



Effects of farmers' seed management on performance and adaptation of pearl millet in Rajasthan, India

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Summary

Pearl millet (*Pennisetum glaucum* [L.] R.Br.) is the staple food and fodder crop of farmers in the semi-arid areas of north-west India. The majority of farmers in western Rajasthan depend on their own seed production and employ different seed production strategies that involve different levels of modern-variety introgression into landraces as well as different selection methods. This study quantifies the effects of three seed management strategies on environmental adaptation and trait performance. Forty-eight entries representing farmers' grain stocks – pure landraces or landraces with introgressed germplasm from modern varieties – as well as 33 modern varieties, multiplied by breeders or farmers, were evaluated in field trials at three different locations over two years under varying drought-stress conditions. Results indicate that the plant characteristics employed by farmers in describing adaptive value and productivity is an effective approach in discriminating the type of millet adapted to stress and non-stress conditions. It was also found that introgression of modern varieties (MVs) leads to populations with a broader adaptation ability in comparison to pure landraces or MVs alone – but only if MV introgression is practised regularly and is combined with mass panicle selection. Under high-rainfall conditions, farmer grain stocks with MV introgression show similar productivity levels as modern varieties. Under lessening rainfall, pure landraces show, in tendency, higher grain yields. In conclusion, farmers' seed management could form an integral part of participatory breeding programs.

Abbreviations: IG – introgression group; LR – pure landrace group; MG – management group; MVs – modern varieties; PPB – participatory plant breeding

Introduction

In many parts of the world, especially in those marginal regions affected by frequent and unpredictable drought, such as parts of Asia and sub-Saharan Africa, farmers still produce their own seed using their own seed management practices. To a large extent, these farmers are able to maintain and develop their traditional crops, and to adapt these crops to changing

needs and circumstances (Almekinders et al., 1994). Modern plant breeding programs so far have had limited success in developing modern varieties (MVs) that are suited to these marginal environments, and which meet the specific needs and preferences of the farmers themselves (Franzen et al., 1996). Evidence has been mounting in recent years that formal plant breeding does not generate the same benefits for farmers living in marginal areas as it does for

those living in more favourable regions (Ceccarelli, 1996). Comparative studies indicate that there are two main approaches for developing breeding strategies that would be better suited to achieving higher genetic gains in marginal environments. The first is decentralisation of the selection process, to address the need for improved adaptation to specific stress conditions (Witcombe, 1996; Ceccarelli et al., 1998). The second key issue is the systemic utilisation of locally adapted genetic material (Ceccarelli, 1994; Witcombe et al., 1996; Yadav & Weltzien, 1997; Yadav et al., 2000). It has been suggested by more than one study to combine these two approaches in a participatory plant breeding (PPB) program that would explicitly involve farmers in the variety development process (Witcombe, 1996; Witcombe et al., 1996; Ceccarelli et al., 1998; Weltzien et al., 1998). PPB strategies are being experimented within regions where formal breeding programs have largely failed (McGuire et al., 1999). In a PPB program, key stages of selection are carried out by the farmers in their own fields, which ensures decentralisation for local adaptation.

If PPB programs are to be successful, then it is necessary that scientists learn more about the farmer's own seed management strategies. Scientists must be able to determine whether these strategies are indeed effective. Up until now very few quantitative studies have examined the potential and effectiveness of farmers' seed selection strategies. Louette & Smale (2000), studying traditional maize varieties in Mexico, concluded that farmer selection of ear characteristics was an effective method for maintaining the variety ideotype of various maize landraces, as well as favouring more productive genotypes. Ceccarelli et al. (2000) have shown that farmer selection in segregating generations of barley in Syria is a successful strategy for increasing yield performance. However, another similar study carried out by Soleri et al. (2000) on maize selection in Oaxaca, Mexico, did not reveal significant response.

Rajasthan seed management systems

Rajasthan is a semi-arid state in the north-west of India. It was chosen for the present project on account of its harsh climatic conditions and its complex social hierarchy. Pearl millet (*Pennisetum glaucum* [L.] R.Br.) represents the staple food and fodder crop of Rajasthan. In the dry, western part of Rajasthan, which fringes the Thar Desert, farmers prefer to grow adapted, traditional landraces of pearl millet (Weltzien &

Witcombe, 1989; Yadav et al., 2000). Kelley et al. (1996) argue that modern pearl millet varieties have a low adoption by farmers in this region because of the MV's poor grain and fodder yield under severe drought stress. Despite the known risks of MVs under harsh climatic conditions, farmers are attracted by the possibilities of higher yield potential under more favourable conditions (Dhamotharan et al., 1997; Weltzien et al., 1998). In order to avoid crop failure in the event of drought, many farmers in western Rajasthan mix only small quantities of modern variety seed into their own landrace seed grain. These farmers who purchase and mix-in modern varieties usually have access to wells, or have more fertile fields, or are confident it will be a favourable season. Because pearl millet is an open-pollinated crop, this practice leads to introgression of modern-variety germplasm into landraces and, therefore, diversification of the farmers' pearl millet crop. We will refer to this mixing practice as 'introgression of MVs'. Some farmers select seed from these diversified landraces. Few farmers select plants from the field. It is more usual to select panicles from the threshing ground (Christinck, 2002). Different members of the farming family inspect the panicles together and select for certain characteristics considered to be important under diverse biotic and abiotic stress situations or for the nutritional qualities of grain and stover. Grain from panicles that show the preferred traits is chosen as seed grain and stored separately. The remaining grain will be used as food. This selection procedure is often carried out by women. We will refer to it as 'panicle selection' in this study. Another selection method is winnowing. This entails the cleaning and separation of bolder, heavier grain for seed purposes (Weltzien et al., 1998). Winnowing is generally carried out after harvest in order to separate husk from grain. Farmers who use food grain for sowing, or who grade their stored seed before sowing, also employ the winnowing method.

Farmers' selection criteria

Farmers in Rajasthan generally divide pearl millet into two categories: local landraces ('desi') and modern varieties ('sankar') (Dhamotharan et al., 1997; Tripp & Pal, 1998). Farmers use morphological and developmental characteristics (e.g. tillering habit, panicle, leaf and grain size, stem diameter, and flowering date) to differentiate pearl millet varieties (Dhamotharan et al., 1997; Christinck et al., 2000). Certain plant types are associated with adaptive abilities under specific

growing conditions. Christinck et al. (2000) showed that plants that show high basal and nodal tillering are considered to indicate high quality fodder and the ability to grow under low-input and harsh environmental conditions. On the other hand, low basal and nodal tillering, thick stems with broad leaves, and large panicles are considered to indicate susceptibility to drought stress and low soil fertility. This latter plant type, however, is considered superior under favourable conditions (Christinck et al., 2000). Other farmers in different parts of Rajasthan also use similar classification systems for judging plant types (Christinck, 2002).

The present study was initiated in order to quantify the effects of farmers' seed management on adaptation and performance of important traits under various stress conditions, with the specific aim of testing the effectiveness of farmers' selection methods and determining the validity of traits as selection criteria.

Materials and methods

Genetic materials

In this study, the term 'modern variety' (MV) describes a pearl millet cultivar which was developed in a breeding program on-station without farmer participation. The term is used for open-pollinated varieties as well as hybrids. 'Grain stock' refers to grain from a farmer's pearl millet crop. If the farmer selects grain for sowing, it is referred to as 'seed grain'. The remaining grain stock will be used as 'food grain'. If the farmer does not perform selection, the grain stock is referred to as 'unselected'.

Pearl millet grain stock samples were collected from four villages in Rajasthan between 1995 and 1997: 48 grain stocks from Kichiyasar (Bikaner district) and Aagolai (Jodhpur district) in western Rajasthan and 21 grain stocks from Nunwa and Udaipur Khurd (Ajmer district) in central Rajasthan. The grain stocks from western Rajasthan comprised mostly landraces adapted to sandy soils and erratic monsoon rains. Farmers from the Ajmer district in central Rajasthan, however, grow mainly the modern variety RCB-IC 911, or composites of the other modern varieties capable of producing high grain yield in better environments. These varieties were distributed to the farmers during earlier research activities of ICRISAT (Weltzien et al., 1998). During these on-farm research activities, farmers were instructed how to facilitate

seed multiplication of a specific variety. This instruction included the distribution of pamphlets illustrating how to select for typical panicles for seed purpose which are found in the centre of the field (E. Weltzien, personal communication). In addition to these farmers' grain stocks, the study also included 12 modern varieties, provided by the ICRISAT pearl millet breeding program and which had been used by farmers in the aforementioned villages in previous on-farm trials (Table 1) (Weltzien et al., 1998). A detailed documentation of these 12 modern varieties is given by Yadav & Weltzien (1998). The 12 MVs and the 21 farmer-multiplied modern varieties (MVF) from central Rajasthan will be treated as modern variety controls in the present study.

Choice of farmers

Eleven families from Aagolai and Kichiyasar provided samples of their pearl millet grain stocks for the experiment. These families represented different socio-economic standings e.g. caste, landholding. Further details about the farming systems of these villages are given by Van Oosterom et al. (1996) and Weltzien et al. (1998). Special emphasis was placed on choosing farmers who had participated in earlier studies, as these farmers had since introgressed the MVs distributed during the last project. Additionally, two farmer families who did not participate in previous trials were also chosen for the reason that they had never consciously introgressed MVs. In general, farmers were chosen on the basis of their reputation for diligent seed management. All participating farmers donated seed and food grain samples or unselected grain samples over three consecutive years between 1994 and 1996. 'Village investigators' who had also participated in these on-farm research activities, assisted in contacting these farmers and choosing new participants.

Classifying farmer households and their seed management strategies

The farmers provided important information on seed management practices e.g. whether introgression of MVs is practised and which selection methods they use. They also gave specific information on their grain stock sample e.g. whether it was food or seed grain, pure landrace or introgressed. These data were combined with other seed management data gathered during previous studies (Weltzien et al., 1998) to form

Table 1. Description of genetic materials examined in this study

Categories	Region of origin	Abbreviation	Grain stock characterisation	Farmers' seed management	Number of stocks		
					Seed	Food	Unselected
Management group	Western Rajasthan	LR	Pure landraces	Winnowing	3	3	8
		IG1	Landraces with occasional introgression of modern varieties	Winnowing	6	6	7
		IG2	Landraces with frequent introgression of modern varieties	Panicle selection	6	6	3
Farmer-multiplied modern variety group	Central Rajasthan	MVF	Farmer-multiplied RCB-IC 911, farmer-generated modern variety composites	Seed multiplied by farmers	21		
Modern variety group	ICRISAT genebank	MV ^a	HHB67 (68), ICMH 356 (69), ICMH 90852 (70), CZ-IC 912 (71), ERajPop C0 (72), RCB-IC 911 (73), IVMV 155 (74), RCB-IC 924 (75), CZ-IC 922 (76), FCB-IC 846 (77), RCB-IC 956 (78), CZ-IC 923 (79)	Released or experimental varieties	12		

^a In brackets entry number.

a scheme for grouping farmers according to their seed management strategies (Table 1).

Three management groups were established for the villages in western Rajasthan: (1) farmers who grow and maintain pure landraces (LR) only, and who prefer a winnowing method for separating seed and food grain; (2) farmers who occasionally introgress modern varieties (IG1), and who also follow the winnowing method when selecting seed grain; (3) farmers who frequently introgress MVs into their own seed stock (IG2), and who mostly practise 'panicle selection' in separating seed from food grain (see Table 1).

Evaluation of field performance

The 48 grain stock samples collected from farmers, plus the 33 modern variety controls, were evaluated in five field trials in western and central Rajasthan during the monsoon seasons of 1997 and 1998. These trials took place at three locations: the Central Arid Zone Research Institute (CAZRI) at Jodhpur (JOD97, JOD98), the Rajasthan Agriculture University Research Station (RAU) at Mandor (MAN97, MAN98), and the CAZRI regional research station at Pali (PAL97). Total seasonal rainfall varied from 478 mm at Pali in 1997 to 190 mm at Mandor in 1998 (Table 2). The 1998 Pali trial had to be abandoned due to severe drought conditions that year.

Based on the amount and distribution of precipitation, PAL97, JOD97 and MAN97 will be referred

to as high-rainfall environments, in which most of the total rainfall occurred before flowering. MAN98 and JOD98 will be referred to as low-rainfall environments, which had more or equal amounts of rainfall after flowering than before the flowering period. Experimental sites are named in short – low and high-rainfall environments or conditions – in the text and the tables of the manuscript.

Each field trial was laid out in a 9 × 9 lattice design with five replications and two-row plots of 4 m length. Row spacing differed among sites from 0.6 m to 0.7 m. 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, and low water-holding capacity (M.C. Bohra, personal communication). While similar Psamment soils are found at Jodhpur, the Pali soils are grey-brown and loamy in texture (Chouhan, 1993). For each trial, 18 kg N ha⁻¹, 46 kg P₂O₅ ha⁻¹ and 43 kg K₂O ha⁻¹ were applied before sowing. Depending on rainfall, either one or two side dressings of 15-20 kg N ha⁻¹ were applied prior to the booting stage. Weeding was carried out either by hand or with the use of a tractor-drawn cultivator. Field observations focused on plant characteristics that are generally used by both farmers and scientists to evaluate pearl millet (Table 3).

Table 2. Description of rainfall situation and amount of seasonal rainfall (mm) before (BF), during (DF) and after (AF) flowering period at experimental stations at Mandor (MAN), Jodhpur (JOD) and Pali (PAL) in 1997 and 1998

Description of rainfall situation		Environment				
		High rainfall			Low rainfall	
Period	Parameter	MAN97	JOD97	PAL97	MAN98	JOD98
BF	Rain [mm]	250.0	253.1	432.5	93.6	96.3
DF	Rain [mm]	67.0	41.0	12.5	4.8	4.1
AF	Rain [mm]	36.4	47.7	33.3	91.6	188.8
Total seasonal rainfall [mm]		353.4	341.8	478.3	190.0	285.1

Table 3. Traits assessed in field trials

Yield and yield traits	Unit	Explanation
Grain yield	g m ⁻²	Grain yield after threshing, based on plot data
1000-grain weight	g	Weight of 1000 grains, based on two samples of 100 grains per plot
Productive tillers	No. m ⁻²	Number of productive panicles per square meter
Harvest index	%	Grain yield in relation to total above-ground biomass per plot
Threshing percentage	%	Grain yield in relation to panicle yield per plot
Stover yield	g m ⁻²	Stover dry matter yield based on plot data
Plant-type characteristics		
Time to flowering	d	Days after sowing until 50% of panicles of a plot reached flowering
Nodal tillering	%	Percentage of plants with nodal tillers (productive and unproductive) in relation to total number of plants per plot
Stem diameter	mm	Measured between the 3 rd and 4 th node of main tillers at physiological maturity, averaged across five random plants
Diversity	1-7 score	Visual variability of plant types; (1 = uniform, 7 = extremely heterogeneous)
Plant height	cm	Measured from stem base to the tip of the spike of main tiller, averaged across 10 random plants
Panicle girth	cm	Diameter measured on widest part of the main tiller panicle, averaged across five random plants
Panicle length	cm	Measured from the base to the tip of main tiller panicle, averaged across 10 random plants
Leaf length	cm	Measured from leaf base to tip of 3 rd leaf downwards from flag leaf, averaged across five random plants
Leaf width	cm	Measured on the widest part of the 3 rd leaf downwards from flag leaf, averaged across five random plants

Statistical analysis

Since it was found that entry and environmental effects were related in a multiplicative manner, as indicated by Tukey's test for non-additivity (Tukey, 1949), the following traits were transformed to a logarithmic scale [$Y' = \ln(Y+1)$]: grain yield, dry matter yield, number of productive tillers, 1000-grain weight, days to flowering, leaf width, stem diameter, nodal tillering, plant height, and panicle girth. Transformed data were used for computing variances and other second-degree statistics, whereas environmental and group means

were calculated from the original (non-transformed) data.

Analyses of variance (ANOVA) for the five individual test environments were performed according to the underlying lattice design. Extreme outliers were declared missing values as defined by Anscombe & Tukey (1963). Estimation of components of variances for environment, entry and entry \times environment interaction was based on an analysis of variance of lattice-adjusted entry means by assuming a random model. The pooled error variance was calculated according to Cochran & Cox (1957). The single experiment ana-

lyses were based on all 81 entries, whereas all further computations were performed with 80 entries, as it was not possible to clearly identify the origin of one particular grain stock. All calculations were performed by the computer program PLABSTAT (Utz, 1993).

Principal-component (PC) analysis was computed on the correlation matrix for 14 traits (excluding grain yield) (Table 3). Eigenvalues and corresponding eigenvectors were computed from the correlation matrix which was calculated from the entry means across environments. The Statistical Analysis System (SAS) procedure PRINCOM was employed for these calculations (SAS, 1997). Entries were plotted according to their scores of the first and second principal-component.

Pattern analysis using the software package GEBEI (Watson et al., 1996) was applied to the environment-standardised (Fox & Rosielle, 1982) grain yield matrix of entry means. The ordination-derived biplot provides a graphical representation of the entry \times environment interaction as well as of the relation between entries and between environments (Kempton, 1984). Angles between environment vectors can be used for interpreting the similarity between environments. Environments with small angles discriminate genotypes in a similar fashion, while those with large angles (approaching 180°) discriminate in an almost opposite fashion. Environments with angles of 90° show no correspondence in ranking. The position and perpendicular projection of entry points onto an environmental vector can be used to characterise the entry's adaptability. Entries plotted in the positive direction of an environmental vector are specifically adapted to this environment. The contrary holds for entries plotted in the opposite direction. Entries found close to the origin of the environment vectors tend to show an average performance across all environments (Basford et al., 1996).

The SAS procedure PROC GLM was used for the combined ANOVAs of management groups (MG). Adjusted entry means were used as input data. The model contained fixed effects for the MG groups and the environments, and random effects for entries. Multiple comparisons among entry means were performed separately for high and low-rainfall environment groups by the SAS procedure PROC MIXED, command LSMEANS, using the Kramer-Tukey adjustment for unbalanced data (Kramer, 1956).

Results

Quality of field trials

Environmental means for yield traits and plant-type characteristics varied over a wide range according to amount and distribution of rainfall (Table 4). The effect of drought was strongest in MAN98 with a 73% reduction of grain yield compared to MAN97. The highest straw yields were observed in MAN97 and JOD98. Harvest index did not differ markedly among environments, except in the most drought-affected environment (MAN89), where a significant reduction occurred. Flowering occurred earliest in PAL97. The longest vegetative growing period was noted for MAN98. Nodal tillering ability was highest in MAN98 and JOD98 where drought spells occurred before flowering and grain filling period. At these locations, between 40 to 60% of the plants developed nodal tillers. Mean values of nodal tillering in environments with high-rainfall conditions (MAN97, PAL97) amounted to only 14%.

The combined ANOVAs revealed significant differences among entries for all traits except grain yield (data not presented). Differences among entries was the main source of variance for diversity score, stem diameter, panicle girth, and leaf width. Significant genotype \times environment interactions were observed for all traits except stem diameter.

Covariation pattern of yield and plant-type traits

Phenotypic relationships of grain yield to yield traits and plant-type characteristics strongly depended on the distribution and amount of rainfall in the individual test environments (Table 5). Nodal tillering, number of productive tillers and diversity score were all positively associated with grain yield in the low-rainfall environments and negatively in the high-rainfall environments. In contrast, stem diameter, leaf width, panicle girth, and 1000-grain weight, had negative correlation coefficients with grain yield under low-rainfall conditions and positive coefficients under high-rainfall.

The first and second principal components collectively explained 81% of the multivariate variation among entries (Figure 1). Each PC presents a linear combination of the original values of 14 traits, excluding grain yield, with coefficients equal to the eigenvectors of the correlation matrix. The strongest (positive or negative) association with the first PC occurred for panicle girth, followed by nodal tillering

Table 4. Environmental means for yield, yield traits and plant-type characteristics

Trait ^a	Environment ^b					Overall mean
	MAN97	JOD97	PAL97	MAN98	JOD98	
Grain yield	272	118	142	73.0	232	167
1000-grain weight	8.37	8.99	7.61	5.65	7.98	7.72
Productive tillers	18.0	12.9	14.6	11.4	22.2	15.8
Harvest index	31.6	30.1	29.7	19.1	33.8	28.9
Stover yield	492	220	261	262	384	324
Flowering	46.5	49.5	46.0	58.7	56.7	51.5
Nodal tillering	14.5	– ^c	14.3	57.2	42.6	32.4
Stem diameter	11.5	9.52	9.82	9.43	10.0	10.1
Diversity	3.56	– ^c	3.77	3.61	3.71	3.67
Panicle girth	8.38	7.61	7.34	6.83	7.57	7.55
Leaf width	3.64	– ^c	3.38	3.41	3.41	3.46

^a For trait units see Table 3.

^b MAN = Mandor, JOD = Jodphur, PAL = Pali; 97, 98 = 1997 and 1998, respectively.

^c Trait not recorded.

Table 5. Coefficients of phenotypic correlations of grain yield to yield traits and plant-type characteristics in high and low-rainfall environments

TRAIT	Environment ^a				
	High rainfall			Low rainfall	
	MAN97	JOD97	PAL97	MAN98	JOD98
1000-grain weight	0.69**	0.75**	0.42**	0.08	–0.25*
Stem diameter	0.62**	0.69**	0.41**	–0.65**	–0.14
Panicle girth	0.70**	0.83**	0.42**	–0.60**	–0.24*
Leaf width	0.38**	– ^b	0.33**	–0.62**	–0.24*
Nodal tillering	–0.65**	– ^b	–0.41**	0.56**	0.27*
Diversity	–0.57**	– ^b	–0.36**	0.32**	0.11
Productive tillers	–0.54**	–0.46**	–0.41**	0.90**	0.48**

*, ** Significant at $p = 0.05$ and $p = 0.01$, respectively.

^a For abbreviations of environments see Table 4.

^b Trait not recorded.

and number of productive tillers, stem diameter, leaf width, and 1000-grain weight (Table 6). Differentiation in these traits was therefore a primary source of overall variation. The highest eigenvectors for the second PC were plant height and panicle length followed by time to flowering and straw yield (Table 6). Management groups LR, IG1 and IG2 were distinct from the MV and MVF controls (Figure 1). Entries of management groups formed two clusters with considerable overlaps. The first contained mainly entries of LR and IG1 with low scores for PC1 and medium ones for PC2; the second, mainly entries of IG2, displayed low scores for PC1 and moderate to high ones for PC2. Entries selected as seed grain within IG2 tend to have higher PC1 values than the food grain entries (data not presented). MVs are mainly found on the right-hand

side of the plot (high PC1 values and variable PC2 values). Modern varieties or farmer-multiplied MVs that displayed lower values for PC1 contained western Rajasthan landrace material in their pedigree or were broad based composites.

Specific environmental adaptation

The first two components of the biplot derived from pattern analysis explained 50% and 23% of the total entry \times environment interaction variance, respectively (Figure 2). Environments with opposite rainfall situations (MAN98 and JOD98 versus MAN97, JOD97 and PAL97) were mainly separated by component1. Component1 values were highly correlated with panicle girth ($r = 0.81$ $p < 0.01$), 1000-grain weight ($r =$

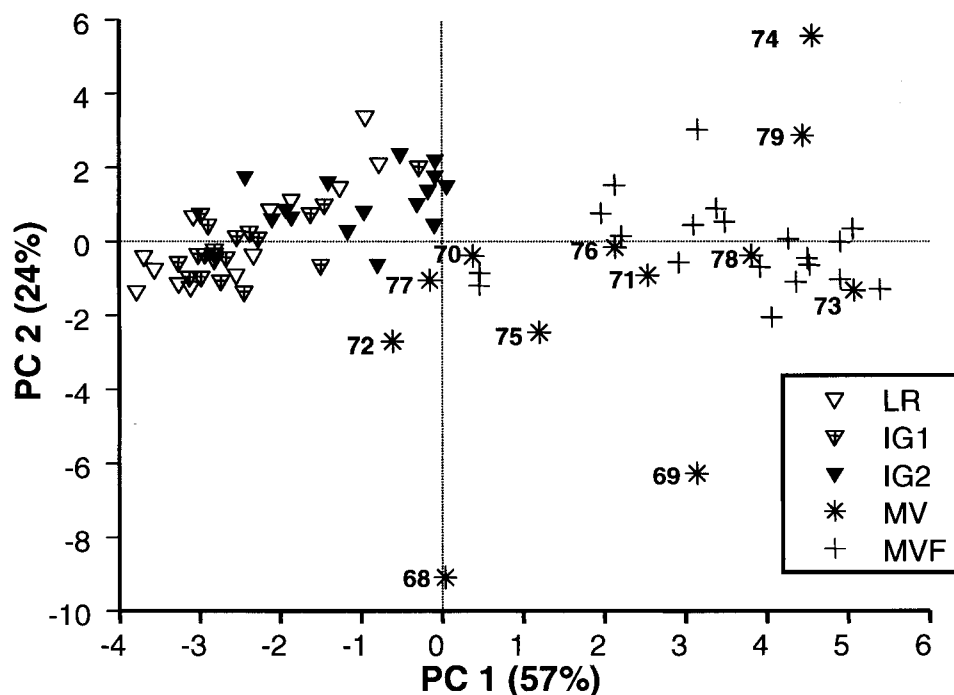


Figure 1. Scores of 80 pearl millet entries for principal components PC1 and PC2 calculated from the correlation matrix of entry means for five yield traits (excluding grain yield) and nine plant-type characteristics. For abbreviations of entry-groups see text. Symbols with numbers identify breeder-multiplied modern varieties.

Table 6. Eigenvectors of five yield traits and nine plant-type characteristics that were jointly analysed

Trait	PC1	PC2
1000-grain weight	0.31	-0.10
Productive tillers	-0.34	-0.05
Harvest index	0.26	-0.32
Threshing percentage	0.19	-0.18
Stover yield	-0.23	0.35
Time to flowering	0.18	0.35
Nodal tillering	-0.34	0.02
Stem diameter	0.33	0.17
Diversity score	-0.26	0.25
Panicle girth	0.35	-0.05
Leaf length	0.24	0.30
Plant height	-0.11	0.49
Panicle length	0.16	0.40
Leaf width	0.32	0.17

0.73 $p < 0.01$), leaf width ($r = 0.69$ $p < 0.01$), and stem diameter ($r = 0.60$ $p < 0.01$). Negative correlations occurred for nodal tillering ($r = -0.62$ $p < 0.01$) and diversity score ($r = -0.50$ $p < 0.01$). The second component, which accounts for 23% of the GE interaction, was moderately correlated with grain yield ($r = 0.47$, $p < 0.01$).

Most of the LR and IG1 entries showed positive interactions with the low-rainfall environments MAN98 and JOD98, as indicated by the proximity of their position points to the component1/component2 values of these environment. Entries classified in IG1 displayed a slightly wider dispersion in the positive direction of component2 than LR and IG2 entries. Compared to groups LR and IG1, the entries IG2 are positioned closer to the origin of the biplot between the space spanned by environment vectors of MAN98 and PAL97. Modern varieties as well as farmer-multiplied MVs were generally associated with the high-rainfall environments MAN97, PAL97 and JOD97. An exception was cultivar 70, which contained landrace germplasm from western Rajasthan in its pedigree.

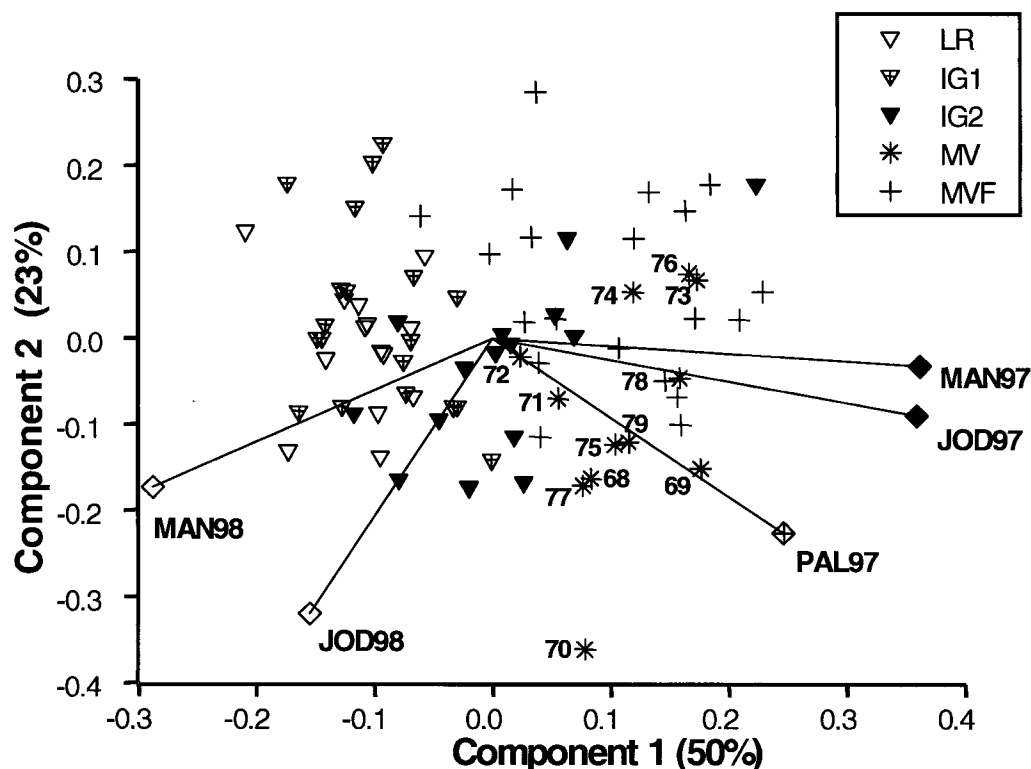


Figure 2. Biplot displaying principal components 1 and 2 obtained by ordination techniques from environmental standardised grain yields of 80 pearl millet entries. For abbreviations of entry-groups see text. Symbols with numbers identify breeder-multiplied modern varieties (MAN = Mandor, JOD = Jodhpur, PAL = Pali).

Table 7. Mean squares due to seed management groups (MG), entries within management groups (T:MG) and the corresponding interactions with environments (E) for yield, yield traits and plant-type characteristics

Trait	Source of variation			
	MG	T:MG	E × MG	E × T:MG
Grain yield ^b	143	20.1	118**	19.0**
1000-grain weight ^b	120**	4.56**	5.99**	1.51
Productive tillers ^b	288**	51.2**	32.1*	13.3
Harvest index ^b	38.7**	6.41	34.3**	6.56**
Stover yield ^b	3.86	19.5*	17.5	11.6
Flowering ^b	0.55	1.99**	1.41**	0.40
Nodal tillering ^a	370**	16.7**	30.1**	46.9
Stem diameter ^b	98.1**	7.26**	1.79	1.26
Diversity ^b	265*	33.4**	33.2**	7.60**
Panicle girth ^b	172**	72.3**	28.2**	1.25**
Leaf width ^a	147**	9.42**	2.04	34.0

*, ** F-test significant at $p = 0.05$ and $p = 0.01$, respectively.

^{a,b} Estimate multiplied by 100 and 1000, respectively.

Effects of seed management on performance

No significant differences or trends were found between the grain stocks of the management groups sampled in the different seasons (1995, 1996 and 1997, data not shown). Mean squares for variation between the management groups LR, IG1, IG2 were significant for all traits apart from grain yield, stover yield and time to flowering (Table 7). Variation of entries within management groups was significant for all traits except grain yield and harvest index. Stover yield and stem diameter were the only traits that did not show significant environment × management group interactions. Food grain was excluded from these calculations.

Groups LR and IG1 performed similarly in both the low and high-rainfall environments (Table 8). Grain yield, 1000-grain weight, productive tillers, and harvest index of groups MV and MVF were significantly higher than groups LR and IG1 in the high-rainfall environments, but groups MV and MVF

Table 8. Means of seed management (LR, IG1, IG2), modern variety (MV) and farmer-multiplied modern variety (MVF) groups for yield, yield traits and plant-type characteristics, averaged across three high-rainfall and two low-rainfall environments

Trait ^a	High-rainfall environment					Low-rainfall environment				
	LR	IG1	IG2	MV	MVF	LR	IG1	IG2	MV	MVF
Grain yield	153a ^b	155a	186ab	210b	203ab	170a	155a	148a	158a	132a
1000-grain weight	7.49a	7.70a	8.46b	9.01b	9.62b	6.44a	6.59a	6.99a	7.02a	7.37a
Productive tillers	17.4a	17.2a	15.6a	13.4b	11.3b	23.0a	20.3a	17.1a	12.7b	9.60b
Harvest index	26.8a	27.2a	29.9b	35.2c	34.8bc	26.2a	25.4a	24.8a	28.8a	27.7a
Stover yield	340a	343a	356a	301a	297a	370a	351a	348a	282b	252bc
Flowering	47.5a	47.4a	46.9a	46.3a	47.6a	55.8a	56.3a	57.4a	57.4a	61.3a
Nodal tillering	25.6a	23.4a	12.7b	3.8c	2.2c	76.2a	70.9a	57.4a	26.4b	13.3b
Stem diameter	9.42a	9.46a	10.3b	10.8b	11.7b	9.05a	8.96a	9.66a	10.2a	11.0a
Diversity	4.44a	4.66a	4.89a	1.96b	2.28b	3.89a	4.54a	5.32a	2.00b	2.47b
Panicle girth	6.73a	6.74a	7.66b	8.71b	9.55c	6.30a	6.34a	6.92a	8.09b	8.78b
Leaf width	3.16a	3.24ab	3.52bc	3.64c	4.07c	3.07a	3.11a	3.44ab	3.60b	3.97b

^a For trait units see Table 3.

^b Group means for individual traits followed by the same letter are not significantly different at $p = 0.05$.

tended to be lower yielding in the low-rainfall environments. The groups LR, IG1 and IG2, representing farmer-managed seed stocks, all furnished higher stover yields than the groups MV and MVF across all environments. This superiority was greater under low-rainfall than under high-rainfall conditions. In regard to plant-type characteristics, groups LR and IG1 differed significantly from groups MV and MVF. For instance, LR and IG1 developed three to six-times more nodal tillers, while the leaves were consistently narrower (Table 8). In the high-rainfall environments, group IG2 differed significantly from groups MV and MVF in having 16% to 40% more productive tillers, two to four-times more nodal tillering, a much higher diversity score but a lower harvest index. Under low rainfall the harvest index of the two groups was similar, while IG2 produced significantly more stover and smaller panicles than MV and MVF.

Comparisons among the three seed-management groups LR, IG1 and IG2 revealed significant changes in plant-type characteristics (data not shown) associated with the amount of introgression of modern varieties. These differences were more prominent under low rainfall. The most distinct introgression effects were: increases in panicle girth, leaf width, phenotypic diversity, and decreasing nodal tillering (Table 8).

Under high-rainfall conditions, groups LR and IG1 had the lowest grain yield, whereas the reverse was observed under low-rainfall conditions. However, none of these differences reached significance. Significant seed management effects for yield traits were

Table 9. Relative performance [%] of seed grain compared to food grain stocks within different seed management groups (LR, IG1, IG2) under high-rainfall (HI) and low-rainfall (LO) conditions

Trait	LR		IG1		IG2	
	HI	LO	HI	LO	HI	LO
Grain yield	98	110	106	103	111	93
1000-grain weight	101	103	104	105	107 ⁺	113
Productive tillers	89	108	92	89	94	88
Harvest index	96	102	103	102	106*	100
Stover yield	103	107	102	100	102	95
Flowering	101	100	101	102*	98	102
Nodal tillering	86	96	93	94	58*	87
Stem diameter	101	102	103	102	101	102
Diversity	98	100	102	115	90	98
Panicle girth	105	98	103	102	107*	105
Leaf width	103	100	106*	103	103	103

⁺, * Performance of seed grain significantly different from food grain at $p = 0.1$ and $p = 0.05$, respectively.

noted for 1000-grain weight and harvest index under high-rainfall conditions (Table 8).

Selection effects should show up in the comparisons between seed and food grain within management groups. Only those entries that were clearly declared as seed grain or food grain by the farmer who provided the seed over three consecutive years (1994–1996) were included in the analysis. In the low-rainfall environments, the LR group tended to have higher grain yield performance in seed grain compared to food grain (Table 9). In groups IG1 and

IG2, on the other hand, yields of the seed grain were, in tendency, less than in the LR group under low rainfall. Grain weight and harvest index were significantly ($p < 0.1$) affected by panicle selection in the high-rainfall environments.

Significant selection effects on the plant-type characteristics occurred only in groups IG1 and IG2. Seed grain stocks of IG1 showed significantly broader leaves under high-rainfall conditions and delayed flowering under low rainfall compared to food grain stocks. Nodal tillering was significantly reduced and panicle girth increased by farmers' selection under high-rainfall.

Discussion

Developmental plasticity

Optimal plant growth and high mean grain and stover yield was recorded at Mandor in 1997. In this year the site experienced sufficient and evenly distributed rainfalls during the pre-flowering vegetative and panicle development phase (Table 2). Similarly high yield levels were recorded for Jodhpur in 1998 despite pre-flowering drought conditions with 59% less rainfall compared to Mandor 1997. The pattern analysis (Figure 2) suggests that those entries with non-synchronous tillering were usually able to take advantage of the relatively high rainfalls after flowering at Jodhpur in 1998. These entries had the advantage of a developmental plasticity, as explained by Van Oosterom et al. (1996). Mahalakshmi & Bidinger (1986) showed that grain-yield loss of the main shoot, because of drought or other damage, can be effectively compensated by an increased number of productive tillers per plant and grains per panicle.

Association between farmers' plant type differentiation and performance

Farmers use morphological and agronomic traits – grain size, number of productive tillers, nodal tillering, stem diameter, panicle girth and leaf width – to classify pearl millet plants. These traits exert a strong discriminating effect in the analysis (Tables 5 and 6). The adaptive role of the described traits was corroborated by the pattern analysis (Figure 2). The correlation of these traits with the coefficients of the first component in the biplot also suggested that the entry-component of the interaction was strongly

associated with the aforementioned traits. These results confirm the effectiveness of the aforementioned traits in discriminating the farmers' grain stocks and modern varieties. Consequently, the special concept of classification held by farmers should be recognised as a competent selection criteria – and one that could be utilised in breeding programs for marginal regions. This finding also supports recommendations by Bidinger & Witcombe (1989) and Van Oosterom et al. (1996) that high tillering should be a selection criterion for drought avoidance. The aforementioned morphological traits should be denoted as 'key traits' for estimating productivity and adaptation, particularly in view of their contrasting correlation with grain yield under low and high-rainfall conditions (Table 5). Sperling et al. (1993), studying selection practices for bean varieties in Rwanda, reported that farmers there look for specific plant types for use under specific growing conditions, as well as plant types that can be used to increase disease resistance. Bellon & Brush (1994), working in Mexico, reported that the Chipas farmers classify their maize varieties according to morphological characteristics associated with agronomic characteristics such as performance in different soils.

Effects of introgression

The characterisation of entries by principal component and pattern analysis demonstrates that farmers in western Rajasthan produce grain stocks specifically adapted to drought conditions. Strong entry \times environment interactions confirmed farmers' perception that modern varieties are not adapted to the stress conditions of western Rajasthan. This may be due to these MVs being developed and tested at research stations under favourable growing conditions. The management strategies of farmers in western Rajasthan revolve around risk avoidance. Use of traditional landraces can ensure food supply during drought. The strategies IG1 and IG2 are specifically implemented in order to increase yield potential and to reduce the risk of total yield loss under extreme stress.

The similar behaviour of entries belonging to groups LR and IG1 (Figures 1 and 2) suggests that gene flow contamination from neighbouring fields may have occurred. Farmers, who provided LR appear to have been only partly successful in keeping their landrace stocks pure. Molecular markers could help to clarify this issue. Nevertheless, group LR excelled in stress tolerance, as judged by its highest performance

in the most severely stressed environments (Table 8). Under higher rainfall, introgression of MV germplasm into group IG1 was not sufficient enough to surpass the LR performance level, which indicates that occasional introgression of modern varieties does not offer significant advancement in regard to adaptation and productivity. Regular introgression (IG2), on the other hand, resulted in seed stock-performance which resemble improved populations or top-cross hybrids based on western Rajasthan landrace material in the biplot in Figure 2. Further, the behaviour of those entries visualised in the biplot indicates that farmers applying the IG2 method were able to reduce the entry \times environment interaction effect. Thus those entries showed more stable yield under stress conditions and a higher yield potential under high-rainfall conditions compared to the other entries. In conclusion, IG2 farmers were able to meet the objectives of their management practices: by regularly introgressing modern varieties, they were able to raise the performance level of their seed stocks under high-rainfall growing conditions. In the low-rainfall environments this same strategy produced grain yields slightly below the LR level.

It should not be overlooked that grain yield improvement is not the sole objective for Rajasthan farmers. Rather, they will forfeit part of their potential grain yield in order to meet other equally important requirements such as stover yield, grain and stover quality. Although regular introgression of modern varieties (IG2) did not affect the characteristically high stover yield levels of western Rajasthan landraces, apparently food and fodder quality decreased, as assessed by indirect plant-type indicators e.g. less tillers, thicker stems and larger leaves (Table 8). Nevertheless, group IG2 possessed a high genetic potential for quality and adaptive traits compared to modern varieties. Thus, the IG2 strategy enables farmers to enhance productivity without abandoning preferred landrace traits and to create new varietal characteristics by combining contrasting plant-types traits in the same population. The trait combinations resulting from the IG2 strategy can allow a population to adapt to favourable climatic conditions as well as to drought stress.

Effects of farmer selection

Selection effects calculated in the present study were generally small. It may be possible that effects will only become evident after observing several generations. In pure landraces, however, there was a trend

towards improved yield traits under low-rainfall conditions (Table 8), which stresses the yield stability of the landrace. The opposite trend was observed for populations introgressed by modern varieties. Farmer selection acts against wild plant-type attributes, which are solely influenced by natural selection. According to Harlan (1975), landraces are in equilibrium with both environment and pathogens. Consequently, the 'pure landrace' can be understood as a stabilised population balanced between the selection forces of fitness and adaptation on the one hand, and moderate artificial selection for productivity on the other. This balance may be invalidated by increased variance in landrace populations due to introgression of modern varieties.

Under high-rainfall conditions, combining modern variety introgression with panicle selection resulted in a significant increase in grain weight and panicle girth as well as a significant reduction of nodal tillering (Table 8). Farmers described these characteristics as key indicators of high grain yield after good rains (Christinck et al., 1998; Christinck, 2002). Recent studies by Cerccarelli et al. (2000) in barley and Louette & Smale (2000) in maize support the feasibility and effectiveness of farmer selection strategies. Louette & Smale (2000) have demonstrated that direct selection for specific maize traits, such as ear characteristics, results in significant selection gain. Similarly, mass selection of pearl millet panicles can be seen as an effective method for improving grain yield, for panicle size and grain weight are highly heritable traits.

Variation within management groups

Significant genetic differences existed between entries within management groups for most of the traits (Table 7). This differences may be partly due to the fact that farmers in India live in diverse socio-economic environments and each farmer has his own personal views regarding farming practices. Additionally, the variable climatic conditions of western Rajasthan most likely support diversifying natural selection and thereby augment the genetic variation among local populations. It is widely recognised that various natural, as well as cultural, factors can lead to crop diversity within a given production system (e.g. Sperling et al., 1993; Bellon & Brush, 1994; Weltzien et al., 1996; Louette et al., 1997; Louette & Smale, 2000).

Consequences for participatory breeding in Rajasthan

Using farmers' selection criteria

Understanding how farmers classify varieties should be a prerequisite for participatory breeding. The present study shows that farmer evaluation is an effective selection criteria. Risk avoidance is their primary aim, followed by nutritional productivity and quality. The experience of farmers can help breeders to define effective selection criteria and to set breeding goals that meet the farmers' specific needs and preferences.

Supporting farmer-breeding

Although the multiple breeding objectives of farmers appear to stand in contrast to formal breeding programs, which are aimed at higher productivity across a wide range of environmental and socio-economic conditions, farmers' pearl millet populations could be enhanced substantially by directly supporting the farmers in their own seed management activities. Breeders could take on an advisory role and provide the farmer with technical information as well as germplasm that would complement local germplasm and thus broaden the genetic base for farmer-preferred traits. National breeding institutes in marginal regions are not normally in the position to carry out such programs alone, as they are usually operating on limited funds.

Farmers' participation in variety development

If farmers' needs are to be addressed in a breeding program, then it's essential that the farmers are involved in that program right from the beginning. Farmers would carry out selection in accordance to their concepts of varieties. Evaluation of materials should be organised in such a way that site-specific adaptive traits will receive adequate weights as selection criteria. This would require a large decentralised set of experimental fields representing the various growing conditions of the target region. Farmers would grow the crops and make local-selection decisions. This approach would also facilitate the participation of female farmers. Moreover, natural selection would act against poorly adapted genotypes. Samples of locally-selected populations would be collected by breeders in order to form an overall gene pool management and for improving traits that require laboratory or controlled-environment techniques.

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