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Farmers' seed management practices open up new base populations for pearl millet breeding in a semi-arid zone of India

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With 6 tables

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Abstract

Farmers in western Rajasthan (north-west India) produce and maintain their landrace populations of pearl millet through their own distinct seed management practices. The objective of this study was to characterize morphological and agronomic variability of different traits between and within three farmers' populations using quantitative–genetic parameters. Populations examined were a typical landrace and two modified landraces, which were generated through farmer introgression of modern varieties with different levels of subsequent selection. From these three populations, 100 random full-sib progenies were evaluated in field trials at two locations in western Rajasthan over two years. Significant genetic variation existed within the three populations. Estimates of heritability were moderate to high for all observed traits. Predicted selection response for grain yield across environments was 1.6% for the typical landrace and 2.2% for both the modified landraces. Results suggest that the introgression of modern varieties into landraces had increased the genetic diversity. Therefore, farmers' current breeding activities could open up new resources for plant breeding programmes aiming at plant improvement for the semiarid zones of India.

Key words: *Pennisetum glaucum* — diversity — farmers' seed management — genetic gain — genetic resources — introgression — landraces — participatory plant breeding

Pearl millet is a drought-tolerant cereal crop well adapted to the semi-arid tropics. In north-west India, particularly in the state of Rajasthan, it is the staple food and fodder crop. Western Rajasthan pearl millet landraces are extremely tolerant to stress conditions, even under the harsh climate of the Thar desert transition zone (Weltzien and Witcombe 1989). In India, pearl millet research and development has been described as a 'great success story' (Khairwal et al. 1999) that has seen immense activity on the part of national and international breeding institutes. In the state of Rajasthan alone no less than 97 pearl millet varieties have been notified for release since 1969 (Tripp and Pal 1998). Socioeconomic studies, however, have shown that farmers in the marginal regions of western Rajasthan consider modern 'improved' varieties (MV) as inferior to local landraces, both in yield performance under stress conditions and in general stover productivity. These farmers have benefited very little from the new varieties (Kelley et al. 1996, Dhamotharan et al. 1997). It can therefore be stated that most of the modern varieties released in Rajasthan have not met the needs and preferences of subsistence farmers (Weltzien and Witcombe 1989, Kelley et al. 1996, Weltzien et al. 1998, Christinck et al. 2000).

Farmers in western Rajasthan place emphasis on a wide range of morphological and developmental plant properties. They use such properties as indirect measures of yield performance and stability, as well as for identifying stover productivity and quality-related aspects (Kelley et al. 1996, Weltzien et al. 1998, Christinck et al. 2000). Until recently, very few formal attempts have been made to understand the specific needs of these farmers and their production systems, or evaluating the ecological conditions of Rajasthan's marginal millet-growing areas (van Oosterom et al. 1996, Dhamotharan et al. 1997). As a result of these attempts, efforts have been made to develop better targeted breeding programmes for the production systems of north-west India (Yadav and Weltzien 1997, Yadav et al. 2000). A common objective of these projects was to develop varieties that combine the capacity to adapt to the various stress conditions of this region with a high yield potential under favourable conditions. A further goal of these projects was to implement elements of participatory plant breeding (PPB). Farmer–researcher collaboration is considered a more effective approach for developing plant material acceptable to Rajasthan farmers (Weltzien et al. 1998).

The present study was conducted as a collaborative project between ICRISAT, various national institutions of India and the University of Hohenheim in Germany. One of the project's main objectives was to understand and examine the effects of farmers' seed management and crop improvement activities in their pearl millet populations. This was achieved by combining quantitative genetic methodology with social science. Farmers' seed management was defined as all the activities of a farming family that influence their seed stock. This mainly comprised introgression of modern varieties, seed selection, and processing.

The purpose of the present study was to evaluate farmer-generated populations and population crosses as base populations for participatory breeding in Rajasthan. Specific objectives were: (1) to characterize morphological and agronomic variability between and within three farmer-generated populations; and (2) to evaluate the usefulness of each population with regard to breeding purposes.

Materials and Methods

Plant materials: The plant material analysed in this study comprised 100 random full-sib progenies that were produced from three different farmers' pearl millet, *Pennisetum glaucum* [L.] R.Br., populations originating from the same village of Aagolai in western Rajasthan. The three base populations will be referred to by the names of the farmers who provided the seed stock samples: Rana Ram (RR), Dhira Ram (DR) and Seemu Bai (SB). Their populations were chosen from a total of 69 farmer populations that were sampled in western and central Rajasthan between 1997 and 1998. These 69 populations had been used to study the effects of farmers' management on adaptation and productivity (vom Brocke et al. 2000). The two populations DR and SB were chosen for the present study because they were the two most 'diversified' seed stocks with regard to plant type. Population RR, on the other hand, was identified by farmers and researchers alike as the most typical landrace in the village of Aagolai (see below). Between 400 and 500 random plants per population were grown at the ICRISAT research centre in Patancheru (Andhra Pradesh) in 1998. About 200 random plant pairs per population were crossed reciprocally for production of full-sib seed. Bagged panicles were pollinated at the full-stigma-emergence stage. Pollen developing under the bag after the crossing was used to fertilize bagged tillers of the plant previously used as male. Crossing was performed during the entire flowering period to avoid selection for earliness.

Background of base populations: Rana Ram, whose landrace seed stock has been produced in his family over many generations, avoids all forms of conscious introgression. Dhira Ram's family, on the other hand, has been introgressing MV seed into their landrace stock for nearly 20 years. The family owns fertile land in a water catchment area. Almost every year they buy MV seed and sow it in a separate field section. This purchased seed comprises 16–20% of the total seed grain used. At harvest, preferred panicles for seed are selected from the entire crop before being bulked together for storage. Based on information from Dhira Ram, selected fractions vary between 3 and 4%. In contrast to Rana Ram and Dhira Ram, farmer Seemu Bai's family owns a small plot of land. Only after experiencing a favourable harvest do they have enough surplus seed for sowing the next season. In most years this family needs to purchase modern variety seed from the market or must ask neighbours for seed. Farmer Seemu Bai, like Rana Ram, does not use the panicle method for selecting seed grain: these farmers winnow grain from their food grain for use as seed. The winnowing method entails the cleaning and separation of bold, heavy grain for seed purposes (Weltzien et al. 1998). Both Seemu Bai and Dhira Ram describe their population as landraces despite the fact that these populations have been modified by modern-variety introgression. These two populations will be referred to as modified landraces.

Field experiments: For the field layout, the 100 full-sib progenies of each population were divided into five sets of 20 entries, and each set was arranged in a completely randomized block design with three replications, resulting in 15 experiments. Further blocking was done by arranging one set of each population in one field section, resulting in five blocks containing three randomized sets. Each plot consisted of a single row 4 m long with 25 cm between plants within the row. Spacing between rows varied among sites from 0.6 m to 0.7 m. Yield and yield components, time to flowering and various morphological traits were assessed. These traits are used by both farmers and breeders to evaluate pearl millet cultivars (Table 1). Yield and yield components were measured on a plot basis. Observations of morphological traits were taken from three to seven plants per row, depending on how many neighbouring plants were available.

Between 1998 and 1999, four field trials were conducted at two experimental stations in western Rajasthan: Rajasthan Agriculture University (RAU) at Mandor and the Central Arid Zone Research Institute (CAZRI) at Jodhpur. These four site–season combinations will be referred to as environments. Total rainfall per season varied from 285 mm at Jodhpur in 1998 to less than 120 mm at Mandor in 1999, underlining the extreme stress conditions for the field trials (Table 2). All experimental fields had sandy soils typical for the region and were regularly cultivated in rotation with legume crops. The predominant soil type at Mandor research station is Psamment, a coarse texture soil composed of 85% sand and 7% clay with a pH of 8.3. At Jodhpur, the soil mostly consisted of sand but with a higher silt content than in Mandor.

Table 1: Traits evaluated in the field trials

Trait	Unit	Explanation
Grain yield	g/m^2	Grain yield after threshing, based on plot data
Productive tillers	no./m^2	Number of productive panicles per square metre
Stover yield	g/m^2	Stover dry matter yield based on plot data
Grain weight	g	Based on two samples of 100 grains per plot
Time to flowering	day	Number of days after sowing until 50% of panicles of a plot reached flowering
Plant height	cm	Measured from stem base to the tip of the spike of main tillers, averaged across seven random plants
Panicle length	cm	Measured from the base to the tip of main tiller panicles, averaged across seven random plants
Panicle girth	cm	Diameter measured on widest part of the main tiller panicles, averaged across five random plants
Stem diameter	mm	Measured between the 3rd and 4th node of main tillers at physiological maturity, averaged across five random plants
Nodal tillering	%	Percentage of plants with nodal tillers (productive and unproductive) in relation to total number of plants per plot

Table 2: Amount of rainfall before, during and after flowering and number of weeks with rainfall exceeding 5 mm at experimental stations in Mandor (MAN) and Jodhpur (JOD) in 1998 and 1999

		Environment			
Period	Parameter	MAN98	JOD98	MAN99	JOD99
Before flowering	Rain (mm)	93.6	96.3	109.0	174.9
	Number of weeks	3	2	2	2
During flowering	Rain (mm)	4.8	4.1	—	7.4
	Number of weeks	0	0	0	1
After flowering	Rain (mm)	91.6	188.8	9.2	—
	Number of weeks	4	5	1	0
Total rainfall [mm]		190.0	285.1	118.2	182.3

Owing to severe environmental conditions, some parts of the trials completely failed or had to be excluded from the analysis because of large gaps between plots and plants, i.e. they were not representative. This was especially the case at Jodhpur in both years. The proportion of excluded plots in all four trials amounted to approximately 10% for population RR, 20% for DR and 30% for SB.

Statistical analysis: Data from the field trials differed markedly in environmental means, while residual variance and means were often positively correlated. Therefore, data for number of productive tillers, grain weight, stover yield, grain yield and time to flowering were transformed to a logarithmic scale. Population means were back-transformed for the purposes of illustration, as suggested by Sokal and Rohlf (1981).

Each population was analysed separately for estimation of variance components due to entries within sets (σ^2_{ts}), for genotype × environment interactions within sets (σ^2_{tsl}) and error (σ^2_{e}) according to a linear, hierarchical random effects model. Variance components were estimated by the restricted maximum likelihood (REML) method using the PROC MIXED procedure of the program package SAS (SAS Institute Inc. 1997). F-tests were performed using the PROC GLM procedure suggested by Cheres et al. (2000). Combined analyses across populations were computed with population effects considered as fixed variables in order to test for statistical significance among population means using the Kramer–Tukey adjustment (Kramer 1956).

Estimates for populations means and variance components obtained by the REML were used in computing the coefficient of error variation (CV) and broad-sense heritability (h^2) in a given set of full-sib families. The genetic superiority of the selection fraction, G, will be used as a measure of the expected response to selection. The selection intensity for small populations was obtained from Falconer and Mackay (1996, Table B) assuming that the five best progenies are selected out of 100. To facilitate comparisons among traits, G is expressed as percentage of the population mean.

Results

Environmental conditions

All locations experienced severe drought stress, although in 1998 drought was only prevalent before flowering, as late rains caused additional productive growth after anthesis resulting in high means for nodal tillers (Table 3). For 1999, rainfall only occurred during the early growing stage and then only on some days. These harsh growing conditions led to extremely low grain yields, ranging from an average of 31.9 g/m^2 at Mandor in 1999 to 138.5 g/m^2 at Jodhpur in 1998. The more severe stress conditions of 1999 resulted in higher coefficients of error variance compared with 1998, particularly for grain yield, number of productive tillers, stover yield, grain weight, and nodal tillering (Table 4).

Population means

Population means for time to flowering and for morphological characters ranked consistently among the environments (Table 3). Grain yield population means did not differ significantly within or across environments. In the combined analysis, the typical landrace RR tended to produce the highest grain yield, whereas the modified landraces showed higher grain weights than RR. For SB, this difference was significant. The modified landrace DR achieved the highest population mean for stover yield: approximately 20% more than the landrace and 25% more than population SB. Interestingly, the modified landrace DR had plants 10 cm taller and stems 13% thicker than the typical landrace. Population DR was also significantly taller than population SB. In all environments, DR flowered one to several days later than RR and SB. Population RR had, on average, 5% more productive tillers and about twice as many nodal tillers than either of the two modified landraces.

Variance components

Estimates of genetic variances were highly significant (P = 0.01) for all traits in each of the three populations (Table 5). The two modified landraces were genetically more variable than the typical landrace. This difference was especially prominent for grain yield, grain weight, flowering, plant height, panicle girth and stem diameter. Modified landrace DR had the greatest estimates for nodal tillering, grain yield, grain weight, and panicle girth; whereas SB was most heterogeneous

Table 3: Means of 100 full-sib progenies each of three farmer populations, one typical landrace (RR) and two modified landraces (DR and SB) for yield, developmental and morphological traits in four environments and across environments

Environment[1]	Population	Grain yield[2] (g/m^2)	Productive tillers[2] (no./plot)	Stover yield[2] (g/m^2)	Grain weight[2] (g)	Flowering[2] (days)	Plant height (cm)	Panicle length (cm)	Panicle girth (cm)	Stem diameter (mm)	Nodal tillering (%)
JOD98	RR	139.3 a[3]	26.3 a	243.2 ab	6.56 a	56.7 a	133 a	19.3 a	5.86 a	7.15 a	76.2 a
	DR	145.8 a	14.7 b	258.5 b	7.88 b	62.1 b	144 b	21.3 b	7.13 b	8.54 b	27.5 b
	SB	130.6 a	16.1 b	220.3 a	7.77 b	59.1 ab	133 ab	21.5 b	7.12 b	7.88 b	34.9 b
MAN98	RR	84.4 a	17.0 a	228.2 a	5.53 a	57.4 a	124 a	19.9 a	5.93 a	8.32 a	87.8 a
	DR	91.8 a	11.4 b	275.9 a	6.49 b	61.6 b	141 b	22.2 b	7.02 b	10.14 b	53.2 b
	SB	90.9 a	11.8 b	254.7 a	6.66 b	58.6 a	137 b	22.5 b	6.96 b	9.46 b	57.1 b
JOD99	RR	65.4 a	11.9 a	99.2 a	6.40 a	48.9 a	123 a	18.6 a	6.18 a	7.26 a	14.9 a
	DR	58.3 a	6.9 a	108.3 a	6.36 a	52.1 a	131 a	20.6 b	7.37 b	9.03 b	3.0 b
	SB	67.2 a	8.3 a	102.8 a	6.67 a	49.1 a	127 a	20.1 b	7.36 b	8.32 b	3.8 b
MAN99	RR	43.2 a	8.7 a	104.7 a	4.79 a	46.2 a	124 ab	18.8 a	5.95 a	7.93 a	—
	DR	28.2 a	4.5 b	120.3 a	4.87 a	48.7 b	130 b	20.4 b	6.70 b	9.48 b	—
	SB	24.3 a	4.4 b	91.2 a	5.26 a	47.3 ab	119 a	19.8 ab	6.67 b	8.92 b	—
Across environments	RR	75.9 a	14.7 a	155.2 a	5.76 a	52.5 a	126 a	19.2 a	5.96 a	7.66 a	58.1 a
	DR	68.9 a	8.5 b	175.0 a	6.32 ab	55.9 b	137 b	21.1 b	7.04 b	9.29 b	28.6 b
	SB	66.1 a	9.0 b	150.8 a	6.51 b	53.5 a	129 ab	20.9 b	7.02 b	8.67 c	31.6 b

[1] JOD = Jodhpur; MAN = Mandor.
[2] Population means back-transformed for illustration.
[3] Population means for individual traits within environments followed by different letters are significantly different at P = 0.05.

Table 4: Coefficients of error variation (%) of 100 full-sib progenies of farmer populations, one typical landrace (RR) and two modified landraces (DR and SB), for yield, developmental and morphological traits in four environments with different amounts of rainfall during the pearl millet season. Estimates for grain yield, productive tillers, stover yield, grain weight and flowering are calculated from logarithmically transformed data

Environment[1] (rainfall, mm)	Population	Grain yield	Productive tillers	Stover yield	Grain weight	Flowering	Plant height	Panicle length	Panicle girth	Stem diameter	Nodal tillering
JOD98	RR	6.32	9.61	3.73	5.32	1.12	8.39	8.49	7.86	9.93	22.69
(285)	DR	6.53	11.14	4.52	6.19	1.38	9.60	9.66	6.73	8.77	58.32
	SB	6.85	10.89	4.53	5.24	1.61	8.84	9.03	7.58	9.77	73.72
MAN98	RR	7.94	10.38	4.41	5.65	1.06	7.79	7.27	6.41	7.87	14.69
(190)	DR	7.16	10.87	5.25	4.75	1.33	7.83	9.01	10.97	9.37	33.35
	SB	7.40	9.92	4.30	5.42	1.19	9.28	10.11	6.61	8.88	29.68
JOD99	RR	10.19	13.71	9.72	7.81	1.27	11.22	7.66	5.83	9.64	90.40
(182)	DR	14.78	19.84	10.01	9.62	1.37	11.30	8.30	7.47	9.75	211.30
	SB	9.47	12.97	8.57	7.50	1.32	12.07	10.02	6.39	9.13	170.18
MAN99	RR	10.79	13.88	15.76	6.23	1.06	6.96	12.11	6.39	6.81	—
(118)	DR	17.20	26.72	13.30	6.91	1.30	9.44	7.80	7.46	8.12	—
	SB	17.43	29.81	10.78	8.11	1.23	7.95	9.11	8.25	8.74	—

[1] JOD = Jodhpur; MAN = Mandor.

Table 5: Estimates of the genetic variance between full-sib progenies within sets (σ^2_{ts}) and their approximate standard errors, estimates of heritability (h^2) and genetic gain relative to the mean (G%), for yield, developmental and morphological traits of 100 full-sib progenies of three farmer population, one typical landrace (RR) and two modified landraces (DR and SB), combined across four environments. Estimates of genetic gains were back-transformed for easier comparison

	σ^2_{ts}			h^2			G%		
Trait	RR	DR	SB	RR	DR	SB	RR	DR	SB
Grain yield[1]	20.54** ± 6.5	60.16** ± 15.2	55.70** ± 15.2	0.53	0.65	0.62	1.62	2.16	2.21
Productive tillers[1]	37.59** ± 7.6	45.26** ± 10.1	63.41** ± 12.9	0.77	0.71	0.78	9.62	16.88	17.41
Stover yield[1]	9.27** ± 2.7	14.27** ± 4.1	30.60** ± 6.9	0.54	0.60	0.74	0.74	0.69	0.89
Grain weight[1]	3.14** ± 1.0	5.25** ± 1.4	4.79** ± 1.2	0.52	0.61	0.67	18.75	17.72	17.20
Flowering[1]	2.09** ± 0.4	4.66** ± 0.7	5.56** ± 0.8	0.93	0.93	0.94	2.08	2.04	2.17
Plant height	21.34** ± 24.9	60.83** ± 12.9	87.08** ± 17.0	0.79	0.75	0.81	9.80	9.93	13.18
Panicle length	2.18** ± 0.4	1.70** ± 0.3	3.40** ± 0.6	0.87	0.83	0.91	14.46	11.31	16.95
Panicle girth	0.15** ± 0.0	0.40** ± 0.1	0.34** ± 0.1	0.92	0.91	0.92	12.58	17.19	16.10
Stem diameter	0.28** ± 0.1	0.37** ± 0.1	0.71** ± 0.1	0.87	0.85	0.91	13.05	12.16	18.69
Nodal tillering[2]	69.70** ± 16.9	132.26** ± 29.7	67.07** ± 28.4	0.76	0.79	0.53	25.24	72.00	38.17

*, ** F-test of respective mean squares significant at P = 0.05 and P = 0.01, respectively.
[1] Logarithmically transformed estimates multiplied by 1000.
[2] Only three locations included in the analysis.

for productive tillering, stover yield, time to flowering, plant height, panicle length, and stem diameter.

Estimates of broad-sense heritability

Heritability estimates based on the standard situation of four locations and three replications, were similar for all morphological traits, mostly ranging between 0.75 and 0.92. Estimates for grain yield, productive tillers, stover yield and grain weight, as well as flowering, varied from 0.53 to 0.93 in the landrace and from 0.60 to 0.94 in the two modified landraces (Table 5). The modified landraces showed higher values than the typical landrace except for number of productive tillers.

Genetic gain

For most traits, the predicted genetic gain was highest in population SB (Table 5). Genetic gain for grain yield, stover yield and flowering were generally very low in all three populations. Estimates for grain yield across all environments were 1.62% for the RR landrace, 2.16% for population DR and 2.21% for SB. Compared with the more moderate climatic conditions of 1998, estimates under drought stress were more than twice as high for the typical landrace (2.31%) and more than four times higher for the modified landraces DR (5.02%) and SB (5.55%). Across environments, genetic gain predicted for morphological traits, as well as for number of productive tillers and grain weight exhibited high values, varying from 9.6% to 25.2% in the landrace, from 9.9% to 72.0% in population DR and from 13.2% to 38.2% in SB.

Correlations among traits

Coefficients of phenotypic correlation between grain yield and the remainder traits, as well as between stover yield and the remainder traits, were estimated for the environments that had the highest and lowest rainfall (Table 6). Grain yield was mainly associated with number of productive tillers and stover yield. Moderate correlations existed for grain weight and early flowering, plant height, panicle length and panicle girth. Most correlation coefficients increased under the extreme stress of MAN99 (see Table 6). In general, the modified landraces exhibited slightly tighter relationships than the landrace.

Table 6: Coefficients of phenotypic correlations of grain yield and stover yield to the respective remainder traits in a typical landrace (RR) and two modified landraces (DR and SB), under mild (JOD98) and severe (MAN99) drought stress conditions[1]

	JOD 98[1]			MAN 99[1]		
Trait	RR	DR	SB	RR	DR	SB
Grain yield						
Productive tillers	0.57**	0.66**	0.49**	0.81**	0.84**	0.89**
Stover yield	0.67**	0.73**	0.66**	0.37**	0.21**	0.40**
Grain weight	−0.02	0.29**	0.10	0.22**	0.43**	0.51**
Flowering	−0.24**	−0.36**	−0.06	−0.50**	−0.61**	−0.48**
Plant height	0.13*	0.27**	0.41**	0.32**	0.31**	0.49**
Panicle length	0.22**	0.20**	0.31**	0.22**	0.12	0.24**
Panicle girth	−0.01	0.09	0.18**	0.24**	0.25**	0.19**
Stem diameter	0.19**	0.22**	0.24**	0.09	0.00	−0.07
Nodal tillering	−0.06	0.26**	0.01	—	—	—
Stover yield						
Productive tillers	0.45**	0.52**	0.45**	0.28**	0.20**	0.39**
Grain weight	−0.01	0.19**	0.08	−0.04	0.04	0.14*
Flowering	−0.07	−0.09	0.09	0.07	−0.01	0.07
Plant height	0.43**	0.52**	0.58**	0.45**	0.30**	0.61**
Panicle length	0.30**	0.27**	0.36**	0.18**	0.10	0.39**
Panicle girth	0.02	0.01	0.16*	0.05	−0.06	0.06
Stem diameter	0.24**	0.32**	0.35**	0.38**	0.21**	0.30**
Nodal tillering	−0.03	0.23**	0.06	—	—	—

*, ** Significant at P = 0.05 and P = 0.01, respectively.
[1] JOD98 = Jodhpur, 1998; MAN99 = Mandor, 1999.

In all populations, stover yield was moderately associated with plant height, and number of productive tillers. The correlation with panicle length and stem diameter was much weaker. Mostly non-significant relationships existed between stover yield and grain weight, time to flowering and panicle girth. For most traits, the coefficients of correlation were higher under less severe drought conditions (JOD98).

Discussion

Effect of environment

Plant breeding programmes conducted under stress conditions are frequently considered to have lower selection gains owing to low heritabilities and small genotypic variances (Atlin and Frey 1990, Simmonds 1991, Bänziger et al. 1997). All trials in this study were carried out under drought conditions, resulting in low mean performance throughout (Table 3). Nonetheless, high coefficients of error variation occurred only under the extreme drought stress of 1999: grain yield, number of productive tillers, stover yield, grain weight, and nodal tillering were especially affected (Table 4). In all other trials, the coefficients of error variation were low for all traits. They may be underestimated, owing to the above-described exclusion of entries from the analysis. Furthermore, despite the unfavourable growing conditions in all environments, genetic variance was significant for each trait, exceeding the genotype × environment interaction variance in nearly all cases (data not shown), resulting in high heritability estimates (Table 5). Higher heritabilities under stress or low-input conditions compared with more favourable environments have also been reported in other studies (Ceccarelli 1996). The average estimate for the genetic superiority of 2% in this study lies in the range of estimates obtained by Rattunde and Witcombe (1993), who subjected six pearl millet composites to multi-locational and multi-year testing. In the present study, however, the additive component of genetic variance could not be separated from the variance among entries, which may have led to an overestimation of the genetic gain, especially for traits with a relatively high measure of dominance. Nonetheless, findings indicate that sufficient genetic variation exists in the populations tested for progeny-based selection.

Effects of farmers' seed management on performance and quantitative–genetic parameters

Populations that underwent farmer introgression and selection activities displayed increased genetic variances and higher performance in all environments, except under the most extreme stress conditions at Mandor 1999. This kind of farmer management proved to be effective only in diversifying the genetic base but not in improving the yielding potential. The higher productivity and stability of landraces in extremely stressed environments was also demonstrated with barley in Syria (Ceccarelli 1996).

The inferiority in grain yield of the modified landraces DR and SB under severe stress (MAN99) appears to support the argument of Weltzien and Witcombe (1989), Ceccarelli (1996) and vom Brocke et al. (2000) that non-landrace material has poor adaptability to severe stress conditions. In the SB population, the seed selection method of winnowing may have compounded the poor adaptability, as selection for large seed size in such a population would favour panicles with poor seed setting. Indeed, grain weight was highest in population SB (Table 3). Yet, the quite large estimated selection responses for grain yield in both modified landraces indicate that tolerance to drought stress may be improved by breeding.

In addition to grain yield, sufficient stover yield is of immense importance to the farmers of western Rajasthan, especially under drought conditions, as there is usually no other available forage (Kelley et al. 1996). Stover yield and grain yield as well as plant height are positively correlated in the three populations, which may in part reflect the unfavourable growing conditions. Presterl (T. Presterl, pers. comm.), working with landraces and modern pearl millet varieties in India, also reported a significant phenotypic correlation (r = 0.51) between grain yield and stover yield under stress conditions in Rajasthan. Under less harsh conditions in Patancheru the correlation was still positive but not significant (r = 0.21). A positive relationship facilitates the combination of grain and stover yield by selection and thus the development of pearl millet cultivars for western Rajasthan that are acceptable to farmers.

Different authors have reported that pearl millet landraces generally have higher stover yields than modern varieties (Bidinger et al. 1994, Kelley et al. 1996). In this study, the modified landrace DR was superior to the typical landrace, with the modified landrace SB being largely equivalent. However, stover yield in the landrace RR was mainly based on extensive nodal tillering and large numbers of productive tillers. While high stover yields in the modified landraces, especially in population DR, resulted from tillers with tall and thick stems. In interviews, Dhira Ram actually expressed a preference for tall plants with long panicles. As a consequence, these traits exhibited reduced variation compared with the non-selected SB population. Under the more favourable conditions of JOD98, stover yield of Dhira Ram's modified landrace was significantly higher than Seemu Bai's. It appears that Dhira Ram had increased the growing period of his population either indirectly by accumulating plants with high stover mass or by introgressing varieties with later flowering. Depending on the environment, flowering occurred up to 6 days later in population DR than in the other two populations. This may be disadvantageous under terminal drought (van Oosterom et al. 1996). The negative correlation between grain yield and time to flowering in MAN99 stresses the significance of drought escape through earliness. As can be seen in the typical landrace of Rana Ram, early flowering is a typical attribute of western Rajasthan landraces, even under drought stress.

A characteristic of many modern varieties is their low tillering ability. Thus, introgressing MVs into landraces generally leads to a reduction of tillering, specifically nodal tillering, as can be seen by comparing the typical landrace RR with the two modified landraces. The lowest population means and the greatest genetic variance for nodal tillering were found in population DR, suggesting that Dhira Ram actually introgressed MVs with low nodal tillering. Most farmers in western Rajasthan value tillering as a mechanism of yield security because, if the panicles of the main tillers are damaged by drought, they can still expect additional yield if late rains occur (Mangat et al. 1999, Christinck et al. 2000). Dhira Ram, on the other hand, will grow wheat after pearl millet in the family's relatively fertile fields in case of sufficient soil moisture. Thus, the family favours a more synchronous maturing crop with less nodal tillering.

Usefulness of farmer-generated populations for variety development

Farmer-generated populations can be used in various ways for variety development. Populations with sufficient adaptation that require little further breeding could be directly made available to other farmers in the region. However, they would probably not be accepted by the formal variety release system of India which demands broad adaptability, as proven by ecologically broad-based multi-environment testing (Packwood et al. 1998). One option would be to release farmer-generated varieties as 'truthfully labelled' varieties (Tripp and Pal 1998). The label would state the identity of such a variety and minimum seed quality standards such as germination and moisture content. Apart from or additional to an immediate release, farmer-generated populations could be employed as base populations for participatory plant breeding programmes.

Among the three populations studied, the high genetic variances found in population SB suggest that it is best suited as a base population for a breeding programme. The farmer's introgression of MVs without regular plant selection might result in more less well-adapted material. Therefore this variances may be overestimated. Before any reasonable yield improvement in this population could be expected, it would first be necessary to perform selection and remove unadapted genotypes.

As described above, Dhira Ram employs the panicle selection method to improve the performance of his preferred traits. Rattunde et al. (1989) found mass selection on a single-plant basis to be an effective method for improving traits with high heritability, such as panicle length, plant height, tillering and seed weight. However, heritabilities based on single-plant observation for grain and stover yield may be too small to achieve adequate selection gain (Hallauer and Miranda 1981). A meaningful measure from the breeder's side would be a progeny-based selection programme to increase heritability and thus accelerate genetic gain to help improve yield under stress.

Higher basal and nodal tillering stand for high adaptation to drought stress, but also for superior food and fodder quality (Christinck et al. 2000). Farmers with small, infertile fields in particular depend on these features. As a result of the increasing use of MVs in Aagolai and elsewhere, uncontrolled introgression might lead to the loss of typical landrace characteristics. Thus, efforts should be made in formal breeding to 'improve' and maintain the local landrace resources. An appropriate *in situ* programme could maintain the allelic richness and specific adaptation of a landrace, as well as safeguard a continuing evolutionary adaptation of pearl millet to environmental and socio-economic changes. In their natural habitats, such germplasm constitutes an invaluable source of tolerance to various abiotic and biotic stresses (Hawtin et al. 1997).

In conclusion, the results of this study demonstrate that Rajasthan farmers maintain and increase diversity in their pearl millet populations through their own seed management strategies. Genetic gains can be expected for all traits studied. Farmers' seed management should be considered as a valuable pre-breeding activity yielding in ideal starting material for improving grain and forage yields in semi-arid India. Farmer participation in the selection process would ensure that farmer preferences and adaptation to their specific environmental conditions is properly addressed.

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