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Genetic variation in drought response of landraces of pearl millet [*Pennisetum glaucum* (L.) R. Br.]

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Abstract

Crop landraces are considered as a good germplasm source for adaptation to prevalent stress conditions. In this study, 105 landraces of pearl millet [*Pennisetum glaucum* (L.) R. Br.] were evaluated under drought stress and optimum (non-stress) conditions to elucidate their response to drought and to identify the traits that are associated with drought tolerance/escape. The landraces differed significantly for flowering time, yield-contributing traits and yielding ability under stress and non-stress conditions. There was a wide range in the drought response index (–8.5 to 13.9) among the landraces and it accounted for 73% of variation in grain yield obtained under stress conditions. Yielding ability of the landraces depended upon different characters in the presence and absence of drought stress emphasising manipulations of different traits for enhancing yield under stress and non-stress conditions. Higher panicle number and greater biomass accumulation proved to be the target traits for improving grain yield under stress but not for enhancing yield under non-stress conditions. Higher individual grain mass was associated with drought escape, while higher grain number panicle^{-1} and harvest index were associated with drought tolerance. The landraces having high degree of drought tolerance have been identified for use in developing drought tolerant cultivars.

Key words : Pearl millet, landrace, drought tolerance, adaptation, stress environments

Introduction

Landraces of pearl millet (*Pennisetum glaucum* (L.) R. Br.) have evolved over many generations under natural selection in environments that include severe drought and high temperature conditions. Consequently the landraces may well possess better adaptation to stress environments than elite improved cultivars [1]. The mechanism(s) of adaptation of landraces to harsh growing conditions is, however, not clearly understood. Therefore, grain yield and its components remain major selection criteria for improving adaptation to stress environments in many millet breeding programmes [2]. However, grain yield achieved in stress environments is not necessarily a good measure of stress tolerance *per se*, as genotypic differences for yield potential and drought escape have large effects on yields under stress [3-4].

Stress tolerance is considered to be the product of many physiological and morphological characters. However, few of them have been demonstrated to be individually causally related to the expression of drought tolerance under field conditions (i.e. crop yield) and the necessary evidence to support their use as selection criteria is often lacking [5]. On the other hand, plant response to stress may provide better alternative selection criteria because whole-plant responses are more easily measured and are more likely to be related to crop performance, than are individual resistance mechanisms [6]. Thus a need exists to identify key plant responses to stress and the relationship of such responses to stress tolerance or susceptibility. Relative performance of landraces under stress and near-optimum growing conditions may help identify the whole-plant responses in landraces that provide a distinct advantage in stress environments. The present study was, therefore, undertaken to assess the magnitude of variation among landraces for stress tolerance, to identify the traits that are associated with tolerance, and to assess the possibility of using these as selection criteria to enhance the adaptation to environmental stress conditions.

Materials and methods

A total of 105 landraces from three North-Western Indian states *viz.*, Rajasthan, Gujarat and Punjab were used in this study. All the landraces and six checks, five of them repeated thrice in each replication, were evaluated in simple 11×11 lattice design with three replications at three locations, *viz.*, Central Arid Zone Research Institute, Jodhpur, Research Station of the Rajasthan Agricultural University at Fatehpur, and the CCS Haryana Agricultural University, Hisar, in 1988 and 1989 under rainfed conditions.

Each entry was sown in two rows that were spaced 50-60 cm apart. The row length was 4m. The plant-to-plant distance within a row was maintained at 15 cm. All the trials were fertilized @ 60 kg N ha^{-1} and 20 kg P ha^{-1}, to eliminate nutrient limitations to the expression of genotype potential/adaptation. Weeds were controlled by 1-2 hand weedings. Type of drought stress in each individual stress environment was determined by observing rainfall distribution, overall crop growth and days to flowering.

Data on time to flowering were recorded as number of days from sowing to appearance of stigma in the main panicle of 50% plants in a plot. Prior to harvesting total number of plants in each plot were counted. All the panicles from each plot were harvested and counted. They were sun-dried for 15 days before weighing. Panicles were threshed and grain weight recorded. Dry stover yield was recorded on plot basis. Stover and panicle weights were added to get biomass yield per plot. Harvest index was calculated as the ratio of grain yield to biomass yield and multiplied by 100, and panicle harvest index as the ratio of grain weight to panicle weight expressed in percentage. 1000-grain mass was recorded from a duplicate sample of 100 grains from bulk harvested from each replication. All data were converted to a m^{-2} basis by dividing by the net plot area (2.0 to 2.4 m^2). Number of grains $panicle^{-1}$ and grain yield $panicle^{-1}$ were derived from primary data.

Test locations were first grouped into stress and non-stress environments depending upon the intensity of drought stress and trial mean grain yield. Based on these criteria Fatehpur 1989, and Jodhpur 1988 and 1989 with the mean grain yield between 15 g m^{-2} and 89 g m^{-2} were termed as stress environments; and Fatehpur, 1988 and Hisar 1988 and 1989 with mean grain yield between 144 g m^{-2} and 182 g m^{-2} as non-stress environments. The mean grain yield of each entry in three stress environments was considered as yield under stress (Y_s) and mean grain yield in three non-stress environments as potential yield (Y_p). Drought response index (DRI) was calculated using the regression model developed by Bidinger *et al.* [7].

Analysis of variance (ANOVA) was done both across all environments and separately for stress and non-stress environments. Correlation analysis was performed to determine the pattern of association between grain yield and component traits in both stress and non-stress environments. The relative contribution of yield potential, drought escape and drought tolerance or susceptibility to measured yield under stress was quantified by multiple regressions. Checks were excluded from the analysis, as they did not represent landrace germplasm.

Results and discussion

Environments were a significant source of variation for all variables (data not presented). Environments were further partitioned into stress and non-stress environments, which differed significantly for all traits. Variation due to trial within stress and non-stress environments also remained significant.

Reduction in grain yield under stress environments was 65% (Table 1), which showed a high intensity of drought in stress environments. The decrease in grain yield under stress was due to reduced panicle number (39%) and grain yield $panicle^{-1}$ (46%). Both grain number $panicle^{-1}$ and individual grain mass contributed almost equally to the reduced yield $panicle^{-1}$. An equal reduction in grain yield and stover yield under stress conditions resulted into almost comparable harvest index in stress and non-stress conditions. Maintenance of similar harvest index by landraces under very severe stress conditions reflects their capacity to produce grain even under the most harsh conditions. This might primarily be due to their unaffected panicle harvest index under stress conditions when compared to non-stress conditions (Table 1).

Table 1. Mean (±SE) grain yield and yield components of pearl millet landraces in the stress and non-stress environments.

Variable	Stress	Non-stress	% reduction in stress
Grain yield (g m^{-2})	56.9±3.7	160.3±4.3	64.5
Panicles m^{-2} (no.)	10.6±0.6	17.3±0.6	38.7
Yield $panicle^{-1}$ (g)	5.4±0.2	9.9±0.3	46.0
Grains $panicle^{-1}$ (no.)	951.7±34.3	1350.0±47.8	29.5
1000-grain mass (g)	5.7±0.1	7.5±0.1	24.6
Biomass (g m^{-2})	339.6±15.9	954.2±19.1	64.4
Stover yield (g m^{-2})	254.5±14.5	701.5±19.2	63.7
Harvest index (%)	16.6±0.9	17.1±1.7	2.9
Panicle harvest index (%)	62.3±1.0	63.3±0.8	1.6

Landraces differed significant ($P < 0.01$) for all traits under stress as well as under non-stress environments (data not presented). The differences among individual landraces for their average yielding ability under stress and nonstress conditions were considerable: the range was from 49 g m^{-2} to 99 g m^{-2} in stress environments and from 95 g m^{-2} to 209 g m^{-2} in non-stress environments. This indicated thar landraces differed not only in their yielding ability under stress conditions but also in their potential yield. There were significant differences among landraces for their flowering time: the range was between 51 to 66 days in stress and 48 to 63 days in non-stress conditions. The differences in flowering time and yield potential (both measured in the non-stress environments) accounted for 27% of variation in yield under stress conditions. This finding is supported by the results of earlier studies in pearl millet and other crops [3, 8]. The DRI then allowed the separation of differences in yield in the stress environments due to differences in drought escape and potential yield from differences due to drought tolerance. The DRI was highly and positively correlated to yield under stress ($r = 0.84^{***}$, $P < 0.001$) but not to yield measured in non-stress conditions ($r = -0.01$) and time to flowering ($r = 0.01$). In fact DRI is designed specifically for use in stress environments and to be independent of yield potential in optimum conditions. Hence, DRI is useful to identify landraces specifically adapted to stress environments. The relative contributions of yield potential, drought escape and drought tolerance to measured yields in the stress were determined by multiple regression of measured yield in stress on these three variables. The contribution of each was determined as the percentage of the regression sum of squares it accounted for. Yield in the absence of stress accounted for 5%, time to flowering for 22%, and DRI for 73% for yield measured in stress environments, suggesting that across variable stress environments adaptation was a greater factor in genotype performance than was either yield potential or crop duration.

There was a good range in DRI value of landraces evaluated (–8.52 to 13.9), thus demonstrating a wide range in their drought response. As many as 26 landraces had DRI value of zero, which indicated that their measured yield in stress was adequately estimated by their yield potential and flowering time, and have no specific response to drought. Thirty-seven landraces possessed positive DRI values indicating that they may well provide base genetic material for improving stress tolerance. The fifteen landraces (IP 3243, IP 3228, IP 3424, IP 3296, IP 3362, IP 3180, IP 3272, IP 3303, IP 3252, IP 3258, IP 11141, IP 3318, IP 3123, IP 3363 and IP 3244) having high DRI values were identified which can be utilized in developing millet populations that possess high degree of drought tolerance that is independent of drought escape and yield potential.

The correlation of grain yield and time to flower was significant and negative (Table 2) indicating that landraces with longer duration tended to have lower grain yield in the environments in this study. It was interesting to note that earliness was as strongly correlated to grain yield in non-stress environments as in stress environments. The relationship between phenology and grain yield depends upon the timing of stress [3, 5]. Although the growing conditions were relatively better under 'designated' non-stress environments, they did not provide an advantage to later flowering landraces.

Table 2. Correlation of component traits with grain yield in pearl millet landraces in stress and non-stress environments

Correlate	Correlation coefficient under	
	Stress	Non-stress
Time to flower	-0.41^{***}	-0.52^{***}
Biomass yield	0.53^{***}	0.40^{***}
Stover yield	0.23^{**}	0.14
Panicle m^{-2}	0.83^{***}	0.38^{***}
Yield $panicle^{-1}$	0.57^{***}	0.43^{***}
Grains $panicle^{-1}$	0.41^{**}	0.50^{***}
1000-grain mass	0.79^{***}	0.14
Harvest index	0.82^{***}	0.69^{***}
Panicle harvest index	0.59^{***}	0.55^{***}

**Significant at $P < 0.01$; ***Significant at $P < 0.001$

The relationship of grain yield and various components differed considerably in stress and non-stress conditions (Table 2). Several yield components were similarly correlated to yield in both growing conditions while some components were more strongly related to yield in stress. Panicle number and biomass were more closely related to grain yield under stress conditions than in non-stress ones (Table 2). Stover yield was only moderately associated with yield under stress but not under non-stress conditions. Individual grain mass was strongly associated with yield in stress but had no correlation under favourable environments. These observations suggest that yielding ability of landraces depends upon different characters, or the ability to maintain expression of different characters, in the presence and absence of stress, which underlines the need to manipulate different set of traits to enhance the grain yield in stress and non-stress conditions. Higher panicle number, greater biomass accumulation, and especially the ability to fill grains under stress seem to be the most important target traits for stress environments while higher grain number per panicle seemed most interesting trait for non-stress environments.

The relationship of grain yield and yield components in stress conditions were re-examined to determine if they were constitutive or adaptive. This was done by comparing the relationship of yield under stress with the yield components measured under non-stress (constitutive) and stress (adaptive) environments. Panicle m^{-2}, 1000-grain mass and harvest index measured in the non stress environments were positively correlated to yield under stress (Table 3) but degree of association was less as compared to when these traits were measured under stress conditions (Table 2). Other traits like grains $panicle^{-1}$ and panicle harvest index and drought escape were positively associated with yield under stress only when they were measured in the stress (Table 2). The reduction in degree of relationship between grain yield in stress environment and yield components when measured in non-stress rather than stress environments suggests that these traits represent the true adaptive response to stress conditions. The results concur with the earlier results [3, 9] that selection for stress tolerance, based on the correlated traits to tolerance, should be done under stress conditions.

Table 3. Correlation of traits measured in non-stress environments to pearl millet yield measured in stress environments

Character	Correlation coefficient
Time to flower	–0.02
Panicle m^{-2}	0.37***
Yield panicle^{-1}	–0.25**
Grains panicle^{-1}	–0.49***
1000-grain mass	0.29**
Harvest index	0.28**
Panicle harvest index	–0.26**

**Significant at $P < 0.01$; ***Significant at $P < 0.001$

Drought escape, stress tolerance and, to a lesser extent potential yield contributed to determining the grain yield under stress. An individual trait that was related to grain yield in the stress environment could, therefore, be a reflection of genotypic differences in their time to flowering (drought escape) or drought index (drought susceptibility/resistance). This was further investigated by correlating those traits measured in stress environments, which were related to yield in the stress, to both time to flowering and drought index (Table 4). Higher individual grain mass was clearly associated only with drought escape, while grain number per panicle and harvest index were associated with drought tolerance but not with drought escape. A higher productive panicle number was associated with both early flowering and drought response. This suggests that brought tolerance is associated with the ability to maintain both a higher panicle number and a higher grain number, and to translocate the accumulated biomass to grain.

Results of the present study clearly established that there exist wide differences among landraces for their drought tolerance that is independent of drought escape and yield potential. Hence landraces need to be evaluated for their tolerance to drought stress, as well as for their yield potential and maturity, before using them in breeding programmes to enhance the adaptation to drought. Different traits were associated with yield measured in stress and non-stress environments, which suggested manipulating different traits for enhancing yield in the presence and absence of stress. Higher panicle number should result in increased yields under stress conditions. Since this trait was primarily a result of drought escape, flowering time should be used as a selection criterion, as it is very easy to measure and has high heritability. Higher grain number per panicle was related to drought resistance but the degree of association was not strong enough to suggest as an alternate selection criterion.

Table 4. Correlation of yield and yield components in stress environments with time to flowering (drought escape) and drought response index (tolerance/susceptibility)

Character	Correlation coefficient with	
	Time to flower	Drought response index
Grain yield (g m^{-2})	–0.41***	0.84***
Panicle m^{-2} (no.)	–0.62***	0.34***
Yield panicle^{-1} (g)	0.09	0.22*
Grains panicle^{-1} (no.)	0.15	0.21*
1000-grain mass (g)	–0.44**	0.00
Harvest index (%)	–0.08	0.41***
Panicle harvest index (%)	–0.70***	0.32**

*Significant at $P < 0.05$; **Significant at $P < 0.01$; ***Significant at $P < 0.001$

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