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Genetic diversification of landrace-based populations of pearl millet (*Pennisetum glaucum* L. R. Br.) to enhance productivity and adaptation to arid zone environments

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Abstract

In the present investigation, 20 crosses of pearl millet (*Pennisetum glaucum* L. R. Br.) and their nine parental combinations consisting of four landrace-based and five elite exotic populations were evaluated in four contrasting seasons within arid ecosystem in order to study their response pattern to a wide range of environmental conditions. In most severe drought year, the landrace-based populations outyielded other two groups by a margin of 33-72%. In favourable conditions, exotic elite populations provided significantly higher grain yield than landraces with average degree of superiority being 25-45% across two seasons. The hybridization between landrace-based and elite populations resulted into enhanced adaptation range of crosses, beyond that of their parents. Individual landraces and elite populations differed significantly in their general combining ability (*gca*) effects though landraces had, in general, more pronounced *gca* effects than elite populations. Landrace Jakharana and elite population ESRC provided their crosses both adaptation to stress conditions and also higher potential productivity. On the contrary, BarPop was established as an appropriate parent for producing cultivars with general adaptation giving high stover yield but with a significant penalty for grain yield. ERajPop appeared more suitable for producing grain type materials while WRajPop emerged suitable to produce dual-purpose materials. The elite populations MC and EC had effects for specific adaptation to drought conditions for grain yield productivity. The populations BSEC established as promising parent for grain yield but not for stover yield across environments. Results demonstrated that there are exploitable differences among landraces and elite populations for their ability to produce genetic material with a variety of combinations for grain and stover productivity and with differential adaptation pattern. Implication of these findings in pearl millet breeding for arid zone conditions is discussed.

Key words: Pearl millet (*Pennisetum glaucum*), drought adaptation, landraces, genetic diversification

Introduction

Modern high yielding cultivars of pearl millet (*Pennisetum glaucum* L.R. Br.) including both single cross hybrids and open pollinated varieties have been adopted by Indian farmers due to their high yield potential, early maturity and resistance to disease but their adoption rate are differential in various regions [1-2]. Improved cultivars adoption is the lowest in the drier arid regions of northwestern India owing to their perceived poor grain and stover yields under severe drought stress [3]. Consequently, traditional landraces are commonly grown as a strategy to reduce the risk of crop failure in seasons with limited and highly erratic rainfall. However, the lower yield potential of landraces than elite cultivars is insufficient to support ever-growing populations in these regions. This accentuates the need to create new source populations that integrate adaptation to drought stress conditions of landraces and high yield of elite material, so that the new materials don't trade increased productivity with reduced yield stability and increased risk of crop failure.

New breeding materials can be derived from either landraces or improved elite breeding populations. Use of landraces as the base material might ensure adaptation but puts a ceiling on degree of improvement in productivity that might be obtained through selection as landraces generally are reported to have limited variation for grain yield *per se* [4]. On the other hand, using elite breeding material may assure the yield potential but leaves behind the difficult task of improving stress adaptation which is poorly understood physiologically. Hence, the introgression of elite genetic material with adapted germplasm is an attractive option for diversifying the genetic base of adapted germplasm as intermating exotic and adapted germplasm maximizes the potential for new valuable recombinants. Elite pearl millet of African origin is potential genetic material for diversification of northwestern Indian landraces because of its high yield potential and adequate levels of disease resistance in addition to its bold and lustrous grains [5]. In the present investigation, response pattern of crosses and their parental populations to a wide range of environmental conditions within arid ecosystem was studied to explore whether stress adaptation of landraces and high productivity of elite exotic populations could be amalgamated in population crosses between adapted germplasm and exotic elite populations. The effects of individual landrace-based population and elite population were also studied.

Materials and methods

The genetic material used for present investigations were pearl millet landrace-based populations and elite early to medium maturing exotic populations developed mainly from African and Indian pearl millet germplasm. The Rajasthan landrace-based populations included Jakharana, Early Rajasthan Population (ERajPop), Western Rajasthan Population (WRajPop) and Barmer Population (BarPop). Landrace populations were chosen to represent a gradient from elite landrace to unimproved types. Jakharana represented the improved type of landrace in terms of productivity and disease resistance. BarPop, on the contrary, represent unimproved typical landrace from western Rajasthan. The exotic elite populations were Early Smut Resistant Composite (ESRC), Smut Resistant Composite (SRC), Early Composite (EC), Medium Composite (MC) and Bold Seeded Early Composite (BSEC).

A set of 20 crosses was made by manually crossing each of four landraces with five elite populations. A minimum of 100 plants from parental populations was used in each cross. The 20 crosses along with nine parental populations were evaluated at the Central Arid Zone Research Institute, Jodhpur during four rainy seasons of 1999-2001 and 2003. Each year the material was evaluated in randomized block design with three replications. Each entry was grown in 4 m long four rows at spacing of 60 cm. The plots were over sown with a tractor-drawn planter and a plant-to-plant spacing of 15 cm was maintained by thinning within two weeks of sowing. Trials received 20 kg/ha N and 8 Kg/ha P_2O_5 at sowing and an additional 20Kg/ha N was top dressed 3-4 weeks after sowing. Weeds were controlled manually.

Days to flowering was recorded as number of days from sowing till the emergence of stigma in the main shoot panicle of 50% plants in a plot. At maturity, the panicles were harvested from entire plot, counted and were dried for two weeks before weighing and threshing. Both grain and dry stover weights were recorded on plot basis. The dry panicle weight and dry stover weight were added to obtain total biomass. The harvest index was calculated as ratio of grain to biomass expressed in percentage.

The individual year data were analyzed using ANOVA. A combined analysis of variance over environments was also conducted. Sums of squares due to crosses were further partitioned into variation due to landraces, elite populations and their interaction. General combining ability (*gca*) for each parental population was estimated as the mean of all crosses involving that parent minus the overall mean. Significance of the parental *gca* was determined by t-test at error d.f.

Results and discussion

Growing environments

The four growing seasons had a considerable variation in the amount and distribution of rainfall (Table 1) which provided a wider range of drought stress ranging from a severe stress in 1999, moderate drought stress in 2000 and near-optimum growing conditions in 2001 and 2003. This resulted into a grain yield productivity of 32 g m^{-2} to 216 g m^{-2}. Thus the results obtained in this study would be applicable in a range of environmental conditions. The reduced productivity in 1999 and 2000 as compared to 2001 and 2003 seasons was due to both lower number of panicles per unit area and lower grain yield per panicle (Table 1).

Performance of landraces, elite populations and crosses

In analysis of variance across years, the genotypes showed highly significant differences among themselves for both grain and stover yields (data not presented). Crosses as well as parents had significantly contributed to the significance of genotypes as indicated by highly significant means squares due to both of these

Table 1. Mean days to flower, grain yield and yield components, rainfall and its distributions during four years of evaluations at Jodhpur

Trait	Unit	1999	2000	2001	2003
Time to flower	days	52.85	48.25	46.34	45.24
Grain yield	gm^{-2}	31.85	65.30	201.81	216.01
Panicles m^{-2}	no.	4.21	7.78	9.85	11.11
Grain yield per panicle	g	7.56	8.39	20.49	19.44
Biomass yield	gm^{-2}	-	309.01	766.65	831.85
Harvest index	%	-	20.87	26.53	25.95
Stover yield	gm^{-2}	-	189.65	463.48	519.83
Rainfall	mm	205.2	255.7	327.9	327.2
Pre-flowering	mm	195.7	231.2	317.3	291.7
Post-flowering	mm	9.5	24.5	10.6	35.5

components. Performance of both parents and crosses was modified significantly over different years as shown by their significant interactions with environments except parent x year interaction for stover yield (data not presented). However, three groups of material showed differential adaptation pattern to changing environmental conditions. In most severe drought year of 1999, the average grain yield performance of landraces was significantly superior to both elite populations and crosses (Fig. 1). The landraces group outyielded overwhelmingly other two groups by a margin of 33-72% which suggested that adaptation, rather than potential yield, was a major determinant of grain yield performance under extreme severe drought conditions. This also probably explains the reason of continued preference of landraces in extremely scanty rainfall regions of western Rajasthan [3]. The cultivation of such adapted landraces minimize the chance of cop failure [6] and provide greater stability in production due to their more heterogeneous and heterozygous nature.

Under moderate drought environment of season 2000, the average grain and stover yields of three groups was at par (Fig. 1). The situation in relatively favourable and near-optimum seasons of 2001 and 2003 was reverse to that observed in severe drought year of 1999 with respect to grain yield performance. Exotic populations provided significantly higher grain yield than landraces (Fig. 1) with average degree of superiority being 25-45% across two seasons, though their average

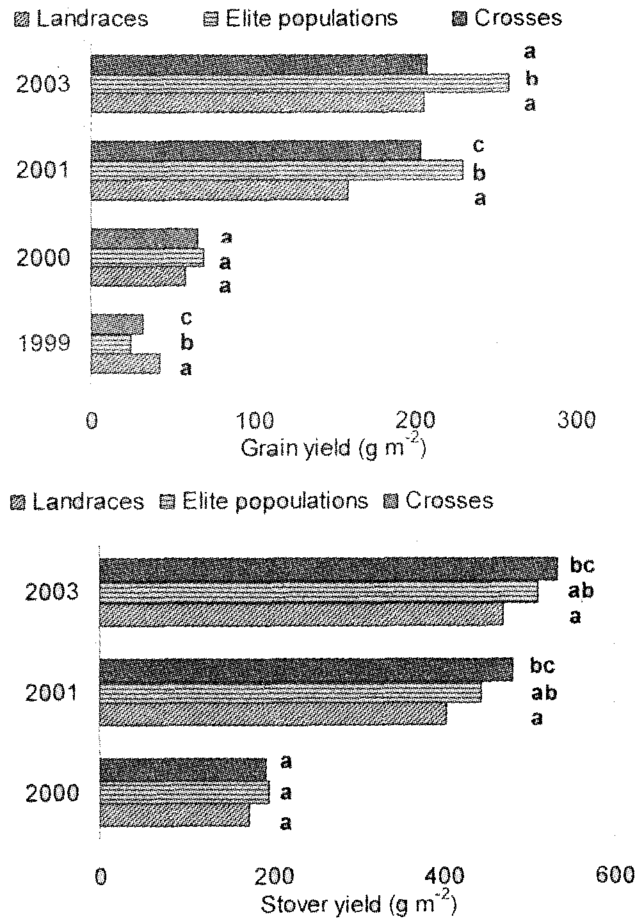

Fig. 1. Mean of grain yield (g m^{-2}) and stover yield (gm^{-2}) of four landraces, five exotic populations and their 20 crosses in four seasons differing in drought intensities (mean values of a trait within a year having different letters differ significantly at P<0.05)

stover yield performance was statistically at par with that of landraces. These results indicated that the high potential yield of material primarily determined the performance under good growing seasons.

Crosses though had significantly lower performance in severe drought of 1999 season than landraces but their mean grain yield performance was significantly improved than that of elite populations (Fig. 1). On the other hand, crosses had no significant disadvantage over either elite or landrace-based populations in 2000 which suggested that crosses tended to get benefited of adaptation of landraces and higher productivity potential of elite populations. In near-optimum environments (2001 and 2003), the population crosses performed significantly better than landraces for stover yield in both years and for grain yield in one of the two years. Thus, the hybridization between landraces and elite populations resulted into enhanced adaptation range of crosses, beyond that of their parents, as they were better able than their landrace parent to capitalize on the additional resources of good growing seasons, and simultaneously had a better capacity than their elite parent to tolerate drought. Presterl and Weltzien [7] also observed that hybridization between adapted landraces and elite populations was beneficial to widen the germplasm base.

Though the average grain yield performance of crosses was between the average performance of landraces and elite populations (Fig. 1), there existed significant variation within landraces and crosses in individual years which led us to critically examine the relative performance of individual landrace and its crosses under diverse growing conditions for grain and stover yields. In seasons of 2000, 2001 and 2003 the grain and stover yield performances of crosses was always greater than their landrace parents except those based on one landrace (WRajPop) for stover yield in 2000 and based on two landraces (BarPop and WRajPop) for grain yield in 2003 (Fig. 2). These data suggested that a reasonable degree of improvement in pearl millet productivity could be expected in the genetic material developed by introgression of elite materials into adapted material.

Effects of elite and landrace-based populations

The highly significant ($P < 0.01$) differences among crosses in their grain and stover yields, biomass and harvest index in both individual year and across years analysis (data not presented) suggested that variation among crosses could be further partitioned into variation due to different sources. Mean squares due to landraces were highly significant for grain and stover yields, biomass and harvest index in all years of evaluation except for grain yield in 1999 and for stover yield in 2003 evaluations suggesting that landraces differed for their combining ability effects for all traits. These effects were, however, significantly modified by environments as indicated by significant landrace x year interactions. It was due to changes in both direction and magnitude of *gca* effects of landraces over different years of evaluations (Table 2).

Landrace Jakharana exhibited positive *gca* effects in all four years for grain yield, the effects being significant in three years, resulting into overall significant and positive effects across years (Table 2). This was due to significant and positive *gca* effects for harvest index

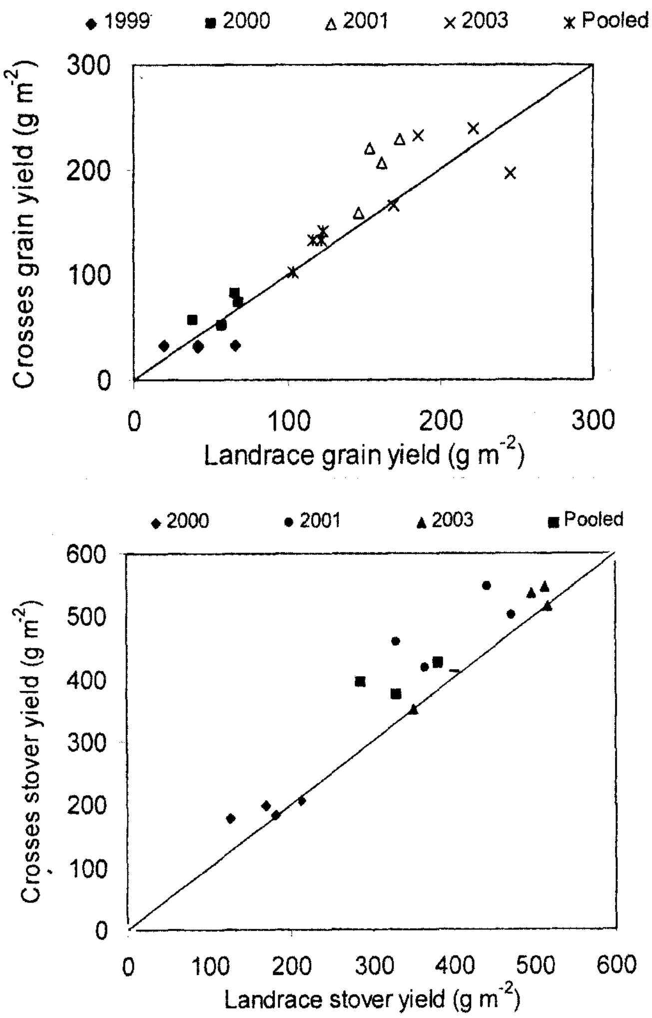

Fig. 2. Relationship (1:1 line) between yield of individual landrace and its crosses evaluated at Jodhpur

coupled with either significant positive or average *gca* estimates for biomass. Thus the landraces Jakharana appeared to provide its crosses both adaptation to stress conditions and also higher potential productivity. On the contrary, BarPop had negative *gca* estimates for grain yield in all four years of evaluation primarily due to poor biomass partitioning by its crosses as indicated by its significant and negative *gca* effects for harvest index. BarPop had either positive significant or average effects for stover yield and thus would be an appropriate parent for producing cultivars with high stover yield but with a significant penalty for grain yield.

ERajPop also had significant negative *gca* effects for stover yield in all years except in 2003 (Table 2) mainly due to its negative *gca* effects for biomass, but grain yield response of its crosses to drought and non drought years varied. It showed negative *gca* effects in two drought years and positive effects in other two non-drought years, though *gca* effects could reach the level of significance in one year only. Overall, it had significant positive *gca* effect for grain yield but significant negative for stover yield and thus ERajPop appeared more suitable for producing grain type materials.

The *gca* effect of WRajPop for grain yield was significant and positive in moderate drought year 2000 (Table 2) but did not significantly differ from zero in 1999 as was expected on the basis of non-significant mean squares due to landraces in this season. The effects were consistent with its *gca* estimates observed for biomass. In fact, *gca* effects for biomass was the primary determinant of *gca* estimates for grain yield in this study as indicated by high positive correlation of *gca* effects for grain yield and biomass (r = 0.84*** PO.01, 0.47** PO.10 and 0.63** PO.10 in 2000, 2001 and 2003, respectively). These results are in agreement with those obtained earlier in the Indian arid zone environments [8, 9]. The WRajPop was able to produce crosses with good biomass across years with overall significant and positive effect for harvest index (Table 2). Consequently, WRajPop was found to be average combiner for stover yield. Therefore, WRajPop established its utility to produce dual purpose materials with significant and positive *gca* for grain yield with average *gca* estimates for stover yield.

The analysis of variance also indicated significant effects of elite populations in four seasons for all traits except for biomass in 2000 and stover yield and harvest index in 2003 and the *gca* effects of elite populations was also significantly modified by environments as shown by significant elite population x year interaction (data not presented). However, these interactions appeared to result in most cases largely due to change in magnitude of *gca* effects of elite populations over years, rather than a significant change in direction of combining ability effects across years (Table 2).

The population ESRC exhibited positive and significant *gca* estimate for grain yield largely due to its high estimates for biomass (except in 2000) with the average estimate for harvest index which led to its overall significant positive estimates for both grain yield and stover yield (Table 2). Thus ESRC was identified as a suitable parent for developing dual purpose genetic materials with general adaptation. The populations SRC also seemed to fall in this category though it did not exhibit as high estimates as ESRC showed for grain yield but it did show higher estimate than ESRC for stover yield. This might be due to its negative effects for harvest index despite of possessing positive estimate for biomass (Table 2).

The elite populations MC and EC proved to be having effects for specific adaptation for grain yield productivity. Both of them had average estimate for grain yield in drought years but negative and significant effects in near optimum conditions (Table 2). The population BSEC had either significant positive or average combining ability effects for grain yield across years but had consistent negative estimates for stover yield. Though its effects for biomass partitioning were significant and positive but lower biomass accumulation capacity of its crosses resulted into a significant disadvantage for stover yield (Table 2). Thus BSEC established far greater promising for grain yield than for stover yield under arid zone conditions.

It was interesting to note that landraces had more pronounced *gca* effects in different contrasting seasons as compared to elite populations. This might be due to the fact that in the present study landraces represented a wide range of plant type than elite populations in terms of their tillering capacity, panicle size and biomass accumulation and its partitioning. The different plant types of pearl millet have been reported to respond in a different way to varying growing conditions [10].

Summary and implication in breeding for drought tolerance

The results of present investigation revealed that landrace-based populations and exotic elite populations make two contrasting groups in terms of adaptation to the arid zone environment. Crosses between these two groups had significant superior performance to exotic populations in extreme drought situations and had no significant disadvantage over either elite populations or landraces under moderate drought conditions which suggested that crosses tended to combine the traits of both parental types, as they performed better than elite composites in the severe drought year and better than landraces in good rainfall years. Thus, these data certainly appeared to make the case for genetic diversification of landraces through introgression of elite genetic material for conditions ranging from drought stress to near optimum conditions. Results also demonstrated that there are exploitable differences in the landraces and elite populations for their ability to produce genetic materials with a variety of combination for grain and stover productivity and with differential adaptation pattern. Certain landraces and elite

Table 2. General combining ability effects of four landraces and five elite populations of pearl millet for gain yield, stover yield, biomass and harvest index in four years of evaluation

Trait	Year	Landraces				Elite populations				
		Jakharana	BarPop	ERajPop	WRajPop	ESRC	SRC	MC	EC	BSEC
Grain yield	1999	1.00	-0.18	-1.24	0.43	5.57**	0.37	-2.11	-0.61	-3.22
	2000	8.32**	-14.95**	-10.04**	16.68**	-5.07	-2.31	-1.57	-2.10	11.05**
	2001	24.45**	-44.08**	2.99	16.64*	17.23*	22.02**	-17.29*	-15.41*	-6.56
	2003	24.60**	-43.15**	30.59**	-12.05*	29.50**	-2.73	-16.50*	-23.99**	13.72*
	Pooled	14.59**	-25.59**	5.57*	5.42*	11.81**	4.33	-9.37**	-10.53**	3.75
Stover yield	1999	-	-	-	-	-	-	.	-	-
	2000	7.47	-7.81	-14.06*	14.41	2.60	12.15	11.29	-10.42	-15.63*
	2001	-22.40*	66.49**	-63.37**	19.27	48.78**	84.38**	-58.85**	7.99	-82.29**
	2003	-0.87	15.11	3.30	-17.54	6.95	1.74	15.63	-6.95	-17.37
	Pooled	-5.27	24.60**	-24.71**	5.38	19.45**	32.76**	-10.65	-3.13	-38.43**
Biomass yield	1999	-	-	-	-	-	-	-	-	-
	2000	19.24**	-32.01**	-25.24**	38.00**	-4.13	11.33	10.10	-16.24*	-1.06
	2001	-1.97	16.69	-61.33**	46.60**	76.17**	141.83**	-106.26**	-14.34	-97.40**
	2003	23.78	-16.77	38.26**	-45.27**	29.17	30.01	10.19	.44.78**	-24.59
	Pooled	13.69*	-10-70	-16.10*	13.11*	33.74**	61.06**	-28.66**	-25.12**	-41.02**
Harvest index	1999	-	-	-	-	-	-	-	-	-
	2000	1.49**	-2.54**	-1.65**	2.71**	-1.25	-1.55*	-1.36	0.48	3.67**
	2001	2.53**	-5.84**	2.02**	1.28**	-0.24	-1.50**	-0.56	-1.48**	3.78**
	2003	2.27**	-4.14**	2.06*	-0.19	1.56	0.42	-1.12	-1.77	0.91
	Pooled	2.10**	-4.17**	0.81*	1.27**	0.02	-0.88*	-1.01	-0.92*	2.79**

- no data; *,** Significant at P< 0.05 and 0.01, respectively.

populations were identified which can be intercrossed and recombined to develop broader composites with high productivity and adaptation with sufficient genetic variation for their successful exploitation in future recurrent selection programme. The landraces Jakharana and WRajPop and elite populations ESRC and SRC can be utilized for making populations with general adaptation for a variety of growing conditions which can cater the need for grain as well as stover. The landrace BarPop and elite population BSEC looked complimentary to each other with good combining ability effects for stover and grain yield, respectively. Therefore, these two should make an interesting material for use in breeding programmes for arid zone environments.

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