Biomass Heterosis as the Basis for Grain and Stover Yield Heterosis in Arid Zone Pearl Millet Hybrids

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ABSTRACT

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] single cross hybrids, bred from high-yielding parental lines in favorable environments, are not well adapted to northwest India's arid zone. The objectives of these experiments were (i) to measure grain and stover yield heterosis in testcrosses of six landrace-based restorer populations and (ii) to understand how heterosis for biomass and harvest index (HI) affects heterosis for grain and stover yields in crosses of these populations. Six restorer populations and their testcrosses on 10 to 13 A1 male-sterile lines were evaluated at two arid zone locations of northwest India. Heterosis was calculated as percentage advantage of testcross hybrids over parental restorer population. The range in individual testcross heterosis varied from –3% to +39% for grain yield and from –22% to +17% for stover yield. Variation in biomass heterosis accounted for 55% of the variation in grain yield heterosis and 84% of the variation in stover yield heterosis. Harvest index heterosis accounted for 38% of variation in grain yield heterosis and 13% of stover yield heterosis with a positive heterosis in HI resulting in negative heterosis in stover yield. The testcrosses with the highest biomass heterosis for each restorer population achieved 20% biomass heterosis level (combined with a mean 12% heterosis in HI), resulting in 32% grain yield heterosis and 18% stover yield heterosis. We concluded that heterosis for biomass was the major determinant of grain and stover yield heterosis in pearl millet.

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Abbreviations: A-line, male-sterile hybrid seed parent; AICPMIP, All India Coordinated Pearl Millet Improvement Project; GCA, general combining ability; HI, harvest index.

Single cross hybrids are currently grown on an estimated 45 to 50% of the 9 million hectares sown annually to pearl millet [*Pennisetum glaucum* (L.) R. Br.] in India (Khairwal and Yadav, 2005). This is a remarkable achievement in a crop grown primarily by small farmers in the driest areas of the country, where the more productive, but less drought-adapted sorghum [*Sorghum bicolor* (L.) Moench] and maize (*Zea mays* L.) do not succeed. Hybrids have played a significant role in raising the national average pearl millet yields from 323 to 731 kg ha^{-1} between the period of 1950–1954 to 2000–2002 (Khairwal and Yadav, 2005). Adoption of hybrids, however, is mainly concentrated in the more favorable areas (better rainfall and deeper soils) of the country; hybrids have not yet significantly replaced landraces or open-pollinated varieties in the less favorable areas.

The main area in which farmers still rely largely on their traditional landraces of pearl millet is the arid (200–400 mm annual rainfall) zone of northwest India (primarily western Rajasthan state), which represents as much as 25% of the pearl millet acreage in the country (Govila et al., 1997; Khairwal and Yadav, 2005). Arid zone farmers generally perceive that available hybrids have a higher risk of failure in poor rainfall years and produce insufficient

Published in Crop Sci. 49:107–112 (2009).
doi: 10.2135/cropsci2008.03.0154

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straw for maintaining animals during the dry season (Kelley et al., 1996; Dhamotharan et al., 1997). These perceptions are supported by research station studies from the arid zone in which traditional landraces or varieties bred from them had significantly greater grain yield than both new hybrids or open-pollinated cultivars in low-yielding environments, as well as significantly higher biomass (straw productivity) (Yadav and Weltzien R., 2000; vom Brocke et al., 2003; Yadav, 2004). Research suggests that the climatic and adaphic factors in the arid zone are strikingly different from those in the rest of the pearl millet growing areas of India (Bidinger et al., 2006), and that successful new cultivars need to be based on adapted (i.e., landrace) germplasm (Presterl and Weltzien, 2003) to perform well under the characteristic drought and temperature stresses of this zone. Current mainstream breeding materials (from the more favorable pearl millet growing zones) do not seem to possess a sufficient level of adaptation to the arid zone (Presterl and Weltzien, 2003; Bidinger et al., 2006).

Although the traditional landrace cultivars of the arid zone provide a source of this adaptation, these often lack sufficient yield potential to compete in improved, nonstress environments, as well as adequate disease resistance, both of which are requirements for cultivar release. The improvement of the grain yield potential of the traditional landrace materials (e.g., by recurrent selection) is conventionally considered to be constrained by a lack of genetic variability for grain yield (Yadav and Manga, 1999; Yadav et al., 2001) and by a characteristic plant type that favors survival over productivity. Recent evidence however, suggests that there is scope to identify landrace germplasm accessions with considerably better yield potential without a sacrifice in adaptation to severe stress (van Oosterom et al., 2006).

An alternative approach to improving both adaptation and yield potential is to use adapted landrace germplasm as the restorer parent in either single cross (inbred × inbred) or topcross (inbred × population) hybrids (Bidinger et al., 1994; Yadav et al., 2000a, 2000b). This approach is a potentially simple way to combine adaptation to arid zone environments from the restorer parent with a higher grain yield potential, through the heterosis achieved in hybrid cultivars. Previous work with hybrids made with unimproved landrace accessions as pollinators on a limited number of seed parents reported an average increase of 15% in growth rate and biomass production in the topcross hybrids, compared to the landrace accessions themselves under typical arid zone conditions (Yadav et al., 2000a; Bidinger et al., 2003). Partitioning of this extra biomass to either grain or stover was largely dependent on the magnitude of heterosis for harvest index (HI; the fraction of total biomass partitioned to the grain), which was partially dependent on the individual seed parent used (Bidinger et al., 2003).

We have bred a series of restorer populations from arid zone landrace germplasm, to provide the base material to test the above approach to produce adapted, higher yielding hybrids for the arid zone, and at the same time make adapted arid zone germplasm available to breeders targeting hybrids for this zone. The objectives of this study were (i) to assess the magnitude of heterosis for both grain and stover yields under arid zone conditions in six of the newly bred landrace-based restorer populations and (ii) to understand how heterosis for biomass and HI affect heterosis for grain and stover yields. The magnitude and expression of heterosis in hybrids made with the restorer population bulks should provide an indication of the heterosis achievable with inbred restorers derived from these populations.

MATERIALS AND METHODS

Restorer Populations and Testcrosses

The restorer populations used in this study were bred from three sources:

- Individual landrace accessions (IP 3228 and IP 3246) that showed good combining ability in a previous experiment (Yadav et al., 2000b).
- Breeding populations (Jakharana and Barmer populations) made from selected landrace accessions of a particular origin or type (Yadav and Weltzien, 1998).
- Adapted open-pollinated varieties (RCB2 and Early Rajasthan Population); RCB2 was bred from selected landraces by the Rajasthan Agricultural University, Jobner, released by the All India Coordinated Pearl Millet Improvement Project (AICPMIP) in 1984 (Khairwal et al., 2004). The Early Rajasthan Population was bred from selected landrace sources and improved by four cycles of recurrent selection (Yadav and Weltzien, 1998); an experimental variety from the last cycle of selection was released by AICPMIP as CZP 9802 in 2002 (Yadav, 2004).

Restorer versions of each of these populations and varieties (considered as the C0 generation) were bred by means of a single cycle of S1 progeny testcross selection, using approximately 200 testcrossed progenies. Approximately 25 S1 progenies were selected on the basis of fertility restoration (assessed on the basis of seed set in bagged panicles) in a male-sterile tester, testcross grain yield, flowering date, and incidence of downy mildew [*Sclerospora graminicola* (Sacc.) Schroet.] in the arid zone. The selected S1 progenies were recombined (using reserve S1 seed) to make the C1 cycle restorer version of each of the original populations or varieties. The C1 bulk was random-mated by hand pollination to form a C2 bulk and bulk pollen from this generation of each restorer population was used to pollinate 10 to 13 male-sterile seed parents (A-lines) to make the testcrosses used in this study. The A-lines had A1 cytoplasmic male sterility system and were based on African and Indian pearl millet germplasm. The present study used a much wider range of seed parent lines than has been used previously, to assess the range in heterosis possible in combination with diverse A-lines, particularly for biomass, which may be the key to improving stover as well as grain yields (Bidinger et al., 2003).

Field Evaluations

Each set of restorer population testcrosses was evaluated at two arid zone locations in a single year. Replicated testcross evaluations of the Early Rajasthan Population and RCB 2 restorer populations were conducted in 2000 with 13 A-lines each. Replicated testcross evaluations of the Jakharana, Barmer, IP 3228, and IP 3246 restorer populations were conducted in 2003 with either 12 (Jakharana and Barmer) or 10 (IP 3228 and IP 3246) A-lines each. All trials also included the restorer populations themselves as entries. In both cases the trials were performed under rainfed conditions at the Central Arid Zone Research Institute (Jodhpur) and the Rajasthan Agricultural University Substation at Nagaur.

The trials in 2000 were performed under high input (for the arid zone) conditions (57 kg ha^{-1} N and 44 kg ha^{-1} P_2O_5 at Jodhpur and 38 kg ha^{-1} N and 39 kg ha^{-1} P_2O_5 at Nagaur). The previous crop in both cases was pearl millet. The trials at both locations were machine sown on 18 July at Jodhpur and on 28 July at Nagaur. Plot size was two rows by 0.6 m by 4.0 m. There were four replications arranged in a 6 (plots per block) by 5 (blocks per replication) alpha design.

The 2003 trials were also performed under high input conditions (50 kg ha^{-1} N and 28 kg ha^{-1} P_2O_5 at Jodhpur and 40 kg ha^{-1} N and 20 kg ha^{-1} P_2O_5 at Nagaur). The previous crop in both cases was also pearl millet. The trials at both locations were machine sown on 7 July at Jodhpur and on 9 July at Nagaur. Both the combined IP 3228 and IP 3246 trial and the combined Jakhrana–Barmer trial were sown in two rows by 0.6 m by 4.0 m plots with five replications in a 5 by 5 lattice design.

The harvest area for all trials was two rows by 3.0 m (3.6 m^2). At harvest, panicles were cut, counted and sun dried in cloth bags. When dry, panicles were weighed and machine threshed, and grain weight was recorded. Stover was cut at ground level, bundled, sun dried in the field for approximately 2 wk, and weighed. Data were used to calculate field dry biomass, grain and stover weights (on a square meter basis), and HI for all entries.

Data Analysis

Data from all trials were analyzed across both locations using the Genstat (Release 10.1, Rothamsted Experimental Station, UK) ReML package with location and rep (and block) as random effects, and A-line, restorer, and A-line × restorer as fixed effects. Heterosis was calculated as the percentage (of the restorer population itself) advantage of the testcross hybrid over the restorer population (Yadav et al., 2000a), which represents the potential exploitable gain in productivity. Heterosis for both grain yield and for stover yield was regressed on heterosis for biomass and HI. The dependant variable in the regression was the mean values for each restorer population ($N =$ 10 to 13) across locations. The analysis was performed using SAS (Version 9.1; SAS Institute, Inc., Cary, NC) PROC REGR in the forward stepwise mode. Partial coefficients of determination for both independent variables were used as an indication of the relative importance of heterosis for biomass or HI in determining heterosis for grain or stover yield.

Table 1. Restorer population per se value, mean (by restorer population) heterosis, and the range for individual testcross hybrid heterosis for biomass and harvest index in six arid zone restorer populations.

Restorer population†	Total biomass			Harvest index		
	Restorer	Heterosis		Restorer	Heterosis	
		Mean	Range		Mean	Range
	g m^{-2}			%		
Early Rajasthan	333 ± 53.2	−3.2	−27.3 to +26.8	31.1 ± 1.3	−0.5	−11.4 to +11.6
RCB 2	308 ± 57.7	+9.6	−9.0 to +33.9	26.1 ± 1.8	+20.5	+4.5 to +36.3
CV	25.8			11.1		
IP 3228	543 ± 75.1	−2.8	−20.3 to +12.5	23.7 ± 1.5	+9.7	−9.1 to +25.2
IP 3246	476 ± 81.6	−11.9	−1.0 to +20.4	24.8 ± 1.3	+18.6	+9.8 to +32.4
CV	10.0			6.0		
Barmer	567 ± 53.4	+7.3	−4.6 to +18.4	20.9 ± 1.2	+29.8	+17.4 to +50.3
Jakharana	593 ± 57.1	−2.2	−12.4 to +8.6	24.7 ± 1.5	+21.5	−7.2 to +36.0
CV	11.2			7.7		
Mean	470	−0.5	−12.4 to +20.1	25.2	+16.6	+0.7 to +32.0

†Comparisons among pairs of populations are not valid as these were grown in different years or trials.

RESULTS AND DISCUSSION

Heterosis for Biomass and HI

For all six sets of testcrosses there was no difference between biomass of the restorer population itself and the average biomass of its testcross hybrids, despite a significant variation in biomass production among the testcrosses in all restorer populations. As a consequence average heterosis for biomass in the testcross hybrids of all six restorer populations was nil (Table 1), but a few individual testcrosses in most of the restorer populations had a significant positive biomass heterosis (Table 1). In each pair of restorer populations, the population with the least biomass productivity had the individual testcross with the highest heterosis, an effect also noted by Mahalakshmi et al. (1992) in a set of topcross hybrids made with a broad range of variety pollinators. The maximum expression of biomass heterosis may be at least partially governed by the differences between the actual biomass productivity of the restorer population and the potential biomass productivity of the test environment.

The lack of an overall biomass heterosis in this study contrasts with an earlier report of testcross hybrids based on a larger set of unimproved landraces as pollinators, but on only two testers, in which there was an average 15% increase in biomass productivity per day (Yadav et al., 2000a). Whether this reflects differences in the restorers (unimproved landraces vs. selected, partially improved populations), the wider range of testers used in these trials, or some other factor unique to this data set is not clear. The study by Bidinger et al. (2003) indicated that a past history of selection for grain yield in pollinator populations tended to result in a positive general combining ability (GCA) for HI, at the expense of a positive GCA for biomass. However, in this data set the biomass heterosis was greater in the more improved restorer populations

(RCB2 and Early Rajasthan Population) than in the least improved (the two IP lines) populations (Table 1). In any case, the range in biomass heterosis in the individual testcross combinations is sufficient to select specific combinations for each restorer population with a sufficient increase in biomass of the restorer to improve grain and/or stover yields in the resulting hybrids.

In contrast to the biomass situation, mean HI in testcrosses was 29.3% as compared to 25.2% of restorer populations. The average increase in the testcrosses with the highest HI in each population was 7.6%. As a result, the average heterosis for HI across all six restorers for HI was positive (16%), and heterosis in several of the restorers exceeded 20% (Table 1). The best of the individual testcrosses achieved heterosis for HI between 12 and 50% for individual restorer populations (Table 1). Thus the major effect of testcrossing the restorer populations to conventionally bred A-lines was an increase in partitioning of dry matter to grain, rather than an increase in total dry matter itself. Our earlier study similarly found most released A-lines used had a positive GCA for HI (Bidinger et al., 2003). This likely reflects the primary selection of the A-lines for combining ability for grain yield, which historically has been achieved by a greater increase in grain relative to biomass in many cereal crops (e.g., Austin et al., 1993). Thus the opportunity for achieving significant grain yield heterosis in hybrids made with pollinators bred from the landrace restorers should be good, but it will be important to focus on specific combinations in which this is not simply achieved at the expense of stover yield, where the latter is also important.

Heterosis for Grain and Stover Yields

The consequence of the increase in HI in the testcrosses was an average 22 g m^{-2} increase in grain yield. Mean grain yield increases varied considerably among the restorer populations, from −5 g m^{-2} with the Early Rajasthan Population to +48 g m^{-2} with the Barmer population. The increase in grain yield in the highest yielding individual testcross ranged from 20 g m^{-2} in the case of the Early Rajasthan Population to 70 g m^{-2} in the case of the Barmer Population, with a mean across all population of 46 g m^{-2}. As a result there was a positive mean heterosis for grain yield, for all but one restorer population, with range of −5 to +40% across populations (Table 2). The mean grain yield heterosis of the best individual testcross in each population averaged nearly 40%, with individual testcrosses achieving even higher values (Table 2). Thus there was good opportunity in most restorer populations to identify individual testcrosses with a significant grain yield increase over the restorer population. Given that these populations represent adapted, and in some cases elite, arid zone landrace germplasm, this level of grain yield heterosis is very encouraging.

However, as a consequence of the absence, on average, of heterosis for biomass (Table 1), heterosis for HI resulted in an average 9 g m^{-2} decrease in stover yield. Mean stover yield differences in the testcrosses of individual restorer populations ranged from −36 g m^{-2} in the case of Jakharana to +16 g m^{-2} in the case of IP 3228. Similar figures for increase in stover yield in the highest yielding individual testcross ranged from 12 g m^{-2} in the Jakharana Population to 63 g m^{-2} in the Early Rajasthan Population, with a mean of 44 g m^{-2}. As a result there was an average (across all restorer populations) stover heterosis of −2.1%, with individual population averages ranging from −10% to +5% (Table 2). The stover yield heterosis of the best individual testcross with each restorer was positive (+3% to +28%), but, with the exception of the Early Rajasthan Restorer Population, was less than half of the magnitude of the grain yield heterosis of the best testcross (Table 2). Where the objective in hybrid breeding is primarily an increase in grain yield relative to the current level in landrace populations, this should be easy to achieve with a range of seed parents. This means that the choice of seed parent(s) can be based on other essential considerations such as the maturity, disease resistance, plant type, etc., of the hybrid. However, where the objective is to maintain or increase simultaneously stover yield and grain yield, it will be necessary to be much more selective in the choice of seed parent.

Modeled Heterosis in Individual Testcrosses

We used stepwise regression modeling to partition the variation in heterosis in both grain and stover yield between the variation in heterosis for biomass and for HI though such analyses might be limited by multicolinearity if the traits, used as predictors, are highly correlated. Interestingly, there was no correlation ($r = 0.05$) between heterosis for biomass and HI across restorer populations showing utility of this analysis in understanding trait relationship. Across populations, biomass heterosis accounted for 55% of the heterosis for grain yield and heterosis for HI accounted for 38% of grain yield heterosis, with the effect of biomass heterosis accounting for between 41% (Jakharana) and 70% (RCB 2) of grain yield heterosis in the individual restorer population testcrosses (Table 3). Similarly, biomass heterosis accounted for an average 84% of heterosis for stover yield (range 74–91%), while heterosis for HI accounted for an average of 13% of stover yield heterosis, with a positive heterosis in HI resulting in a negative heterosis in stover production in this case (Table 3).

Thus, despite the generally positive heterosis for HI in all but one of the restorer populations, heterosis for HI actually had a smaller positive effect on grain yield heterosis than did biomass heterosis, and had a negative effect on stover yield heterosis. Despite the lack of a significant average increase in biomass in the restorer population testcrosses across all testcross combinations, heterosis for biomass was still the main determinant of grain and stover yield heterosis among individual testcrosses. Stover productivity carries a greater weight for many farmers in the arid zone than it does for farmers in higher rainfall zones who have greater feed resources as stover is the main source of feed to maintain both large and small ruminants during the long dry season (Kelley et al., 1996). Thus these data support the contention of Bidinger et al. (2003) that GCA for biomass productivity should be the major criterion for parental selection in hybrid breeding for the arid zone.

Table 2. Restorer population per se value, mean (by restorer population) heterosis, and range for individual testcross hybrid heterosis for grain and stover yield in six arid zone restorer populations.

Restorer population†	Grain yield			Stover yield		
	Restorer	Heterosis		Restorer	Heterosis	
		Mean	Range		Mean	Range
	$g\ m^{-2}$	%		$g\ m^{-2}$	%	
Early Rajasthan	109 ± 20.3	−5.2	−38.0 to +17.4	168 ± 26.7	+2.8	−27.8 to +26.8
RCB 2	86 ± 17.4	+30.2	+3.1 to +60.6	179 ± 32.3	−0.4	−21.7 to +28.3
CV	30.4			27.5		
IP 3228	135 ± 22.8	+13.5	−6.3 to +31.3	349 ± 47.9	−8.8	−27.8 to +8.6
IP 3246	126 ± 25.5	+16.1	+3.6 to +37.2	301 ± 51.4	+5.3	−18.5 to +20.7
CV	12.2			10.5		
Barmer	121 ± 14.2	+39.5	+15.1 to +58.4	387 ± 38.6	−1.9	−13.3 to +12.8
Jakharana	155 ± 21.6	+14.1	+5.5 to +27.8	377 ± 34.6	−9.6	−23.4 to +3.4
CV	15.3			11.2		
Mean	122	+18.0	−2.8 to +38.8	294	−2.1	−22.1 to +16.8

†Comparisons among pairs of populations are not valid as these were grown in different years or trials.

Realized Heterosis in the Best Testcross Combinations

One option for targeting biomass heterosis in the breeding of inbred restorers from the base populations would be to focus on selecting inbred or partially inbred lines with specific combining ability for biomass productivity in combination with preselected seed parents. Assuming that there is within-population variability in the restorer populations for specific combining ability for biomass with specific seed parents, this approach should easily achieve the 20% target for increased biomass (compared to the original restorer population) in hybrids made with such inbred restorers. We identified the seed parent that produced the testcrosses with the highest biomass heterosis for each restorer population, and compared the effects of biomass heterosis on heterosis for grain and stover yields. Heterosis was also measured in these testcross combinations for total value of crop, based on a weighted (4:1) average of the relative market value of pearl millet grain and stover per kilogram (P. Parthasarathy Rao, ICRISAT, personal communication, 2007). Mean biomass heterosis for the six selected combinations was 21%, more or less as expected, but interestingly there was also useful heterosis for HI in all but one of the testcross combinations (Table 4). As a consequence, mean grain yield heterosis of the best testcross combination for each restorer population was 33% and mean stover yield heterosis was 18%, for a mean heterosis for total crop market value of 37%, for the selected combinations (Table 4). There was considerable variation among the restorer populations in the performance of the best testcross combination, but in most cases the increases in the grain and stover yield and total crop value were substantial.

Table 3. Heterosis for grain and stover yield as a function of heterosis for biomass and harvest index in the testcross hybrids of six landrace-based restorer populations. Data are partial coefficients of determination (CD) from stepwise regressions of percent heterosis in grain and stover yields on percent heterosis in biomass and harvest index.

Restorer population†	Grain yield partial CD		Stover yield partial CD	
	Biomass	Harvest index	Biomass	Harvest index
Early Rajasthan	0.67	0.21	0.74	−0.21
RCB 2	0.70	0.21	0.82	−0.10
IP 3228	0.65	0.33	0.87	−0.10
IP 3246	0.44	0.49	0.91	−0.10
Barmer	0.46	0.53	0.81	−0.17
Jakharana	0.41	0.53	0.91	−0.07
Mean	0.55	0.38	0.84	−0.13

†Comparisons among pairs of populations are not valid as these were grown in different years or trials.

Table 4. Measured percent heterosis in grain and stover yields in the individual testcross with the greatest biomass heterosis for each of the landrace-based restorer populations.

Restorer population†	Seed parent	% Heterosis for individual components				
		Total biomass	Harvest index	Grain yield	Stover yield	Total value‡
Early Rajasthan	ICMA 97333	26.7	−9.1	17.4	37.7	26.8
RCB 2	ICMA 89111	33.9	10.9	46.9	28.3	54.0
IP 3228	ICMA 94555	12.5	13.5	24.0	8.6	26.2
IP 3246	ICMA 97444	25.2	15.0	37.2	20.7	42.4
Barmer	ICMA 93333	18.4	19.4	43.2	12.8	46.4
Jakharana	ICMA 96333	8.6	22.6	27.8	0.7	28.0
Mean		20.9	12.1	32.8	18.1	37.3

†Comparisons among pairs of populations are not valid as these were grown in different years or trials.

‡Heterosis in the value of the whole crop, based on a weighted average of the market values of grain and stover (1.00 × heterosis for grain yield plus 0.25 × heterosis for stover yield).

Results of the present study showed that there was a wide range in heterosis for grain and stover yields in testcrosses over their parental landrace population. Variation in biomass heterosis was the major determinant of this heterosis. Harvest index heterosis accounted for substantial variation in grain yield heterosis but positive heterosis in HI resulted in negative heterosis for stover yield.

Acknowledgments

This work is an output of the ICAR-ICRISAT Partnership Research Project on Pearl Millet. The authors would like to thank Messrs. M. M. Sharma, D. Dharani, and P. V. D. Maheshwar Rao for their assistance in carrying out the breeding operations and field experiments reported here; Ms. Rehka Baddam for assistance with data analysis; and the Director of Research of the Rajasthan Agricultural University for permission to use University field facilities at Nagaur.

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