RESEARCH

Hybridization of Indian Landraces and African Elite Composites of Pearl Millet Results in Biomass and Stover Yield Improvement under Arid Zone Conditions

O. P. Yadav* and K. N. Rai

ABSTRACT

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is an important cereal crop of arid and drier semiarid regions of south Asia and Africa valued for both grain and stover. Drought is the most common production constraint in these regions. Drought-resilient landraces are widely grown but their cultivation results in a yield penalty under favorable conditions. Both high productivity and adaptation to drought stress are essential for cultivars targeted for arid regions. This study was conducted to assess whether crosses between Indian pearl millet landraces and African elite composites offer any advantage over landraces. Twenty-five crosses produced by hybridizing five Indian landraces with five African elite composites were evaluated for three seasons (2006–2008) at Jodhpur, India. Improvement in crosses was quantified by measuring midparent heterosis and differences between crosses and their parental populations. On an average, crosses had significantly higher biomass and stover yield than both landraces and composites but had grain yield similar to the parental populations. There was differential magnitude and direction of midparent heterosis for various traits: heterosis was positive for biomass (10%) and stover yield (12%) but negative for harvest index (–7%). Although there was little overall heterosis for grain yield, a few individual crosses had significant grain yield heterosis up to +33%. More than one-third of the crosses had greater grain and stover yields than their landrace parent, resulting in a mean advantage of 18% in their total crop value over landraces. These results indicate that hybridization of Indian landraces with elite composites based on African germplasm is an attractive and useful strategy to enhance biomass, stover, and grain productivity under drought-prone conditions.

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Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is an important cereal crop of arid and drier semiarid regions of south Asia and Africa grown over 26 m ha (FAO and ICRISAT, 1996). It is valued for both grain and stover as its grain is the major source of dietary carbohydrates of human diet and stover forms the major component of livestock ration during the dry period of year. Stover might become as important as grain in drought years (Kelley et al., 1996) when sale of animals or dairy products remains the primary source of income.

A number of improved high-yielding cultivars, including hybrids and open-pollinated varieties, have been released (Khairwal et al., 2009). They have been adopted by Indian farmers to a great extent in areas with higher rainfall and greater potential for crop productivity (Govila et al., 1997; Khairwal and Yadav, 2005). As a result, pearl millet productivity has been tripled during the last four decades (Yadav et al., 2011). However, the arid zone of Rajasthan in northwestern India, which occupies 25% of the pearl millet acreage of the country and 10% of the world acreage, has not fully benefited from improved cultivars largely because of their poor adaptation to the prevailing drought stress, high temperatures, and low soil fertility levels of arid zones (Yadav and Weltzien, 2000; Bidinger et al., 2009). This is not surprising, as most cultivars have been bred for and selected in relatively favorable, high yield potential environments,

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and farmers perceive a higher risk of crop failure under severe drought stress with improved cultivars (Christinck, 2002). The farmers' perception was validated by results of research station studies from arid regions (Yadav, 2004; Yadav and Bidinger, 2008; Bidinger et al., 2008). Hence, stress-adapted landraces are largely cultivated by Rajasthan farmers as a strategy to minimize the chances of crop failure (Christinck, 2002). At the same time, however, landraces are inherently lower yielding and often fail to capitalize on inputs, resulting in a significant yield penalty in better growing seasons (van Oosterom et al., 2003; Yadav and Bidinger, 2007; Yadav, 2008a). Landraces are no longer adequate to feed the ever-growing human population. Thus, pearl millet cultivars targeted for arid regions need to possess high yield potential and adaptation to drought stress.

Elite composites of African origin possess high yield potential, adequate levels of disease resistance, and bold and lustrous grains (Andrews and Anand Kumar, 1996) and also possess other agronomic traits that are complementary to Indian landraces (Yadav et al., 2005). However, African pearl millet landraces from western and central Africa have late maturity and are more sensitive to daylength limiting their adaptation to Indian arid conditions. Hence hybridization of Indian pearl millet landraces and African elite composites could be a more useful strategy to generate genetic material that could amalgamate yield potential and stress adaptation. The present study was conducted to assess the performance of crosses between Indian pearl millet landraces and African elite composites vis-à-vis that of their landrace parents and to quantify the magnitude of improvement in crosses for grain and stover productivity under arid zone conditions.

MATERIALS AND METHODS

Genetic Material

Five landraces from the northwestern state of Rajasthan, India, and five elite composites based on African germplasm were chosen for this study. Landraces LR108 (IC 329045), LR184 (IC 329821), LR221 (IC 331738), LR235 (IC 331752), and LR238 (IC 331755) were collected from drought-prone western and central parts of Rajasthan during 2000 through 2003 (Yadav, 2008b) and are characterized by extensive tillering, thin stems, small panicles, and small seed size. The five high-yielding elite composites (HHVBC, CZP 923, SRC II, MCSRC II, and MCNELC) were developed at ICRISAT, Patancheru, India. They are based on African germplasm (hereafter referred to as African elite composites) and have few tillers, thick stems, large panicles, and large seeds (Yadav and Weltzien, 1998). All landraces were crossed with each composite by manual pollinations to produce 25 F_1 crosses. The crosses were performed by taking advantage of protogynous nature of flowering in pearl millet using at least 100 plants from each parental population. The pollens collected from one parental population were dusted on panicles at full-stigma emergence stage of the other parental population. On the day following pollination, the pollinated panicles were observed for stigma drying to ensure successful cross-fertilization. In addition, 2 cm portion of the top as well as base of pollinated panicles was discarded before threshing of panicles to avoid any self-pollinated seed.

Field Evaluation

The 25 crosses, along with 10 parental populations, were evaluated for 3 yr during 2006 through 2008 at the Central Arid Zone Research Institute, Jodhpur, Rajasthan, India. The evaluations were done under rainfed conditions using a randomized complete block design with three replications. Trials were sown after receiving the first major seasonal rains. Each entry was grown in two 4-m long rows with a distance of 60 cm between rows. Seeds were planted with a tractor-drawn planter and plants within rows were thinned to a spacing of 15 cm 2 wk after sowing.

Trials received fertilizer applications of 40 kg N and 20 Kg P_2O_5 ha^{-1}. Full P and half N applications were made at the time of sowing and the remaining half of N was applied as topdressing within 4 wk of sowing on receipt of rains. Weeds were controlled by manual hoeing three times during the crop season. There were no major incidence of diseases and insect pests. Distribution of rains and visual observation on crop growth and development were used as criteria to describe drought stress.

Data Recording and Analysis

Flowering data were recorded on plot basis as number of days from sowing until 50% of plants in a plot had stigmas emerged on their main panicle. At maturity, all panicles from an entire plot were harvested, counted, dried in the field for 3 wk, weighed, and threshed; grain weight was then recorded. The stover was cut at the ground level, bundled and sun-dried for 3 wk and weighed. Panicle and stover weights were added to obtain biomass. Biomass, grain, and stover yields were converted to grams per square meter. Harvest index was calculated as ratio of grain to total biomass, expressed in percentage. The weight of 1000 grains was measured on each plot. The yield and grain number per panicle were derived from recorded traits.

Data were analyzed for individual years and across years using SPAR 2.0 (SPAR, 2004). All entries were divided into three groups, namely, landraces, elite composites, and crosses. Mean performance of each group was compared with other groups through single degree of freedom contrasts following Gomez and Gomez (1984). Midparent heterosis was calculated as percent deviation in performance of a cross from the average performance of its parental populations. To measure potential gain in productivity of crosses over landraces, heterosis was also calculated as percent improvement in performance of cross over its landrace and elite parents. Improvement was also measured for total crop value, based on a weighted (3:1) average of the relative market value of pearl millet grain and stover in western Rajasthan as suggested by Bidinger and Yadav (2009) and Yadav et al. (2009).

RESULTS

Evaluation Seasons

The average maximum temperature during crop seasons ranged between 33.7 and 35.5°C while mean minimum temperature was between 24.8 and 26.6°C (Fig. 1). The 3 yr of evaluations differed in total amount of rainfall and its distribution. Total rainfall during 3 yr of evaluation was 36 to 49% less than long-term average rainfall (360 mm) at Jodhpur. Evaluations in all seasons were affected by drought stress both at vegetative and reproductive stages of growth of experiments. In 2006, moisture stress developed during postflowering stage due to only 11 mm of rain falling after average flowering time of the trial, leading to low mean harvest index (19%) and grain yield (81 g m^{-2}) (Table 1). In 2007 evaluation, a prolonged dry spell of 3 wk resulted in water stress early in the growing season, which affected crop growth leading to delayed flowering. The postflowering rains were higher (62 mm) in 2007 than in 2006, but the crop still experienced water stress during the reproductive stage. Thus, both harvest index (19%) and grain yield (100 g m^{-2}) were low. During the 2008 season, only 13 mm of rain occurred during grain filling and the crop faced a prolonged spell of drought (Fig. 1) and likely ran out of water. The trial was on the verge of extermination and hence a life-saving irrigation of approx. 25 mm was applied, although it did not fully alleviate the drought stress. Thus, the test material was exposed to combinations of water stress that are common in arid zones.

Performance of Parental Populations and Crosses

In spite of the occurrence of drought, experimental coefficients of variation for biomass, grain yield, and stover yield was 10 to 17% (Table 1). This suggested that there was good control over experimental variation. In the ANOVA, both parents and crosses were significant sources of variation for all traits and performance of both groups was modified significantly by years except parental variation for biomass, stover yield, panicle grain yield, and panicle grain number (Table 2). There was significant variation among the parental populations for all traits. Variation among entries within landraces and composites was also significant for all traits except harvest index, grain yield and grain number per panicle, and 1000-grain weight in landraces and grain number in composites.

There was in general a wider range among F_1 crosses for grain yield, grain number per panicle, grain yield per panicle and 1000-seed weight, in comparison to parental populations. Landraces, on an average, flowered 3 d earlier than composites and crosses (Table 3). Biomass of crosses was significantly higher than both landraces and composites. However, crosses had lower harvest index than landraces but similar to elite composites (Table 3). Both biomass and harvest index of landraces and composites

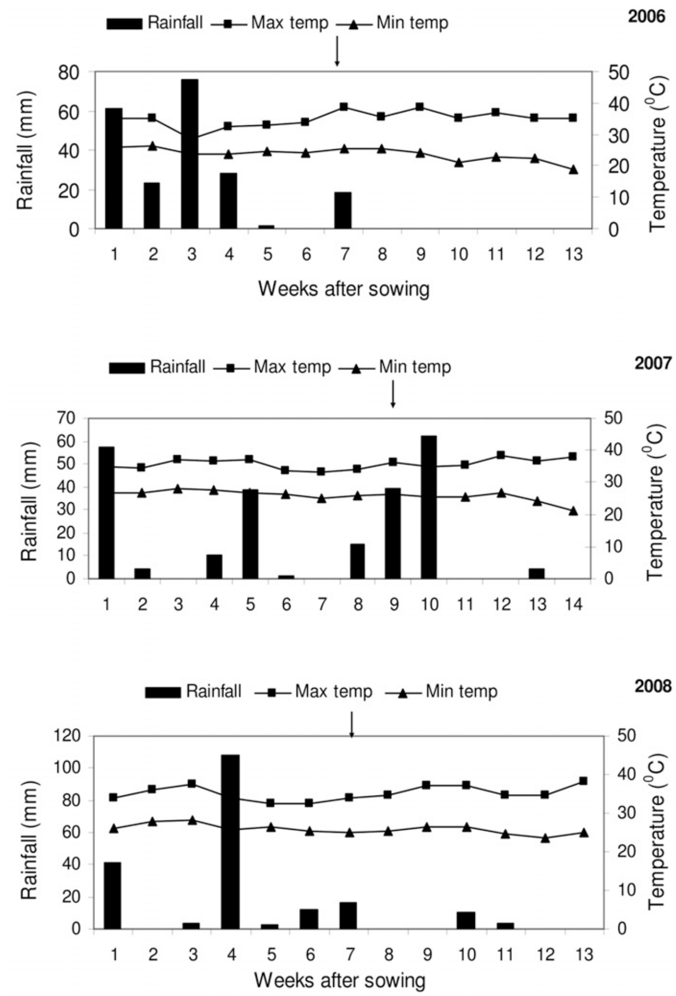

Figure 1. Distribution of rainfall and range in maximum and minimum temperatures during three crop seasons at Jodhpur, Rajasthan, India. Arrows indicate average flowering time of entries.

Table 1. Trial means and range for various traits during 3 yr of evaluations at Jodhpur, Rajasthan, India.

	2006		2007		2008	
Trait	Mean	Range	Mean	Range	Mean	Range
Time to flower, days	46.6	41.7–52.0	60.5	59.3–63.7	48.6	45.7–52.0
Biomass yield, g m^{-2}	414.9	347.8–629.5	532.2	391.5–738.7	766.4	587.6–994.5
Harvest index, %	19.4	10.3–24.5	18.8	11.9–24.8	24.2	19.4–25.1
Stover yield, g m^{-2}	287.1	263.9–420.0	334.9	257.0–493.1	507.0	382.0–659.7
Grain yield, g m^{-2}	80.5	34.5–100.3	100.1	69.9–125.1	185.5	134.9–271.0
Biomass CV%	11.6		9.9		12.5	
Grain yield CV%	15.4		17.2		11.8	
Stover yield CV%	12.4		13.5		15.6	

Table 2. Mean squares from ANOVA for time to flower, biomass, stover yield, grain yield, and yield components.

Source	df	Time to flower	Biomass yield	Harvest index	Stover yield	Grain yield	Panicles m^{-2}	Grain yield per panicle	Grain no. per panicle	1000-grain weight
Environments (E)	2	6106.5**	3338313**	909.6**	1444161**	294788**	86.7**	2099.5**	31370280**	45.33**
Parents (P)	9	50.0**	27744**	36.0**	16583**	1582**	93.0**	64.6**	981765**	1.26**
Crosses (C)	24	16.4**	17553**	54.7**	7985**	3131**	13.5*	14.1**	475769**	1.61**
P vs. C	1	80.6**	182829**	131.8**	127561**	368	56.2**	41.2**	1181956**	0.09
E × P	18	6.2**	3152	32.0**	1778	772**	3.2*	8.4	164757	2.19**
E × C	48	5.5**	21343**	24.2**	11427**	1697**	5.1**	8.4 **	251876**	1.33**
E × P vs. C	2	5.6*	22694*	48.8**	24199**	272	3.1	2.9	383120	1.41*
Error	204	1.64	4891.1	7.35	3350.0	302.3	1.78	5.14	136774	0.328

*Significant at probability level of 5%.

**Significant at probability level of 1%.

Table 3. Mean values and range of traits in 25 crosses between five parental landraces and five parental elite composites during 3 yr of evaluations at Jodhpur, Rajasthan, India.

	Crosses		Landraces		Composites	
Trait	Mean	Range	Mean	Range	Mean	Range
Time to flower, days	52.8b†	50.6–55.6	50.2a	47.8–53.7	53.2b	51.3–54.4
Biomass yield, g m^{-2}	592.7c	501.7–679.0	550.7b	460.3–626.6	528.0b	467.9–568.3
Harvest index, %	19.7a	15.1–23.9	21.4b	19.7–22.8	20.9ab	16.7–23.2
Stover yield, g m^{-2}	397.8c	347.2–463.0	366.2b	307.9–422.4	340.3a	306.7–393.7
Grain yield, g m^{-2}	116.7a	84.1–154.3	117.8a	97.7–131.9	110.4a	99.5–131.3
Panicles m^{-2}, no.	9.3b	6.7–11.5	12.5c	8.5–15.5	7.8a	6.8–9.7
Grain yield per panicle, g	12.6b	10.4–15.7	9.4a	8.2–10.8	14.1c	12.5–15.4
Grain number per panicle	1918b	1567–2400	1505a	1317–1694	2060c	1911–2355
1000-grain weight, g	6.6b	5.8–7.4	6.3a	6.1–6.5	6.8c	6.4–7.3

†Mean trait values within a row of crosses, landraces, and composites suffixed by different letters are significantly different at $p < 0.05$.

were comparable. These combinations of biomass and its partitioning resulted into significantly higher stover yield of crosses than their parental populations and similar grain yield of landraces, composites, and their crosses. However, formation of grain yield was different, particularly between landraces and elite composites. Landraces produced significantly higher number of panicles than composites (Table 3). On the other hand, grain yield per panicle was significantly higher in composites, mainly due to their greater grain number per panicle compared to landraces. Panicle number of crosses was significantly higher than that of composites but significantly lower than that of landraces. Crosses had significant improvement over landraces in grain yield per panicle and seed size.

Heterosis in Crosses

There was differential magnitude and direction of heterosis for various traits. On an average, mean midparent heterosis was positive for biomass and stover yield and negative for harvest index but there was little heterosis for grain yield (Table 4). Mean midparent heterosis for biomass was positive in crosses of all landraces and varied between +7% in crosses of LR238 to +18% in LR108 crosses (Table 4). The mean biomass heterosis across landraces was +10% and seven crosses showed significant positive heterosis for biomass. Maximum heterosis in crosses of each landrace varied from +14 to +36%. In contrast to biomass, the overall heterosis for harvest index was negative (–7%) with nine crosses having significant negative heterosis. However, a few crosses (based on 3 out of 5 landraces) did have positive midparent heterosis with a magnitude of up to +22% in the cross based on LR238 (Table 4).

As indicated by mean per se performance of parental populations and crosses (Table 3), there was little overall heterosis for grain yield (Table 4). However, mean midparent heterosis in crosses varied considerably between –11% in crosses of LR184 and +8% in crosses based on LR238 with three crosses each having significant positive and negative heterosis. The best cross of LR238 had midparent heterosis as high as +33% with mean heterosis of best crosses of all landraces being +15%.

Stover yield was found to be a highly heterotic trait, although the magnitude of heterosis, like other traits, varied considerably (+6% in crosses of LR235 to +23% in

Table 4. Mean and range in midparent heterosis (%) in crosses for biomass, harvest index, grain yield, and stover yield in 25 crosses between five landraces and five elite composites.

Landrace parent	Midparent heterosis (%)							
	Biomass		Harvest index		Grain yield		Stover yield	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
LR108	18.3	–9.4 to +36.2**	–9.9	–22.0** to +3.5	4.0	–11.2 to +14.7*	22.7	11.2 to +42.1**
LR184	8.6	+1.7 to +21.8*	–17.6	–21.8** to –13.6	–10.6	–20.8** to +2.9	14.6	+5.9 to +29.2**
LR221	8.3	+8.3 to +20.8**	–7.2	–13.6 to –3.0	0.2	–7.9 to +10.5	12.1	+6.1 to +25.8**
LR235	8.3	–3.5 to + 13.5*	0.7	–5.1 to +11.7	7.8	+3.6 to +13.4	6.3	–10.0 to +15.0
LR238	7.3	–4.6 to + 17.3*	0.6	–14.8 to +21.6**	8.2	–15.1 to +32.5**	9.8	–0.7 to +22.4*
Mean	10.2	–1.5 to + 21.9	–6.7	–15.5 to +4.0	1.9	–10.3 to +14.8	13.1	+2.5 to +26.9

*Significant at probability level of 5%.

**Significant at probability level of 1%.

crosses of LR108) (Table 4). The mean midparent heterosis was +13% and seven crosses had significant positive heterosis. LR108 and LR184 produced the most heterotic crosses with mean heterosis of +23 and +15%, respectively. The best cross of LR108 had +42% heterosis with mean heterosis of best crosses of each landrace being +27%.

Potential Benefit of Crosses

Not all crosses had significant superiority for biomass, stover, and grain yields over their parental populations. Among crosses that had significant improvement, there existed a wide range in degree of heterosis (Table 5). For biomass, 11 crosses exhibited positive significant heterosis over elite composites while six crosses had significant heterosis over landrace parents. The average magnitude of improvement in biomass in such crosses was 24% for biomass with maximum heterosis over parental populations being up to 37 to 41%. In contrast, none of crosses showed improvement over its landrace parent in biomass partitioning (harvest index), although three crosses had significant better partitioning of biomass than their elite parents. Most of the crosses had positive heterosis for stover yield. Two-thirds of crosses had significantly better stover yield than one of the parents and three had significantly higher stover yield than their both parents. The degree of superiority of the individual cross for stover yield was as high as 40 to 45%. The grain yield improvement over landraces was significant in four crosses and over elite composites in three crosses and these crosses provided 19 to 30% yield advantage over yield of their parental populations. A few crosses, for example, LR108 × SRC II, LR184 × 923, and LR184 × HHVBC, had positive heterosis over their landrace parent for grain yield despite having negative heterosis for harvest index, which might have been due to a very high magnitude of positive heterosis for biomass (23 to 37%). The combined advantage in both stover and grain yield of crosses over parental populations translated in an overall advantage of 18 to 32% with respect to total crop value in best one-third crosses. Grain yield heterosis over landrace parent in crosses was due to higher grain yield per panicle (mean heterosis +35%), which in turn appeared predominantly because of positive heterosis for grain number per panicle (+28% heterosis), although there was overall positive heterosis (+6%) for grain size as well (data not presented).

DISCUSSION

The mean grain yield and biomass of landraces was numerically but not significantly greater than elite composites (Table 3). However, the present study indicated a significant advantage of landraces for stover productivity. Stover yield is an important consideration in pearl millet cultivar adoption in arid regions with high probability of severe drought stress (Kelley et al., 1996) and under these conditions sale of animals or dairy products is the primary source of income (Hall et al., 2004). These results also explain the reason for continued preference of landraces by arid zone farmers (Bhatnagar et al., 1998; Khairwal and Yadav, 2005) with which they harvest as much grain as with elite material and simultaneously have some additional stover.

The lower grain number per panicle and smaller seed size of high-tillering landraces, as observed in this study, reflect the mechanism of their survival under drought stress (van Oosterom et al., 2003, 2006). On the other hand, producing higher grain number per panicle and larger seed size under a range of conditions is a part of the yield formation process of low-tillering elite material (Bidinger and Raju, 2000) and these traits are reflection of their better grain filling ability. Such trends were also observed in our study (Table 3). Crosses appeared to combine higher panicle number of landraces and greater grain yield per panicle of elite composites, both of which are major yield components in pearl millet (Bidinger et al., 1993; Solanki et al., 2001). The greater grain number per panicle and larger seed size of crosses than those of

Table 5. Heterosis (%) over landrace (LR) and elite composite (EC) for biomass, harvest index, stover yield, grain yield, and whole crop value in crosses of pearl millet.

	Heterosis (%)									
	Biomass yield		Harvest index		Stover yield		Grain yield		Whole crop value†	
Cross	Over EC	Over LR	Over EC	Over LR	Over EC	Over LR	Over EC	Over LR	Over EC	Over LR
108 × HHVBC	22.5*	15.7*	–16.1*	–27.1**	27.3*	24.5*	0.4	–13.1	9.4	–5.0
108 × 923	9.7	22.4*	2.7	4.1	15.0	21.6*	7.6	22.8*	12.6	29.9
108 × SRC II	35.3**	37.0**	–14.8*	–15.9*	45.2**	39.0**	12.7	16.0*	27.6	28.8
108 × MCSRC II	4.0	19.4*	20.1*	–12.2	0.8	23.8*	16.5	2.3	16.8	10.2
108 × MCNELC	3.9	15.3	–16.0*	–18.3*	11.6	21.3*	–14.5	–7.4	–10.6	–0.4
184 × HHVBC	20.7*	22.7*	–17.1*	–16.4*	28.0*	30.4*	1.9	3.8	11.2	13.8
184 × 923	2.7	23.3*	–20.0*	–5.9	10.9	22.1*	–15.1	13.9	–11.5	21.2
184 × SRC II	0.01	9.0	–23.8**	–12.6	13.2	12.7	–24.3*	–8.3	–20.0	–4.1
184 × MCSRC II	–7.9	13.6	–9.7	–23.4*	–5.5	20.6	–16.8	–13.9	–18.6	–7.1
184 × MCNELC	–5.1	13.2	–26.2**	–16.7*	2.3	15.8	–29.3**	–9.8	–28.5	–4.6
221 × HHVBC	41.2**	5.4	–4.0	–7.8	47.6**	9.5	25.9*	–1.6	41.6	1.5
221 × 923	10.5	–2.5	–8.1	2.9	19.1	–4.3	1.0	4.2	7.3	2.8
221 × SRC II	16.7*	–6.5	–9.0	–0.7	26.7*	–7.9	–0.6	–7.6	8.1	–10.2
221 × MCSRC II	9.1	–0.9	–3.3	–21.9*	11.1	3.5	4.0	17.4*	7.6	–16.2
221 × MCNELC	17.3*	2.8	–11.6	–4.9	26.9*	4.6	1.0	–1.1	9.8	0.3
235 × HHVBC	24.8*	–0.1	–0.7	–7.0	25.0*	–2.8	16.5	–6.8	24.7	–7.7
235 × 923	16.8*	10.4	–9.1	–0.7	25.9*	5.7	5.8	11.7	14.4	13.6
235 × SRC II	18.5*	1.7	–1.6	4.7	23.3*	–6.3	9.5	4.3	17.2	2.2
235 × MCSRC II	–2.0	–4.8	26.7*	–0.1	–8.8	–11.1	18.8	–3.3	15.9	–7.0
235 × MCNELC	14.4	7.6	–2.6	2.0	19.6*	3.1	13.3	13.5	19.8	14.5
238 × HHVBC	32.1**	5.3	20.2*	5.7	29.1*	7.6	49.4**	11.3	59.0	13.7
238 × 923	–1.6	–7.4	–11.7	–9.4	4.7	–5.5	–14.9	–15.3*	–13.3	–17.1
238 × SRC II	22.0*	4.3	–14.8*	–14.8*	36.2**	11.0	3.4	–7.1	15.3	–3.4
238 × MCSRC II	10.3	6.4	42.9**	5.8	0.8	5.5	52.6**	14.5*	52.9	16.2
238 × MCNELC	6.2	–0.5	–5.1	–6.5	10.9	2.7	0.1	–5.4	3.7	–4.4
Mean	12.9	8.6	–4.5	–7.9	17.9	9.9	5.0	1.4	10.9	3.4

*Significant heterosis at probability level of 5%.

**Significant heterosis at probability level of 1%.

†Heterosis in the value of the whole crop is based on a weighted average of the market values of grain and stover (1.00 × heterosis for grain yield plus 0.33 × heterosis for stover yield).

landraces suggest better grain filling ability of crosses than of landraces. Thus, introgression of elite composites into adapted landraces can result in new valuable recombinants with respect to these yield components.

Heterosis benefited crosses and the magnitude and direction of heterosis varied for different traits. While heterosis was high and positive for biomass (+10%) and stover yield (+13%), it was negative for harvest index (–7%). These values of heterosis are much lower than those previously reported (80 to 150%) in crosses of inbred parents (Virk, 1988; Khairwal and Singh, 1999). However, it needs to be recognized that heterosis in this study was measured over open-pollinated parental populations or their midparental value; whereas heterosis in pearl millet for different productivity traits has historically been quantified using inbred parental lines. Such heterosis estimates are often inflated as pearl millet is a highly cross-pollinated crop and suffers due to inbreeding. Only a few studies have quantified heterosis over open-pollinated parental populations and the magnitude of heterosis observed for biomass (10%) and stover yield (12%) in present study compared well with those reported by Yadav et al. (2000) and Yadav (2006) who observed 10 to 15% increase in biomass and stover yield in landrace-based testcrosses.

The absence of heterosis for grain yield and harvest index was surprising and contrasted with earlier reports of significant heterosis (15–22%) for these traits in testcrosses based on landrace pollinators (Yadav et al., 2000; Bidinger et al., 2005; Yadav and Bidinger 2008; Bidinger and Yadav 2009). Whether this reflects differences in landraces used in this study, productivity of evaluation environments, or some other factor unique to this data set is not entirely clear.

However, these results can partly be explained by differences between landraces and crosses in their ability to produce productive tillers. As deduced from trial planting density (11.1 plants m^{-2}) and observed panicle number (Table 3), the average number of productive tillers per plant was 1.13 in landraces and 0.84 in crosses. Landraces are reported to produce a main panicle even under severe drought stress, which is not the case with other non-landrace elite material (van Oosterom et al., 2003, 2006). This situation might have resulted in relatively greater partitioning of biomass of landraces to grain than stover giving a significant advantage to landraces over crosses leading to negative heterosis for harvest index. In spite of this, a few individual crosses based on most of the landraces had significant high positive grain yield heterosis. This means that low overall heterosis for grain yield was mainly due to mutual cancellation of positive and negative heterosis of crosses, an observation also noted by Prestrel and Weltzien (2003). These authors further contended that low heterosis in such diverse crosses might be explained through coadapted genes, at many loci, interacting in an epistatic manner.

Even though not all crosses showed improvement over parental populations, many showed substantial improvement for both grain and stover yields and thus in their total crop value. Average improvement in total crop value of top one-third (9 out of 25) of crosses was 18% over landraces and 31% over elite parents. Thus there was good opportunity for identifying individual crosses with a significant grain and stover yield increase over landraces. The potential benefit in crop value of best crosses was as high as 30% over landraces and more than 50% over elite composites. Given that these landraces represent germplasm adapted to arid zones, the level of heterosis for total crop value is very encouraging. Therefore, such crosses are potential genetic material to broaden the germplasm base and to develop material for drought prone environments.

A good proportion of crosses showing considerable improvement in productivity indicated that hybridization of Indian landraces with African elite composites could produce genetic material that amalgamates drought tolerance of traditional landraces with high yield potential of elite genetic material. Research results in other crops (Godshalk and Kauffmann 1995; Vetelainen et al., 1997) also support our finding of using exotic materials to add favorable traits that might be absent in local materials. Results obtained here also lend support to prevalent farmers' practices in western Rajasthan of introgression of traditional landrace with modern cultivars (Christinck, 2002) to increase the diversity (vom Brocke et al., 2002, 2003a) and to expand the range of adaptation of their seed stocks (vom Brocke et al., 2003b).

Results of the present study showed that hybridization of Indian landraces with African elite composites is an attractive and useful option to enhance both grain and stover productivity under drought-prone conditions. Although this study was conducted in Indian arid zone, the approach can be useful to other breeding programs targeting similar environments, such as the Sahelian zone of west and central Africa, where the production constraints of pearl millet are similar to those encountered in northwestern India. The use of landraces in hybridization programs is a modest way of conservation of the valuable traits found in fast-eroding traditional genetic resources. Retaining such traits will assure that the benefits of centuries of human and natural selection for adaptation to the stresses of arid zone environments will remain available for future generations.

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