Role in crosses	Rust reaction	Source
ICMV3771	Male	Resistant	ICRISAT-ESA
Manganara	Male	Resistant	UKZN
Okashana2	Male	Resistant	ICRISAT-ESA
ITMV8001	Male	Resistant	ICRISAT-WSA
SDMV94001	Male	Resistant	ICRISAT-ESA
Shibe	Male	Resistant	ICRISAT-ESA
Exbornu	Female	Susceptible	ICRISAT-WSA
CIVT9206	Female	Susceptible	ICRISAT-WSA
GGB8735	Female	Susceptible	ICRISAT-WSA
ICMV221	Female	Susceptible	ICRISAT-ESA
ICMV221white	Female	Susceptible	ICRISAT-ESA
KatPM1	Female	Susceptible	ICRISAT-ESA
OKOA	Female	Susceptible	UKZN
SDMV96053	Female	Susceptible	ICRISAT-ESA
Sosank	Female	Susceptible	UKZN
Okollo	Female	Susceptible	UKZN

2.2 Experimental Sites and Field Layout

The crosses were developed at the National Semi Arid Resources Research Institute (NaSARRI)-Serere in the first rains of 2012 (March-July). The 60 F₁ crosses and 76 parents were evaluated at Serere and Kitgum and two seasons. Both sites were characterised as hot spots for rust, with sandy soils and being in semi-arid zones. The Kitgum site is located at 03°13'N, 032°47'E, and 969 m.a.s.l. while the Serere site location was 01°32'N, 033°27'E, 1140

m.a.s.l. The test materials were replicated twice and planted in a 4×19 alpha design. The materials were planted in $8 \text{ m} \times 5 \text{ m}$ plots at a spacing of $60 \text{ cm} \times 30 \text{ cm}$ and a nutrient regime of $\text{N}40 \text{ kg ha}^{-1}$, $\text{P}30 \text{ kg ha}^{-1}$ and $\text{K}35 \text{ kg ha}^{-1}$, applied in two splits, adopted (Khairwal et al., 2007). The plants were inoculated with freshly harvested uredospores from earlier planted susceptible genotypes.

2.3 Data Collection and Analysis

Data was collected on 36 randomly selected plants per plot using the 'Descriptors of pearl millet' (IBPGR & ICRISAT, 1993). The traits considered were; rust severity determined using the modified Cobb's disease severity scale (0-100%) (Tooley & Grau, 1984), panicle length (cm), panicle girth (cm), panicle area (cm^2), 1000-grain weight (g), plant height (cm), days to 50% flowering, days to 50% anthesis, flower-anthesis interval calculated (days), days to 50% physiological maturity, total number of tillers, number of productive tillers, biological yield per plant (g), harvest index, leaf length (cm) and leaf breadth (cm) of third leaf from plant top, leaf area (cm^2), grain productivity (kg ha^{-1}) and area under disease progress curve $\text{AUDPC} = \sum[(x_{i+1} + x_i)/2] [t_{i+1} - t_i]$ (Singh & King, 1991). The AUDPC was calculated from rust severity data collected for five weeks at five day interval from time first rust disease symptoms were observed. Data analysis was done using the SAS computer software, version 9.2 (SAS Institute Inc., 2012), with analyses of variance for the measured traits determined based on Proc GLM. Using the same model, the components of variance for estimating gene action were determined in SAS with Proc varcomp. The variances for the male (GCA_m) parents, female (GCA_f) parents and crosses (SCA_{mf}) were used as direct estimates for additive and non-additive gene actions for the parents and crosses, respectively as suggested by Dabholkar (1992). The variance components were also used to estimate the narrow sense and broad sense heritability for the traits. In the model, the parents, crosses and sites were fixed factors, while the random factors were; seasons, replications, blocks (nested within reps and seasons and sites) and the interactions of parents with seasons and sites. A modification of the Arunachalam (1974) fixed effects model was used to estimate the effects of the test materials across the two seasons and two sites.

The model:

$$Y_{ijk} = \mu + g_i + g_j + s_{ij} + e_k + (ge)_{ik} + (ge)_{jk} + (se)_{ijk}b_{(\text{rek})} + (g_i \times g_j \times s_{ij} \times e_k)e_{ijk} + \epsilon_{ijk} \quad (1)$$

Where, Y_{ijk} = performance of the cross made with i^{th} male line and j^{th} female line in the k^{th} environment; μ = overall mean; g_i = effect of i^{th} male line; g_j = effect of j^{th} female line; s_{ij} = interaction of the i^{th} male line with the j^{th} female line; e_k = effect of the k^{th} environment; $(ge)_{ik}$ = interaction of g_i and e_k ; $(ge)_{jk}$ = interaction of g_j and e_k ; $(se)_{ijk}$ = the interaction of s_{ij} and e_k ; $b_{(\text{rek})}$ = effect of blocks nested in reps, season and location; $(g_i \times g_j \times s_{ij} \times e_k)e_{ijk}$ = four-way interaction of parents, crosses and sites; ϵ_{ijk} = random error.

The general combining ability (GCA) effects for the male and female parents were determined using parental means *inter se* while the specific combining ability (SCA) effects were estimated using the means of the progeny (Singh & Chaudhary, 1985; Kurt & Evans, 1998). The GCA effects of the male and female parents were estimated as the difference between the grand mean and the mean of the parents for the trait. The SCA effects of each cross were calculated as a deviation of the cross mean from the grand mean of all the crosses adjusted for corresponding GCA effects of parents.

Calculation of the combining ability effects:

$$\text{GCA}_{\text{male}} = X_{\text{male}} - \mu;$$

$$\text{GCA}_{\text{female}} = X_{\text{female}} - \mu;$$

$$\text{SCA}_{\text{male} \times \text{female}} = X_{\text{male} \times \text{female}} - E(X_{\text{male} \times \text{female}}) \quad (2)$$

Where, GCA_{male} and $\text{GCA}_{\text{female}}$ are the general combining of the male and female parents, respectively; $\text{SCA}_{\text{male} \times \text{female}}$ is the specific combining ability for the crosses; X_{male} and X_{female} are the means for male and female parents, respectively; μ is the overall mean; X_{male} , X_{female} and $X_{\text{male} \times \text{female}}$ are respective observed means for the male, female parents and the crosses; $E(X_{\text{male} \times \text{female}})$ is the predicted or expected mean value of the cross given by $E(X_{\text{male} \times \text{female}}) = [\text{GCA}_{\text{male}} + \text{GCA}_{\text{female}} + \mu]$.

The percentage of heterosis and better parent heterosis were computed using the means of the parents and the crosses as shown in the formulae:

$$\text{Mid-parent heterosis (MP)} = [(X_{\text{male} \times \text{female}} - \text{MP}) \times 100]/\text{MP} \quad (3)$$

$$\text{Better-parent heterosis (BP)} = [(X_{\text{male} \times \text{female}} - \text{BP}) \times 100]/\text{BP} \quad (4)$$

Where, $\text{MP} = (X_{\text{male}} + X_{\text{female}})/2$.

Broad sense heritability was calculated as:

$$\sigma^2_{(g)}/\sigma^2_{(P)} \times 100 \quad (5)$$

Narrow sense heritability was calculated as:

$$\sigma^2_{(A)}/\sigma^2_{(P)} \times 100 \quad (6)$$

Where,

$\sigma^2_{(P)} = \sigma^2_{(A)} = \sigma^2_{\text{female}(A)} + \sigma^2_{\text{male}(A)} + \sigma^2_{\text{male} \times \text{female}} + \text{random error}$ (all variance components determine from Proc varcomp anova table.

$$\begin{aligned} \sigma^2_{(g)} &= \sigma^2_{\text{female}(A)} + \sigma^2_{\text{male}(A)} + \sigma^2_{\text{male} \times \text{female}(D)} \\ \sigma^2_{(A)} &= \sigma^2_{\text{female}(A)} + \sigma^2_{\text{male}(A)} \end{aligned} \quad (7)$$

3. Results

3.1 Pooled Analysis of Variance

For grain yield, significant ($p \leq 0.05$) effects were observed for parents and crosses (Table 2). The site and season \times male interactions also had significant effects on grain yield, while site and season \times female interactions had no significant ($p > 0.05$) effect on grain yield. Table 2 further shows a relatively high coefficient of determination ($R^2 = 0.64$) although the coefficient of variance was relatively high. The site effects were highly significant for rust severity at 50% physiological maturity and AUDPC. Only female \times season and female \times site interactions were significant for rust severity. The main effects of male parents, site and season \times male interactions were also significant. Significant effects were also observed for the three way interaction of male, site and seasons. Highly significant ($p \leq 0.001$) to significant ($p > 0.05$) variations were observed for the male main effects for all the traits except panicle area, percentage of productive tillers, thousand grain weight, total number of tillers and number of productive tillers. For the female main effects all the traits were significant except for 1000-grain weight and harvest index. The interactions between female and male parents were also significant for all the traits except for days to 50% anthesis, panicle area, 1000-grain weight, leaf area and harvest index.

Table 2. Analysis of variance mean squares for traits pooled across sites

Source of variation	DF	Traits related to reproductive phase							
		GY	RUST	AUDPC	FLO ₅₀	ANT ₅₀	FAI	PSM ₅₀	PAR
Site	1	3458486.61*	60915.32**	4261084.66**	798.30**	123.57*	344.70**	698.27*	22043305.41**
Block (Season \times site \times rep)	8	7901438.01**	20212.08**	166698.27**	334.88**	532.88**	27.21**	753.18**	6177113.57**
Male	5	1989356.55*	8684.55**	102987.234*	90.90**	116.64**	2.80*	225.99**	138303.49ns
Female	9	1211649.81*	7961.73ns	29573.76ns	69.16**	91.22**	2.48*	192.37**	292797.32*
Female \times male	44	1507374.04*	11684.94*	36526.30ns	23.21*	27.75ns	2.06*	51.24*	154816.01ns
Site \times female	9	1865350.94ns	8576.45ns	24592.02ns	11.29ns	21.63ns	1.99*	94.64*	71555.90ns
Season \times female	10	1656209.21ns	13264.62**	18311.32ns	59.51**	74.00**	2.67*	139.56**	807846.56**
Season \times site \times female	10	2496250.39*	13216.13**	27401.45ns	34.93*	35.51*	4.01*	129.23*	1344518.02**
Site \times male	5	2211695.22*	5409.24**	183630.86*	17.35ns	32.27*	2.51ns	60.99ns	350640.57*
Season \times male	5	1844002.59*	10299.35*	175076.06*	13.34ns	8.19ns	0.31ns	69.89ns	214997.17*
Season \times site \times male	5	1874388.21ns	12104.17ns	189210.51**	30.42*	24.13ns	1.45	78.57ns	166708.48ns
Site \times female \times male	44	1330138.85ns	11175.11ns	28751.53ns	22.04*	28.24*	1.59ns	60.98ns	310099.14**
Season \times female \times male	44	1679336.79*	10665.09*	23525.27ns	18.13ns	23.87ns	1.92*	61.93ns	199953.43**
Season \times site \times female \times male	44	1518669.84ns	10247.94ns	32329.43ns	18.29ns	22.02ns	1.18ns	65.89ns	193304.52*
Error	233	1171949.2	10819.23	44161.85	15.47	18.73	1.38	64.02	160987.7
Total mean square		33716296	215235.98	5343860.5	1557.21	1180.65	398.25	2746.76	32626947
R-square		0.64	0.8	0.62	0.73	0.73	0.76	0.71	0.85
%CV		36.37	11.67	17.68	6.85	6.94	22.74	9.08	9.73

Note. LSD testing at $\alpha = 0.05$; ** = significant with $p \leq 0.001$, * = significant with $p \leq 0.05$, ns = non-significant.

GY = grain yield (Kg plant⁻¹), AUDPC = Area under disease progress curve, RUST = rust severity at 50% physiological maturity, FLO₅₀ = days to 50% flowering, ANT₅₀ = days to 50% anthesis, FAI = flower-anthesis interval (days), PSM₅₀ = days to 50% physiological maturity, PAR = panicle area (cm²).

Table 2. Continued

Source of variation	DF	Traits related to vegetative phase							
		PLH	TOT	PRT	PRO	LAR	1000GWT	HI	BY
Site	1	18905.18**	703.36**	1.17**	44667.57**	670535.50**	214.13**	12691.96**	6.06**
Block (Season × site × rep)	8	10068.14**	20.12**	122.59**	13857.06**	201922.16**	206.88**	3339.71**	25.42**
Male	5	1182.15*	11.54ns	45.21ns	3032.60ns	90107.01*	1.76ns	641.56*	37.72ns
Female	9	2017.24*	14.49*	41.24*	3757.12*	47850.02*	6.73ns	558.35ns	31.52*
Female × male	44	1322.63*	10.26*	66.64*	4271.56*	50117.64ns	5.75*	915.58ns	20.69*
Site × female	9	1189.24ns	16.08*	59.72ns	3755.11ns	24633.81 ns	2.18 ns	550.22ns	16.68ns
Season × female	10	884.48*	12.05*	52.00ns	3125.42ns	70556.28*	12.15*	1146.23*	14.30*
Season × site × female	10	2621.20**	5.74ns	50.86*	3142.20*	143684.47**	11.24*	1127.345*	36.84ns
Site × male	5	1280.28ns	9.86 ns	56.45ns	2491.81ns	44563.826*	27.60**	169.37*	11.82ns
Season × male	5	899.84*	11.59ns	61.58ns	3141.75ns	87594.60*	41.17**	1239.76*	48.27*
Season × site × male	5	836.35ns	14.60*	82.03*	2271.54*	41205.20ns	34.73**	585.28*	9.86*
Site × female × male	44	1035.75ns	10.57*	55.92*	4441.56*	57943.27ns	5.68ns	757.46*	27.58ns
Season × female × male	44	1119.25*	7.23ns	55.18ns	3870.99ns	61417.44*	4.06ns	913.577*	23.73ns
Season × site × female × male	44	1596.45**	8.40ns	55.09*	3819.39ns	63255.42*	4.67ns	700.43*	22.45ns
Error	233	819.66	6.94	52.97	3847.65	45821.23	5.55	744.35	24.1
Total mean square		45777.82	862.79	383.11	103493.34	1701207.90	584.27	26081.15	357.04
R-square		0.71	0.67	0.65	0.63	0.69	0.77	0.72	0.66
%CV		17.96	18.1	19.41	20.76	14.52	16.75	27.72	29.62

Note. LSD testing at $\alpha = 0.05$; ** = significant with $p \leq 0.001$, * = significant with $p \leq 0.05$, ns = non-significant.

PLH = plant height (cm), TOT = total number of tillers, PRT = number of productive tillers, PRO = %productive tillers, 1000 GWT = thousand grain weight (g), BY = biological yield (Kg plant⁻¹), HI = %harvest index, LAR = leaf area (cm²).

3.2 General Combining Ability Effects for the Parents

The estimates of general combining ability (GCA) effects for the male parents are shown in Table 3. The male parent ITMV8001 had the highest positive combining ability effects for grain yield. The same male parent had positive general combining ability estimate for days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, plant height, total number of tillers and harvest index; but showed negative GCA effects for days to 50% flowering, number of productive tillers, percentage of productive tillers, panicle area, 1000-grain weight, biological yield and leaf area. ITMV8001 also had desirable negative GCA effects for area under disease progress curve (AUDPC) and rust severity at 50% physiological maturity. The male parents with poor GCA effects for most traits were ICMV3771 and Manganara. Okashana2 and SDMV94001 were poor combiners for AUDPC and plant height, days to 50% flowering, days to 50% anthesis, flower-anthesis interval, percentage of productive tillers and leaf area. Shibe was respectively a good combiner for grain yield, panicle area, percentage of productive tillers, plant height, harvest index, number of productive tillers, days to 50% physiological maturity and days to 50% anthesis and the best general combiner for AUDPC. Three male parents (ITMV8001, SDMV94001 and Shibe) were good combiners for grain yield and only ICMV3771 and SDMV94001 combined well for 1000-grain weight. One male parent (SDMV94001) combined well for biological yield and only one parent (ICMV3771) had a positive and relatively high general combining ability effect for leaf area. In addition, most male parents had positive GCA effects for harvest index.

The results for GCA effects for the female parents are shown in Table 4. All the female parents had desirable positive GCA effects for days to 50% flowering, days to 50% anthesis, number of productive tillers and 1000-grain weight biological yield and majority had desirable negative GCA effects for AUDPC and rust severity at 50% physiological maturity. However, many female parents also expressed undesirable negative GCA effects for grain yield, flower-anthesis interval, days to 50% physiological maturity, plant height, total number of productive tillers, percentage of productive tillers, panicle area, harvest index and leaf area. The highest GCA effect was registered in SDMV96053 for grain yield followed by Sosank for panicle area.

Table 3. Estimates of general combining ability for male parents

Male parents	Traits							
	GY	AUDPC	RUST	FLO ₅₀	ANT ₅₀	FAI	PSM ₅₀	PLH
ICMV3771	-142.38	2.33	9.95	1.27	-0.65	-0.09	-0.58	-0.37
Manganara	-143.79	7.79	-7.15	0.52	-1.19	-0.02	-2.27	-7.15
Okashana2	-75.12	53.87	-11.02	-1.69	-0.26	-0.02	-0.9	5.18
ITMV8001	248.32	-21.92	-9.31	-0.15	2.33	0.37	2.77	0.93
SDMV94001	19.17	13.42	8.16	-2.17	-0.32	-0.10	0.74	0.04
Shibe	93.79	-55.48	9.40	-0.77	0.09	-0.12	0.22	1.40
	TOT	PRT	PRO	PAR	1000GWT	BY	HI	LAR
ICMV3771	0.18	0.71	6.85	-39.42	0.28	-0.07	0.39	63.68
Manganara	-0.01	-0.69	-4.93	55.11	-0.18	-0.40	-2.99	-31.06
Okashana2	-0.56	-1.01	-3.63	27.92	-0.06	-0.39	-3.04	-5.16
ITMV8001	0.52	-0.04	-4.11	-21.71	-0.03	-0.40	0.05	-2.31
SDMV94001	0.17	0.80	-2.82	-45.51	0.17	1.30	4.16	-15.30
Shibe	-0.3	0.23	8.65	23.59	-0.16	-0.07	1.42	-9.86

Note. GY = grain yield (kg plant⁻¹), AUDPC = Area under disease progress curve, RUST = rust severity at 50% physiological maturity, FLO₅₀ = days to 50% flowering, ANT₅₀ = days to 50% anthesis, FAI = flower-anthesis interval (days), PSM₅₀ = days to 50% physiological maturity, PLH = plant height (cm), TOT = total number of tillers, PRT = number of productive tillers, PRO = % productive tillers, PAR=panicle area (cm²), 1000GWT = thousand grain weight (g), BY = biological yield (kg plant⁻¹), HI = % harvest index, LAR = leaf area (cm²).

Table 4. Estimates of general combining ability for female parents

Female parents	Traits							
	GY	AUDPC	RUST	FLO ₅₀	ANT ₅₀	FAI	PSM ₅₀	PLH
Exbornu	-113.93	2.68	-9.57	1.42	1.80	0.42	1.14	4.11
CIVT9206	28.33	30.03	15.19	0.67	0.69	-0.04	2.49	4.12
GGB8735	31.50	-30.61	19.63	-1.54	-1.66	-0.18	-0.31	-13.04
ICMV221	-94.73	25.08	-8.46	0.01	0.01	-0.06	-0.65	-2.63
ICMV221white	-24.43	32.72	-7.84	-2.02	-1.93	0.03	-3.80	-1.61
KatPM1	-54.45	-8.85	-7.04	-0.62	-1.01	-0.45	-1.44	-2.68
Okoa	-32.70	-3.57	-6.89	0.15	0.63	0.34	-0.19	5.27
SDMV96053	380.89	-20.13	-6.76	-0.65	-1.29	-0.08	-1.40	2.82
Sosank	44.28	-19.43	-9.99	1.35	1.40	-0.01	0.84	-4.60
Okollo	-164.77	-7.88	21.79	1.26	1.35	0.04	3.27	8.29
	TOT	PRT	PRO	PAR	1000GWT	BY	HI	LAR
Exbornu	-0.65	-1.10	-1.48	-25.15	0.29	0.38	-4.41	-10.74
CIVT9206	-0.17	0.81	-8.02	31.61	-0.86	1.28	4.04	15.02
GGB8735	0.01	1.55	17.78	-92.60	-0.26	2.83	4.31	-51.24
ICMV221	-0.47	-0.93	-2.45	33.65	0.06	0.37	-2.93	59.00
ICMV221white	0.40	0.03	-1.25	-76.15	0.35	0.47	-1.27	-28.01
KatPM1	-0.46	-0.94	-4.99	51.20	0.31	0.34	-0.11	-15.98
Okoa	0.67	0.33	-1.16	5.39	0.60	0.41	-2.51	12.20
SDMV96053	1.04	0.43	-2.89	-46.79	-0.31	0.37	-2.29	-13.03
Sosank	-0.22	-0.92	-8.42	176.65	0.04	0.35	-0.75	-19.46
Okollo	-0.16	0.74	12.93	-57.85	-0.18	1.04	5.91	52.24

Note. GY = grain yield (kg plant⁻¹), AUDPC = Area under disease progress curve, RUST = rust severity at 50% physiological maturity, FLO₅₀ = days to 50% flowering, ANT₅₀ = days to 50% anthesis, FAI = flower-anthesis interval (days), PSM₅₀ = days to 50% physiological maturity, PLH = plant height (cm), TOT = total number of tillers, PRT = number of productive tillers, PRO = % productive tillers, PAR=panicle area (cm²), 1000GWT = thousand grain weight (g), BY = biological yield (kg plant⁻¹), HI = % harvest index, LAR = leaf area (cm²).

3.3 Specific Combining Ability Effects for Fifteen Best Selected Crosses

Results for the specific combining ability (SCA) for grain yield, rust and other selected traits are shown in Table 5. The selected best fifteen crosses, all had desirable positive SCA effects for grain yield, days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, total number of tillers, plant height, number of productive tillers, percentage of productive tillers, panicle area, 1000-grain weight, harvest index and leaf area. The genotype 4 × 14 (ITMV8001 × SDMV96053) showed the highest SCA effect for grain yield while genotypes 1 × 9 (ICMV3771 × GGB8735) and 5 × 16 (SDMV94001 Okollo) exhibited the highest desirable negative SCA effects for AUDPC and rust severity at 50% physiological maturity, respectively. In addition, desirable negative SCA effects were observed for AUDPC and severity at 50% physiological maturity for the other crosses.

Table 5. Estimates of specific combining ability effects for the best fifteen crosses

Crosses and traits							
Cross	GY	Cross	AUDPC	Cross	RUST	Cross	FLO ₅₀
4×14	1941.46	1×9	-149.45	5×16	-38.36	5×7	3.98
3×11	559.10	5×13	-123.61	6×9	-38.35	3×14	2.70
6×10	553.43	6×16	-104.49	5×9	-37.23	3×9	2.59
3×12	432.67	5×11	-101.13	1×16	-36.05	1×12	2.56
5×12	403.79	6×8	-88.40	6×8	-33.40	1×14	2.33
2×16	346.91	4×12	-70.44	1×8	-33.36	3×16	2.30
2×15	315.04	1×13	-64.32	4×16	-23.00	6×8	1.74
6×8	311.04	5×15	-59.78	2×9	-22.75	6×9	1.69
4×16	307.25	4×10	-59.77	4×9	-21.15	2×15	1.69
6×9	292.30	3×10	-54.12	2×16	-20.39	4×10	1.35
5×13	269.98	1×12	-51.11	3×9	-20.24	3×11	1.32
6×7	215.86	6×10	-49.61	4×8	-19.17	1×16	1.20
5×15	212.96	3×7	-46.7	3×16	-16.72	1×13	1.16
3×16	209.15	2×9	-46.62	2×8	-14.85	2×7	1.13
2×11	185.33	2×7	-46.58	3×8	-14.72	6×11	1.05
Cross	ANT ₅₀	Cross	FAI	Cross	PSM ₅₀	Cross	PLH
5×7	4.36	6×13	1.00	5×8	5.03	3×11	24.90
3×14	3.39	5×12	0.77	1×9	4.23	1×12	24.80
1×12	3.00	4×10	0.65	1×12	4.16	6×8	23.17
3×9	2.64	6×11	0.56	2×13	4.10	5×9	21.12
1×14	2.53	2×10	0.54	3×14	3.94	1×13	16.35
2×15	2.13	3×10	0.54	1×14	3.50	4×16	14.77
3×16	2.12	1×12	0.51	6×16	3.25	6×15	11.79
4×10	2.00	4×13	0.51	5×7	3.01	5×14	11.34
6×8	1.93	2×15	0.49	4×7	2.48	5×7	11.2
1×16	1.60	5×13	0.48	3×9	2.10	2×8	10.82
6×11	1.43	1×16	0.46	2×15	1.82	1×15	10.51
6×9	1.29	1×7	0.38	6×11	1.72	4×10	9.73
4×13	1.25	1×9	0.36	4×12	1.56	3×16	9.60
5×13	1.15	1×8	0.34	2×7	1.40	6×9	9.40
5×11	0.97	3×14	0.31	5×10	1.30	1×7	9.40

Table 5. Continued

Crosses and traits							
Cross	TOT	Cross	PRT	Cross	PRO	Cross	PAR
1×7	2.27	1×9	10.85	1×9	99.83	3×15	289.61
5×13	2.25	5×8	9.66	6×16	84.53	4×12	284.24
4×14	2.09	6×16	6.69	5×8	17.67	1×16	223.48
5×9	2.08	4×14	3.10	5×12	12.63	2×8	221.54
4×11	1.56	4×11	2.06	3×15	10.73	5×12	193.44
2×10	1.47	2×10	1.36	2×11	10.32	6×10	184.57
1×15	1.13	2×7	1.30	4×10	10.03	1×11	179.68
4×13	1.11	4×13	1.25	4×14	9.70	3×10	161.71
1×9	1.05	3×12	1.01	5×15	8.78	3×14	127.25
6×10	0.89	5×13	0.91	4×7	8.44	5×7	123.43
3×11	0.86	3×11	0.9	3×12	7.88	2×9	121.08
2×7	0.83	3×15	0.77	2×14	7.77	1×13	117.6
6×12	0.82	2×15	0.76	4×11	7.46	6×15	114.74
2×16	0.60	4×10	0.73	2×8	7.24	6×8	92.24
6×7	0.58	1×15	0.69	2×13	6.98	4×13	88.42
Cross	1000GWT	Cross	BY	Cross	HI	Cross	LAR
5×9	1.83	5×9	7.98	5×8	39.00	1×10	369.91
1×8	1.83	5×8	2.83	6×16	37.14	5×9	103.25
4×16	1.47	6×16	2.81	1×9	27.41	5×13	96.22
3×15	1.25	3×14	0.58	2×11	7.28	3×11	74.56
1×16	1.01	1×9	0.58	3×10	6.64	4×14	70.92
2×13	0.96	4×11	0.56	4×7	4.96	1×12	65.47
6×14	0.79	2×7	0.51	4×10	4.14	2×7	65.03
3×7	0.76	2×10	0.50	1×15	3.86	3×15	57.72
4×13	0.73	3×11	0.46	3×13	3.70	3×7	55.52
1×12	0.72	4×15	0.44	2×14	3.69	5×14	40.79
1×7	0.65	2×15	0.43	4×15	3.21	4×12	40.26
3×11	0.61	3×7	0.41	5×14	2.59	2×8	39.15
5×14	0.59	4×14	0.39	2×13	2.50	6×16	34.25
2×11	0.57	3×15	0.38	4×12	2.13	4×11	34.18
5×12	0.50	2×11	0.38	1×12	2.07	5×11	32.22

Note. 1-6 = male parents; 7-16 = female parents; 1 = ICMV3771, 2 = Manganara, 3 = Okashana2, 4 = ITMV8001, 5 = SDMV94001, 6 = Shibe, 7 = Exbornu, 8 = CIVT9206, 9 = GGB8735, 10 = ICMV221, 11 = ICMV221white, 12 = KatPM1, 13 = Okoa, 14 = SDMV96053, 15 = Sosank, 16 = Okollo.

3.4 Gene Action and Heritability

The types of gene action, narrow sense heritability and broad sense for grain yield and other selected traits under the influence of rust are presented in Table 6. Figure 1 shows the percentage contribution of each type of gene action to total genetic variation. For grain yield, additive gene action due to female parents ($\sigma^2_{\text{female}(A)}$) accounted for 32% of the total variation as well as additive gene action due to the male parents ($\sigma^2_{\text{male}(A)}$) (32%), the non-additive gene action ($\sigma^2_{\text{female}\times\text{male}(D)}$) accounted for 36%. The sum of additive gene action for male and female parents was 64%. For rust severity at 50% physiological maturity the order existed $\text{SCA} > \text{GCA}_{\text{male}} > \text{GCA}_{\text{female}}$. The graphical presentation in Figure 1 further shows the strength of gene action contribution of GCA and SCA in following order $\text{GCA}_{\text{female}(A)} > \text{GCA}_{\text{male}(A)} > \text{SCA}_{\text{female}\times\text{male}(D)}$ for days to 50% flowering, days to 50% anthesis, plant height and number of productive tillers. However, non-additive gene action ($\text{SCA}_{\text{female}\times\text{male}(D)}$) was predominant over the additive gene actions ($\text{GCA}_{\text{female}(A)}$ and $\text{GCA}_{\text{male}(A)}$) for grain yield, AUDPC, rust severity at 50% physiological maturity, panicle area, harvest index and leaf area. Additive gene action due to female parent was predominant for 1000-grain weight and leaf area while additive gene action due to male parents was predominant for flower-anthesis interval, days to 50% physiological maturity and biological yield. The expression

of total number of productive tillers was controlled mainly by additive gene action due to the female parent and dominance, with minimal effect of the male parents. Narrow sense heritability was much lower than the broad sense heritability for most traits (Table 6). Traits with narrow sense heritability of less than 10% were AUDPC, total number of productive tillers and biological yield while rust severity at 50% physiological maturity, flower-anthesis interval and harvest index had narrow sense heritability of less than 20%. The majority of the traits had narrow sense heritability higher than 20% and these included grain yield, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, plant height, number of productive tillers, percentage of productive tillers, panicle area, 1000-grain weight, harvest index and leaf area.

Table 6. Components of gene action and heritability for the selected traits

Traits	Variance components			h ² (%)	H ² (%)
	$\sigma^2_{\text{male(A)}}$	$\sigma^2_{\text{female(A)}}$	$\sigma^2_{\text{female}\times\text{male(D)}}$		
GY	40859.40*	42196.80*	45911.80*	22.33	47.02
RUST	1.68**	0.71ns	1.76*	11.26	27.82
AUDPC	91.08*	482.79ns	718.08**	3.02	10.56
FLO50	1.11**	1.87**	0.29n*	34.43	41.05
ANT50	1.21**	1.87**	0.08ns	31.27	32.84
FAI	0.13*	0.07*	0.09*	16.13	29.54
PSM50	3.53**	2.62**	0.81*	38.51	48.64
PLH	152.70*	186.76*	88.75*	37.42	56.98
PRT	0.28ns	0.48*	0.09*	30.96	38.19
TOT	0.01ns	0.13*	0.13*	4.74	14.34
PRO	25.08ns	29.87*	45.54*	23.9	63.52
PAR	65408.00ns	78742.00*	87434.50ns	32.16	71.17
1000GWT	1.37ns	1.77ns	1.76*	26.61	56.47
BY	0.05ns	0.02*	0.04*	7.2	33.64
HI	4.71*	6.87ns	8.25ns	19.29	46.79
LAR	4200.50*	5297.10*	4965.20ns	35.18	71.96

Note. GY = grain yield (kg plant⁻¹), AUDPC = Area under disease progress curve, RUST = rust severity at 50% physiological maturity, FLO₅₀ = days to 50% flowering, ANT₅₀ = days to 50% anthesis, FAI = flower-anthesis interval (days), PSM₅₀ = days to 50% physiological maturity, PLH = plant height (cm), TOT = total number of tiller, PRT = number of productive tillers, PRO = %productive tillers, PAR = panicle area (cm²), 1000GWT = thousand grain weight (g), BY = biological yield (kg plant⁻¹), HI = %harvest index, LAR = leaf area (cm²).

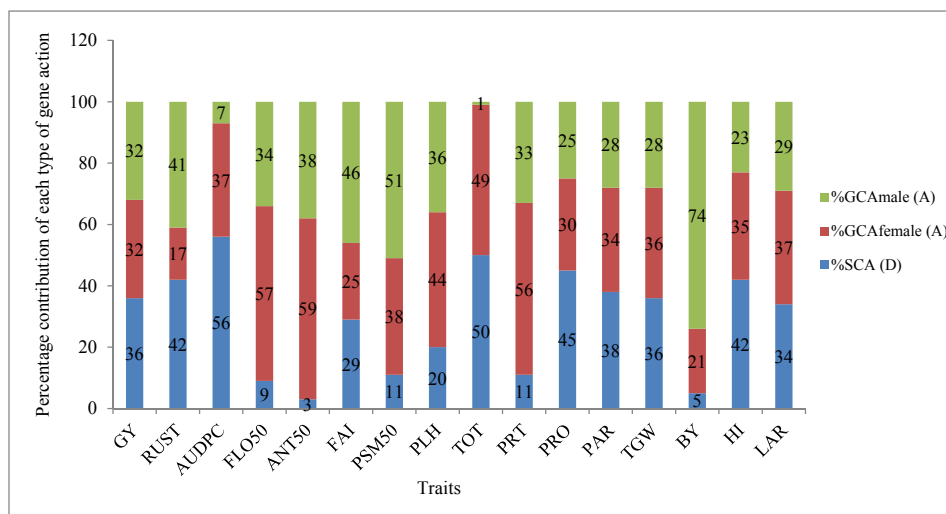


Figure 1. Percentage contribution of type of gene action for each trait

3.5 Better-Parent Heterosis

Trait-specific results for fifteen genotypes showing superior performance relative to the better performing parents are shown in Table 7. The cross 4 × 14 (ITMV8001 × SDMV96053) exhibited very high better parent heterosis (92.72%) for grain yield relative to other crosses which also had positive better parent heterosis. Crosses 3 × 11 (Okashana2 × ICMV221 white) and 6 × 10 (Shibe × ICMV221) also performed better than their better parents increasing grain yield by more than 22%. The other crosses had levels of better-parent heterosis of less than 20%; with crosses 5 × 8 (SDMV94001 × CIVT9206) and 6 × 7 (Shibe × Exbornu) showing the lowest heterosis of less than 5% for grain yield. Desirable negative better parent heterosis was observed for rust severity at 50% physiological maturity and AUDPC. In addition, relatively high heterosis was registered for rust severity at 50% physiological maturity (48-59%) when compared with AUDPC (10-29%). All the fifteen selected crosses performed much better than their better parents for rust resistance. Generally, crosses involving male parents 4 (ITMV8001), 5 (SDMV94001) and 6 (Shibe) dominated the list of better performers for most traits. In addition, relatively low better parent heterosis (< 7%) was observed for days to 50% flowering, days to 50% anthesis and days to 50% physiological maturity for most of the crosses. The results in Table 7 show that low levels of heterosis were registered for AUDPC while relatively high better-parent heterosis for rust was observed in all the fifteen crosses selected. Results for mid-parent heterosis showed the same pattern.

Table 7. Better-parent heterosis for the best fifteen crosses per trait

Crosses and traits							
Cross	GY	Cross	AUDPC	Cross	RUST	Cross	FLO50
4×14	92.72	1×9	-28.79	3×9	-59.21	5×7	6.85
3×11	25.09	6×16	-25.87	4×16	-59.20	3×14	3.83
6×10	22.19	6×8	-22.12	4×8	-58.88	4×15	3.54
3×12	18.83	5×13	-20.06	4×9	-57.70	1×12	3.42
5×12	17.71	6×10	-16.28	2×9	-56.64	6×8	3.27
6×8	16.37	4×12	-15.10	5×16	-55.4	3×16	3.11
6×9	15.62	5×11	-13.43	5×9	-55.06	1×14	2.95
5×13	12.03	4×10	-12.65	6×9	-54.83	4×7	2.70
5×15	11.34	5×15	-12.5	3×8	-53.22	4×8	2.70
2×16	9.99	2×9	-12.41	3×16	-50.96	4×10	2.28
2×15	8.30	6×11	-11.81	2×16	-50.61	4×13	1.64
5×9	6.83	1×13	-10.74	1×15	-49.89	6×10	1.60
4×16	6.47	2×14	-10.69	6×8	-49.63	5×10	1.57
6×7	4.80	6×7	-10.66	1×8	-48.41	3×9	1.54
5×8	4.71	1×12	-9.47	1×16	-48.02	4×16	1.01
Cross	ANT50	Cross	FAI	Cross	PSM50	Cross	PLH
5×7	6.29	6×13	15.91	5×8	6.37	6×8	15.03
3×14	3.38	4×13	15.38	5×7	4.20	3×11	14.16
4×15	3.30	4×10	10.86	4×16	4.19	1×12	13.97
1×12	3.29	4×14	10.62	1×9	4.15	1×13	9.70
6×8	3.20	3×10	9.49	4×7	3.99	4×16	9.34
4×10	3.11	2×10	9.45	6×16	3.75	3×16	8.79
3×16	2.95	2×15	9.25	1×12	3.14	5×14	7.00
4×13	2.92	6×11	8.43	3×14	2.91	5×7	6.87
4×8	2.53	1×16	7.32	1×14	2.43	3×14	6.68
4×7	2.14	5×13	6.82	2×13	2.09	1×7	5.52
1×14	2.07	5×12	6.17	4×15	2.06	5×9	5.07
3×9	1.57	3×14	5.70	3×9	1.36	3×7	4.92
1×16	1.52	4×7	5.22	4×8	1.10	6×15	4.53
2×15	1.48	3×7	5.22	6×8	0.99	4×10	4.43
5×13	1.32	1×7	5.22	5×9	0.73	6×10	4.02

Table 7. Continued

Crosses and traits							
Cross	TOT	Cross	PRT	Cross	PRO	Cross	PAR
1×7	37.08	6×16	95.84	6×16	92.59	3×15	43.10
4×14	31.42	4×14	44.53	5×8	11.45	4×12	42.27
5×9	31.00	4×11	31.31	1×9	10.72	2×8	40.37
5×13	30.59	4×13	17.94	5×12	9.07	6×10	34.50
4×11	27.14	5×13	17.05	4×10	7.00	1×16	31.76
2×10	21.54	1×9	14.80	4×14	6.71	3×10	31.43
4×13	20.51	5×8	14.44	2×11	6.28	5×12	23.84
1×9	16.97	2×10	7.63	4×7	5.06	1×11	20.02
2×7	12.35	1×13	3.92	4×11	3.90	6×8	19.29
1×15	12.27	2×7	3.68	5×7	3.80	6×15	19.02
4×12	9.77	6×14	1.20	3×12	3.46	2×7	17.71
6×10	8.67	3×12	-0.08	2×14	3.44	5×7	14.34
6×12	7.58	6×11	-0.90	3×15	2.76	1×13	13.63
4×8	7.20	3×11	-1.66	5×14	2.45	3×14	13.50
2×16	6.18	2×14	-2.23	2×13	2.39	4×13	11.64
Cross	1000GWT	Cross	BY	Cross	HI	Cross	LAR
5×9	12.48	3×14	41.78	6×16	98.93	1×10	89.16
4×16	10.44	4×11	33.04	1×9	75.06	4×14	13.90
3×15	9.45	5×9	32.50	2×11	13.65	5×9	12.89
1×12	7.88	6×16	26.35	3×10	12.08	3×11	11.26
1×8	7.71	2×7	23.87	5×8	11.68	1×16	10.97
1×7	7.34	2×10	19.45	1×15	9.29	3×7	10.82
1×16	6.63	1×9	17.82	4×15	7.50	1×12	10.41
2×13	6.00	3×11	15.55	4×12	6.18	3×15	9.25
3×7	5.51	5×8	15.27	1×12	5.81	4×12	5.83
4×13	5.40	3×7	1.32	4×10	3.70	6×7	3.15
5×12	5.25	4×15	-0.90	2×14	2.36	6×14	2.09
3×11	4.34	2×15	-3.94	3×13	2.17	4×11	1.48
6×14	3.89	2×11	-4.06	4×7	1.70	5×11	1.05
5×10	3.82	2×13	-7.99	4×9	0.94	5×13	0.19
2×11	3.08	4×14	-8.25	5×14	0.80	2×7	0.08

Note. 1-6 = male parents; 7-16 = female parents; 1 = ICMV3771, 2 = Manganara, 3 = Okashana2, 4 = ITMV8001, 5 = SDMV94001, 6 = Shibe, 7 = Exbornu, 8 = CIVT9206, 9 = GGB8735, 10 = ICMV221, 11 = ICMV221white, 12 = KatPM1, 13 = Okoa, 14 = SDMV96053, 15 = Sosank, 16 = Okollo.

4. Discussion

4.1 General Performance of the Parents and Crosses

The pooled analysis of variance results indicated a highly variable environment in which the genotypes were tested. The significantly different effects of genotypes and environment interactions indicated a high level of environmental variation for expression of heterosis. This implies that stability analysis was important in order to identify which environments were suitable for particular crosses. Similar effects of strong environmental influence were also reported by Bidinger et al. (2003) and Sharma and Shrikant (2006) when testing materials for heterosis. More importantly, they indicated why selection for improved grain yield in marginal environments has been primarily based on selection for a higher harvest index rather than increased productivity. However, differences were observed in the per se performance of all the genotypes tested. This variation expresses the effect of heterosis. Similar effects of crosses outperforming the parents have been reported in many studies. Penthani et al. (2004) and Chavan and Nerkar (1994) reported crosses performing better than parents while

Yadav et al. (2000) reported the same observation for top cross hybrids. F1 hybrids being more resistant to rust than the parents have also been reported by Lakshmana et al. (2010). The hybrids performing better than the parents has also been reported for 1000-grain weight, plant height and days to 50% flowering (Ouendeba et al., 1993). The 1000-grain weight (Kelly et al., 1996; Van Oosterom et al., 1996), harvest index (Bidinger et al., 2003) and flower-anthesis interval (Miralles et al., 1998; Saini & Westgate, 2000; Bidinger & Raju, 2000a) are some of the most important traits determining grain yield; thus selection for the traits may increase grain yield. In this study all the parents and hybrids had relatively high harvest index (HI > 28%) (Yagya & Bainiwal, 2001; Van Oosterom et al., 2006) and hence this set of materials could be advanced to breed for high harvest index, a trait also largely associated with resistance to drought.

4.2 Combining Ability Effects and Gene Action

The analysis of variance showed significant differences in combining ability of the parents and crosses under the influence of rust. Variation was observed for both male and female parents for grain yield, days to 50% flowering, flower-anthesis interval, days to 50% physiological maturity and plant height. The results indicated that the parents used for genetic analysis were diverse; as also reported by Naik et al. (1996) when they studied the combining ability for grain yield and its components. The GCA was higher than SCA for grain yield, rust severity at 50% physiological maturity, plant height, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, total number of tillers, percentage of productive tillers, panicle area, leaf area, 1000-grain weight, harvest index, and biological yield. These traits can be improved through simple selection schemes such as pedigree or recurrent selection because it is easy to predict short-term response to selection (Vengadessan, 2008). The AUDPC had SCA higher than general combining ability, and thus improvement can be achieved through breeding for hybrids. Similar observations were reported for some traits. Bhadalia et al. (2012) reported additive gene action for grain yield, plant height and harvest index while Izge et al. (2007) reported additive gene action for 1000-grain weight. Contrasting results have been reported for panicle dimension (Singh & Sagar, 2001) and 1000-grain weight (Gotmare & Govila, 1999; Sheoran et al., 2000; Pethani et al., 2004; Bhadalia et al., 2012). Pannu et al. (1996) reported predominance of non-additive gene action for 1000-grain weight.

In addition, based on Hallauer and Miranda (1988) classification of heritability, relatively high broad sense heritability estimates were observed for most traits including grain yield. Similar reports were also made by Borkhataria et al. (2005) and Solanki et al. (2002) though Sachan and Singh (2001) indicated the contrary for 1000-grain weight. It implies that the non-additive and environmental effects may be important in the expression of the traits (Vengadessan, 2008). However, as also reported in this study, Pethani et al. (2004) reported additive gene action for days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, plant height and number of productive tillers; though contrary to Bhadalia et al. (2012) findings. Bhadalia et al. (2012) reported preponderance of non-additive gene action for days to 50% flowering and days to 50% physiological maturity. In addition, there was high narrow sense heritability for the traits, as also noted by Bhoite et al. (2008). This may indicate simple inheritance of the traits as reported by Azhaguvel et al. (2003). Thus the traits may be improved through schemes like recurrent selection or pedigree selection. Likewise inbred lines with improved levels of the traits may be developed as suggested by Vengadessan (2008).

4.3 Heterosis

Results showed that the magnitude of heterosis was cross-dependent for all the traits considered. Most of the best crosses had better-parent heterosis of 11% to 25%, though few were within the range (20 to 30%) at which a hybrid is considered to be good (Axtell et al., 1999). The high positive heterosis for grain yield in cross ITMV8001 × SDMV96053 may be due to the high positive heterosis expressed for days to 50% flowering, total number of tillers, number of productive tillers and leaf area. Yadav et al. (2000) first reported high heterosis of 88% though in later studies Yadav (2006) reported lower levels of 42% while Davda et al. (2012) reported 41% standard heterosis and presence of heterobeltiosis. In addition, Karthigeyan (1994) reported 49% heterosis for grain yield, while Ouendeba et al. (1993) reported 36-81% for better-parent heterosis. On the contrary, Bidinger et al. (2003) reported negative heterosis for grain yield. Heterosis was exploited by Wilson et al. (2001) to produce hybrids with increased levels of resistance to pearl millet rust. Results in the current study showed high levels of heterosis for rust at 50% physiological maturity (-48% to -59%); reflecting the importance of non-additive gene action also as suggested by Pannu et al. (1996). However, lower levels were recorded for better-parent heterosis (-10% to -29%) for AUDPC. Lower AUDPC has also been reported in other studies (Lal Ahamed et al., 2004.); indicating that selecting for AUDPC may not be reliable for increasing resistance to rust relative to selecting for rust severity at 50% physiological maturity. Relatively high better-parent heterosis were achieved for panicle area, total number of tillers as also reported by Pethani et al. (2004), percentage of productive tillers, number of productive tillers as reported by Karthigeyan (1994), biological yield, harvest index as also

reported by Bidinger et al. (2003). A high harvest index in hybrid seed parents is desirable because it is a measure of grain filling and fodder production strength of the seed parent (Bidinger et al., 2003).

5. Conclusion

The significantly important interactions of the genotypes with the environment showed the relevance to characterise the test materials across environments. The male parents ITMV8001, SDMV94001 and Shibe and female parents SDMV96053, Sosank, CIVT9206 and GGB8735 had high and positive GCA effects for grain yield. These parents could be used in breeding schemes like recurrent selection that target population improvement. The male parents Manganara and Okashana2 and female parents Exbornu, ICMV221 and ICMV221white were the best general combiners for rust and could be used to breed for rust resistance. The hybrids ITMV8001 × SDMV96053, Okashana2 × ICMV221white, Shibe × ICMV221, Okashana2 × KatPM1 and SDMV94001 × KatPM1 were the best genotypes for grain yield while ICMV3771 × GGB8735, SDMV94001 × Okoa, Shibe × Okollo, SDMV94001 × ICMV221white and Shibe × CIVT9206 were the best specific combiners for rust resistance. The preponderance of additive gene action for days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, number of productive tillers and plant height means these traits could be improved through schemes like recurrent selection. Traits including grain yield, 1000-grain weight, panicle area and leaf area had preponderance to both additive and non-additive gene action and could thus be improved through schemes like recurrent selection and hybrid breeding. In contrast, traits like rust severity at 50% physiological maturity, AUDPC, biological yield, total number of tillers and percentage of productive tillers had preponderance to non-additive gene action, relatively low narrow sense heritability and low genetic coefficient of variation. Thus these traits could be improved through hybrid breeding. Hybrids ITMV8001 × SDMV96053, ITMV8001 × SDMV96053, Okashana2 × ICMV221white, Shibe × ICMV221, Okashana2 × KatPM1 and SDMV94001 × KatPM1 that expressed high better-parent for grain yield could be promoted for high grain yield. Hybrids Shibe × GGB8735, SDMV94001 × GGB8735, ICMV3771 × Okollo, ITMV8001 × GGB8735, Manganara × GGB8735, Okashana2 × GGB8735, ITMV8001 × Okollo, ITMV8001 × CIVT9206, ICMV3771 × CIVT9206, Shibe × CIVT9206 and SDMV94001 × Okollo could be developed as rust resistant hybrids.

References

- Angarawai, I. I., Kadams, A. M., & Bello, D. (2008). Gene effects controlling heritability of downy mildew resistance in Nigerian elite pearl millet lines. *World Journal of Agricultural Sciences*, 4(5), 545-549.
- Ali, G. M., Murtaza, N., Collins, J. C., & McNeilly, T. (2006). Study of salt tolerance parameters in pearl millet *Pennisetum americanum* L. *Journal of Central European Agriculture*, 7(2), 365-376.
- Arulselvi, S., Mohanasundaram, K., & Selvi, B. (2009). Genetic analysis of grain quality characters and grain yield in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. *Crop Research (Hisar)*, 37(1/3), 161-167.
- Arunachalam, V. (1974). The facility behind the use of modified line × tester design. *Indian Journal of Genetics and Plant Breeding*, 34, 280-287.
- Axtell, J., Kapran, I., Ibrahim, Y., Ejeta, G., & Andrews, D. J. (1999). Heterosis in sorghum and pearl Millet. In J. G. Coors & S. Pandey (Eds.), *The Genetics and Exploitation of Heterosis in Crops* (pp. 375-386). American Society of Agronomy, Crop Science Society of America Inc., 5585 Guilford Rd., Madison, WI 53711, USA. <http://dx.doi.org/10.2134/1999.geneticsandexploitation.c35>
- Azhaguvel, P., Hash, C. T., Rangasamy, P., & Sharma, A. (2003). Mapping the d1 and d2 dwarfing genes and the purple foliage color locus p in pearl millet. *Journal of Heredity*, 94(2), 155-159. <http://dx.doi.org/10.1093/jhered/esg025>
- Bänziger, M., & Cooper, M. (2001). Breeding for low input conditions and consequences for participatory plant breeding: Examples from tropical maize and wheat. *Euphytica*, 122, 503-519. <http://dx.doi.org/10.1023/A:1017510928038>
- Bhadalia, A. S., Dhedhi, K. K., & Joshi, H. J. (2012). Genetic analysis of grain yield and its attributes in pearl millet. *Agricultural Science Digest*, 32(2), 153-155.
- Bhadalia, A. S., Dhedhi, K. K., Joshi, H. J., & Sorathiya, J. S. (2014). Combining ability studies through diallel analysis in pearl millet [*Pennisetum glaucum* (L.) R.Br.]. *International Journal of Agricultural Sciences*, 10(1), 57-60.
- Bhatnagar, S. K., Yadav, O. P., & Gautam, R. C. (1998). Research achievements in pearl millet (*Pennisetum glaucum*). *Indian Journal of Agricultural Science*, 68, 423-430.

- Bhoite, K. D., Pardeshi, S. R., Mhaske, B. M., & Wagh, M. P. (2008). Study of genetic variability in pearl millet (*Pennisetum glaucum* L.). *Agricultural Science Digest*, 28(2), 115-117.
- Bidinger, F. R., & Raju, D. S. (2000a). Mechanisms of adjustment by different pearl millet plant types to varying plant populations. *Journal of Agricultural Science*, 134, 181-189. <http://dx.doi.org/10.1017/S0021859699007418>
- Bidinger, F. R., Yadav, O. P., Sharma, M. M., Van Oosterom, E. J., & Yadav, Y. P. (2003). Exploitation of heterosis for simultaneous improvement in both grain and stover yields of arid zone pearl millet [*Pennisetum glaucum* (L.) R. Br.]. *Field Crops Research*, 83(1), 13-26. [http://dx.doi.org/10.1016/S0378-4290\(03\)00006-6](http://dx.doi.org/10.1016/S0378-4290(03)00006-6)
- Borkhataria, P. R., Bhatiya, V. J., Pandya, H. M., & Valu, M. G. (2005). Variability and correlation studies in pearl millet. *National Journal of Plant Improvement*, 7(1), 21-23.
- Chaudhary, V. P., Dhedhi, K. K., Joshi, H. J., & Mehta, D. R. (2012). Combining ability studies in line × tester crosses of pearl millet [*Pennisetum glaucum* (L.) R. Br.]. *Research on Crops*, 13(3), 1094-1097.
- Chavan, A. A., & Nerkar, Y. S. (1994). Heterosis and combining ability studies for grain yield and its components in pearl millet. *Journal of Maharashtra Agricultural Universities*, 19(1), 58-61.
- Christinck, A. (2002). *This seed is like our-selves-a case study from Rajasthan on the social aspects of biodiversity and farmers' management of pearl millet seed* (p. 190). Margraf Verlag, Weikersheim, Germany.
- Davda, B. K., Dhedhi, K. K., & Dangaria, C. J. (2012). Evaluation of heterosis in pearl millet under rainfed conditions. *International Journal of Plant Sciences*, 7(1), 74-78.
- Dabholkar, A. R. (1999). *Elements of biometrical genetics*. Kalyani Publishers, New Delhi, India.
- Falconer, D. S. (1989). *Introduction to Quantitative Genetics*. Oliver and Boyd, London. UK.
- FAO. (2004). *Pennesitum americanum* (L.) Leeke: species description. Food and Agriculture Organization of the United Nations. Retrieved October, 2004, from <http://www.fao.org/ag/AGP/AGPC/doc/Gbase/DATA/Pf000297.htm>
- Girgi, M., Breese, W. A., Lörz, H., & Oldach, K. H. (2006). Rust and downy mildew resistance in pearl millet (*Pennisetum glaucum*) mediated by heterologous expression of the *afp* gene from *Aspergillus giganteus*. *Transgenic Research*, 15(3), 313-324. <http://dx.doi.org/10.1007/s11248-006-0001-8>
- Gotmare, V. L., & Govila, O. P. (1999). Gene effects for grain characters in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. *Indian Journal of Genetics and Plant Breeding*, 59(3), 301-308.
- Govindaraj, M., Rai, K. N., Shanmugasundaram, P., Dwivedi, S. L., Sahrawat, K. L., Muthaiah, A. R., & Rao, A. S. (2013). Combining ability and heterosis for grain iron and zinc densities in pearl millet. *Crop Science*, 53, 507-517. <http://dx.doi.org/10.2135/cropsci2012.08.0477>
- Hallauer, A. R., & Miranda Fo, J. B. (1988). *Quantitative genetics in maize breeding* (2nd ed.). Iowa State University Press, Ames, Iowa.
- IBPGR & ICRISAT. (1993). *Descriptors for pearl millet* [*Pennisetum glaucum* (L.) R. Br.]. International Board for Plant Genetic Resources, Rome, Italy; International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.
- Izge, A. U., Kadams, A. M., & Sajo, A. A. (2007). Agronomic performance of selected cultivars of pearl millet [*Pennisetum glaucum* (L.) R. Br.] and their hybrids in North-Eastern Nigeria. *Journal of Agronomy*, 6(2), 344-349. <http://dx.doi.org/10.3923/ja.2007.344.349>
- Karthigeyan, S. (1994). *Studies on heterosis and combining ability in sweet pearl millet* [*Pennisetum glaucum* (L.) R. Br.] (M.Sc. (Ag) Thesis, Tamil Nadu Agricultural University, Coimbatore, India).
- Kelley, J. D., Parathasarathy Rao, P., Weltzien, E. R., & Purohit, M. L. (1996). Adoption of improved cultivars of pearl millet in an arid environment: Straw yield and quality considerations in western Rajasthan. *Experimental Agriculture*, 32, 161-172. <http://dx.doi.org/10.1017/S0014479700026077>
- Khairwal, I. S., Rai, K. N., Diwakar, D., Sharma, Y. K., Rajpurohit, B. S., Nirwan, B., & Bhattacharjee, R. (2007). *Pearl millet: Crop management and seed production manual* (p. 104). International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.
- Kumhar, S. R. (2007). Combining ability and heterosis in early-maturing pearl millet [*Pennisetum glaucum* (L.) R. Br.] hybrids. *Crop Research (Hisar)*, 34(1/3), 47-52.

- Kurt, O., & Evans, G. M. (1998). Genetic basis of variation in linseed (*Linum usitatissimum* L.) cultivars. *Turkish Journal of Agriculture and Forestry*, 22, 373-379.
- Lal Ahamed, M., Singh, S. S., Sharma, J. B., & Ram, R. B. (2004). Evaluation of inheritance to leaf rust in wheat using area under disease progress curve. *Hereditas*, 141, 323-327. <http://dx.doi.org/10.1111/j.1601-5223.2004.01794.x>
- Lakshmana, D., Biradar, B. D., & Lingaraju, S. (2010). Studies on inheritance of resistance to rust in pearl millet. *Karnataka Journal of Agricultural Sciences*, 23(3), 485-486.
- Legesse, W., Pixley, K. V., & Botha, A. M. (2009). Combining ability and heterotic grouping of highland transition maize inbred lines. *Maydica*, 54, 1-9.
- Lubadde, G., Tongoona, P., Derera, J., & Sibiya, J. (2014). Major pearl millet diseases and their effects on on-farm grain yield in Uganda. *African Journal of Agricultural Research*, 9(39), 2911-2918. <http://dx.doi.org/10.5897/AJAR2013.7208>
- Miralles, D. J., Katz, S. D., Colloca, A., & Slafer, G. A. (1998). Floret development in near isogenic wheat lines differing in plant height. *Field Crops Research*, 59, 21-30. [http://dx.doi.org/10.1016/S0378-4290\(98\)00103-8](http://dx.doi.org/10.1016/S0378-4290(98)00103-8)
- Naik, V. R., Ravikumar, R. L., & Madhav Rao, T. (1999). Combining ability studies for grain yield and its components in pearl millet (*P. typhoides*). *Kanartaka Journal of Agricultural Sciences*, 9(4), 635-641.
- Ouendeba, B., Ejeta, G., Nyquist, W. E., Hanna, W. W., & Kumar, A. (1993). Heterosis and combining ability among pearl millet landraces. *Crop Science*, 33, 735-739. <http://dx.doi.org/10.2135/cropsci1993.0011183X003300040020x>
- Parmar, R. S., Vala, G. S., Gohil, V. N., & Dudhat, A. S. (2013). Studies on combining ability for development of new hybrids in pearl millet [*Pennisetum gaucum* (L.) R. BR.]. *International Journal of Plant Sciences (Muzaffarnagar)*, 8(2), 405-409.
- Pannu, P. P. S., Sokhi, S. S., & Aulakh, K. S. (1996). Resistance in pearl millet against rust. *Indian Phytopathology*, 49(3), 243-246.
- Pereira, A. V., Daher, R. F., Pereira, M. G., Ledo, F. J. da S., de Souza Sobrinho, F., do Amaral Junior, A. T., ... Ferreira, C. F. (2006). Analysis of diallel crosses between elephant grass *Pennisetum purpureum* Schum. and pearl millet *Pennisetum glaucum* L. R. Br. 1. Morphoagronomic characteristics. *Acta Scientiarum Agronomy*, 28(2), 267-275.
- Pethani, K. V., Atara, S. D., & Monpara, B. A. (2004). Heterosis and combining ability for plant and seed characters in pearl millet. *National Journal of Plant Improvement*, 6(2), 115-118.
- Rai, K. N., Gupta, S. K., Bhattacharjee, R., Kulkarni, V. N., Singh, A. K., & Rao, A. S. (2009). Morphological characteristics of ICRISAT-bred pearl millet hybrid seed parents. *Journal of SAT Agricultural Research*, 7, 1-7.
- Rai, K. N., Yadav, O. P., Rajpurohit, B. S., Patil, H. T., Govindaraj, M., Khairwal, I. S., ... Kulkarni, M. P. (2013). Breeding pearl millet cultivars for high iron density with zinc density as an associated trait. *Journal of SAT Agricultural Research*, 11, 1-7.
- Rasal, P. N., & Patil, H. S. (2003). Line \times tester analysis in pearl millet. *Agricultural Science Digest*, 23(3), 171-174.
- Sachan, C. P., & Singh, S. K. (2001). Genetic variability and association of character for quality traits in pearl millet (*Pennisetum typhoides* L.). *Progress in Agriculture*, 1(1), 79-81.
- SAS Institute. (2012). *User's guide: The SAS Statistics System for Windows Release Version 9.2*. SAS Institute, Inc. Cary, NC, USA.
- Saini, H. S., & Westgate, M. E. (2000). Reproductive development in grain crops during drought. *Advances in Agronomy*, 68, 59-96. [http://dx.doi.org/10.1016/S0065-2113\(08\)60843-3](http://dx.doi.org/10.1016/S0065-2113(08)60843-3)
- Satija, D. R., & Thukral, S. K. (1985). Genetic analysis of phytic acid content in pearl millet. *Theoretical and Applied Genetics*, 70(6), 693-696. <http://dx.doi.org/10.1007/BF00252299>
- Shanmuganathan, M., Gopalan, A., & Mohanraj, K. (2006). Genetic analysis of pearl millet for phytic acid content. *The Journal of Agricultural Sciences*, 2(2), 1-5. <http://dx.doi.org/10.4038/jas.v2i2.8126>

- Sharma, P. C., & Pareek, R. S. (1993). Variability of southwest monsoon in west Rajasthan during last two decades. *Mausam*, 44, 389-391.
- Sharma, L. D., & Shrikant, L. S. (2006). Heterosis for grain yield in pearl millet [*Pennisetum glaucum* (L.) R. Br. emend stuntz]. *SABRAO Journal of Breeding and Genetics*, 38(1), 47-52.
- Sheoran, R. K., Govila, O. P., Malik, J. S., & Singh, B. (2000). Estimates of gene effects for quantitative traits in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. *International Journal of Tropical Agriculture*, 18(2), 173-176.
- Singh, R. K., & Chaudhary, B. D. (1985). *Biometrical methods in quantitative genetics analysis*. Kalyani Publishers, New Delhi-Ludhiana, India.
- Singh, Y. P., Khairwal, I. S., & Singh, S. (1991). Genetic analysis for physiological traits in pearl millet. *Crop Improvement*, 18(2), 132-134.
- Singh, S. D., & King, S. B. (1991). Pearl millet rust: Present status and research needs. *International Journal of Tropical Plant Diseases*, 9, 35-52.
- Singh, R., & Sagar, P. (2001). Genetic analysis of grain yield and its components in pearl millet. *Madras Agricultural Journal*, 88(7/9), 512-514.
- Solanki, Y. P. S., Khairwal, I. S., & Bidinger, F. R. (2002). Genetic variability, heritability and genetic advance in three pearl millet composites. *Forage Research*, 28(3), 174-176.
- Tooley, P. W., & Grau, C. R. (1984). Field characterisation of rate reducing resistance to *Phytophthora megasperma* f.sp. *glycinea* in soybean. *Phytopathology*, 74, 1201-1208. <http://dx.doi.org/10.1094/Phyto-74-1201>
- Van Oosterom, E. J., Weltzien, R. E., Yadav, O. P., & Bidinger, F. R. (2006). Grain yield components of pearl millet under optimum conditions can be used to identify germplasm with adaptation to arid zones. *Field Crops Research*, 96, 407-421. <http://dx.doi.org/10.1016/j.fcr.2005.08.008>
- Van Oosterom, E. J., Whitaker, M. L., & Weltzien, R. E. (1996). Integrating genotype environment analysis, characterisation of drought patterns, and farmer preferences to identify adaptive plant traits for pearl millet. In M. Cooper & G. L. Hammer (Eds.), *Plant adaptation and crop improvement* (pp. 383-402). CAB International/IRRI/ICRISAT.
- Velu, G., Rai, K. N., Muralidharan, V., Longvah, T., & Crossa, J. (2011). Gene effects and heterosis for grain iron and zinc density in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. *Euphytica*, 180(2), 251-259. <http://dx.doi.org/10.1007/s10681-011-0387-0>
- Vengadassan, V. (2008). *Genetic and QTL analyses of sink size traits in pearl millet [Pennisetum glaucum (L.) R. Br.]* (Ph.D Thesis, Tamil Nadu Agricultural University, Coimbatore).
- Venkata, A. R. P., Kusuma Kumari, P., Santosh Mohan Dev, T. S., Subba Rao, M. V., & Manga, V. (2012). Genetic analysis of sodium content and Na/K ratio in relation to salinity tolerance in pearl millet *Pennisetum glaucum* (L.) R. Br. *Journal of Crop Science and Biotechnology*, 15(3), 195-203. <http://dx.doi.org/10.1007/s12892-011-0078-3>
- Wilson, J. P. (2000). Pearl millet diseases: A compilation of information on the known pathogens of pearl millet, *Pennisetum glaucum* (L.) R. Br. *Agriculture Handbook No. 716*. U.S. Department of Agriculture, Agricultural Research Service.
- Wilson, J. P., Gates, R. N., & Panwar, M. S. (2001). Dynamic multiline population approach to resistance gene management. *Phytopathology*, 91(3), 255-260. <http://dx.doi.org/10.1094/PHYTO.2001.91.3.255>
- Yadav, O. P. (2006). Heterosis in crosses between landraces and elite exotic populations of pearl millet [*Pennisetum glaucum* (L.) R. Sr.] in arid zone environments. *Indian Journal of Genetics*, 66(4), 308-311.
- Yadav, O. P., Weltzien-Rattunde, E., Bidinger, F. R., & Mahalakshmi, V. (2000). Heterosis in landrace-based topcross hybrids of pearl millet across arid environments. *Euphytica*, 112(3), 285-295.
- Yagya, D., & Bainiwal, C. R. (2001). Genetic analysis of crosses among pearl millet populations. *International Sorghum and Millets Newsletter*, 42, 68-70. <http://dx.doi.org/10.1023/A:1003965025727>

Copyrights

Copyright for this article is retained by the author(s), with first publication rights granted to the journal.

This is an open-access article distributed under the terms and conditions of the Creative Commons Attribution license (<http://creativecommons.org/licenses/by/3.0/>).