Grain yield components of pearl millet under optimum conditions can be used to identify germplasm with adaptation to arid zones

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Abstract

There is evidence that high-tillering, small-panicled pearl millet landraces are better adapted to the severe, unpredictable drought stress of the arid zones of NW India than are low-tillering, large-panicled modern varieties, which significantly outyield the landraces under favourable conditions. In this paper, we analyse the relationship of arid zone adaptation with the expression, under optimum conditions, of yield components that determine either the potential sink size or the ability to realise this potential. The objective is to test whether selection under optimal conditions for yield components can identify germplasm with adaptation to arid zones in NW India, as this could potentially improve the efficiency of pearl millet improvement programs targeting arid zones. We use data from an evaluation of over 100 landraces from NW India, conducted for two seasons under both severely drought-stressed and favourable conditions in northwest and south India. Trial average grain yields ranged from 14 g m^{-2} to 182 g m^{-2}. The landraces were grouped into clusters, based on their phenology and yield components as measured under well-watered conditions in south India. In environments without pre-flowering drought stress, tillering type had no effect on potential sink size, but low-tillering, large-panicled landraces yielded significantly more grain, as they were better able to realise their potential sink size. By contrast, in two low-yielding arid zone environments which experienced pre-anthesis drought stress, low-tillering, large-panicled landraces yielded significantly less grain than high-tillering ones with comparable phenology, because of both a reduced potential sink size and a reduced ability to realise this potential. The results indicate that the high grain yield of low-tillering, large-panicled landraces under favourable conditions is due to improved partitioning, rather than resource capture. However, under severe stress with restricted assimilate supply, high-tillering, small-panicled landraces are better able to produce a reproductive sink than are large-panicled ones. Selection under optimum conditions for yield components representing a resource allocation pattern favouring high yield under severe drought stress, combined with a capability to increase grain yield if assimilates are available, was more effective than direct selection for grain yield in identifying germplasm adapted to arid zones. Incorporating such selection in early generations of variety testing could reduce the reliance on random stress environments. This should improve the efficiency of millet breeding programs targeting arid zones.
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1. Introduction

Pearl millet is an important dual-purpose, staple crop in the crop-livestock production systems of the arid zones of Rajasthan, NW India. Severe drought stress is a regular feature in this environment, but its timing and intensity are unpredictable (Sharma and Pareek, 1993; van Oosterom

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et al., 1996). Consequently, district average grain yields are generally <0.4 tonnes ha^{-1} (Singh, 1997). In areas where the crop is likely to experience mid-season drought stress, minimising the risk of a crop failure is more important than yield potential per se, and farmers preferentially grow landraces that produce many but small productive panicles (Kelley et al., 1996; van Oosterom et al., 1996; Dhamotharan et al., 1997; Bhatnagar et al., 1998; Christinck, 2002). A small main shoot panicle increases tiller survival under drought and minimises the delay in flowering under drought, although production of many grain-bearing basal tillers per se does not significantly increase the range of flowering within a crop (van Oosterom et al., 2003). By contrast, in the wetter areas of Rajasthan, where pre-flowering drought stress is unlikely to occur, low-tillering cultivars that have been bred for high yield potential through investment in large panicles and large grain size are widely adopted (Kelley et al., 1996; van Oosterom et al., 1996). These differences in adaptation are supported by reports of (non-significant) crossover interactions for grain yield between high-tillering landraces and improved cultivars, grown in severely drought-stressed and more favourable arid zone environments (Bidinger et al., 1994; vom Brocke et al., 2003).

Breeding for improved productivity in environments with high levels of drought stress remains a challenge for plant breeders. Genotype × environment (GE) interactions can reduce the rate of progress of crop improvement programs, particularly if they are of the crossover type (Basford and Cooper, 1998). The presence of such crossover interactions led Simmonds (1991) and Ceccarelli (1996) to conclude that adaptation to harsh environments requires in situ selection. Given the high level of unpredictability of many drought prone environments and the limited number of locations and years that can be sampled in field evaluations of segregating materials, it is unlikely that in situ selection trials can adequately sample the long-term distribution of stress patterns (Chapman et al., 2002). To the degree that direct selection for grain yield in such field trials results in selection for adaptation to the subset of environments sampled by the experiments, rather than in selection for adaptation to the long-term prevalent stress patterns, progress in the improvement of productivity across the whole spectrum of probable environments will be slowed. In contrast, selection for improved adaptation to stress should be more effectively targeted (and have reduced negative consequences for favourable environments), if knowledge of the physiological basis of adaptation could be incorporated into selection objectives. The dissection of a complex trait such as stress adaptation into simpler component traits may provide a means to do this (Richards et al., 2002), by identifying, under optimum conditions, traits that confer adaptation to stress conditions. If such underlying component traits are functionally related to grain yield under stress and show a high level of genetic variation with a low GE interaction, indirect selection for these component traits

would permit a direct linkage between the phenotypic expression of grain yield and the genetic control of its underlying component traits (Hammer et al., 2005). This should improve the efficiency of selection programs.

Grain yield in pearl millet is highly correlated with grain number (Bidinger and Raju, 2000). Final grain number in cereals is predominantly determined by the fraction of surviving florets, rather than the maximum number of floret primordia initiated (e.g. Miralles et al., 1998, for wheat), as floret number generally exceeds final grain number (Stephenson, 1981). Hence, grain number is determined during a brief period around anthesis (Saini and Westgate, 2000), when the success or failure of individual developing florets is dependant upon the growth of the non-grain part of the reproductive organ (Kirby, 1988). Grain number is therefore a function of the reproductive growth rate around flowering (Craufurd and Bidinger, 1989; Zinselmeier et al., 1999; Vega et al., 2001; van Oosterom and Hammer, 2006), when the non-grain part of the panicle (structural panicle mass, SPM) is the main reproductive sink. Consequently, strong correlations between SPM and final grain number have been observed for wheat (Fischer, 1993; Miralles et al., 1998) and sorghum (van Oosterom and Hammer, 2006). The SPM represents the amount of resources the crop has allocated as a sink for subsequent post-flowering reproductive growth in a given environment, and can thus be considered a measure of potential grain yield in that environment. As SPM m^{-2} is the product of panicle number m^{-2} and the average SPM per panicle, contrasting yield architectures (combination of tillering pattern and panicle size) can attain a similar potential sink size.

The efficiency with which the potential sink size is realised is represented by the grain yield per unit SPM, which is the product of grain number per unit SPM and individual grain mass. Grain number per unit SPM depends upon both assimilate supply during the early stages of grain development and on genetic factors. For example, a reduction in grain number per unit SPM has been observed for wheat following drought stress around anthesis (Robertson and Giunta, 1994; Demotes-Mainard et al., 1996). Genetic differences in grain number per unit SPM can result from selection for increased yield potential, or, at least in pearl millet, as an adaptive strategy to marginal environments (Bidinger and Hash, 2004). In pearl millet, a low grain number per unit SPM (in the absence of stress) represents a conservative yield strategy that permits partial replacement of grain numbers (and thus potential yield) lost to stress at flowering, by reserving some resources for the rapid production of nodal tillers (tillers produced from the upper nodes that have a very short developmental period and depend upon assimilation from the parent stem for sink development and realisation) if moisture conditions improve after flowering (van Oosterom et al., 2002; Bidinger and Hash, 2004). Finally, individual grain mass depends on the amount of assimilates available per grain (Borrás et al., 2003) and their actual translocation to the grain. The

efficiency with which the potential sink size is realised is hence determined during grain filling, when the SPM has been fixed. This separation of processes in time allows the analysis of yield potential and stress adaptation of germplasm with contrasting yield architectures in environments with variable timing of drought stress.

In this paper, we establish the presence of significant crossover GE interactions for grain yield between optimum and severely drought-stressed environments in a set of 105 pearl millet landraces, and analyse yield components to establish potential underlying physiological causes for these interactions. The objective is to determine whether selection for yield components under optimal conditions can identify germplasm with adaptation to arid zones. This should reduce the need for variety testing under random rainfall conditions, and thus improve the efficiency of millet breeding programs targeting arid zones.

2. Materials and methods

2.1. Landraces

The landraces used in this study were collected in 1977, 1978, and 1983 in the states of Rajasthan, Punjab, and Gujarat in NW India. The region is characterised by a steep west to east rainfall gradient, with long-term annual rainfall ranging from <200 mm in the west to >600 mm in the east. Landraces were collected by choosing farmer's fields for sampling at regular intervals, or whenever a different type of landrace was observed. A random sample of 5–25 panicles from one farmer's field constituted an accession, but where plants with specific traits (e.g. purple glumes or purple grains) were observed within a field, such panicles were grouped into a separate accession. A total of >1000 accessions were collected and entered into the ICRISAT and National Board for Plant Genetic Resources (NBPGR) genebanks.

From the collection of landrace accessions in the ICRISAT genebank, a subset was selected for detailed evaluation and grown for an initial evaluation in the post-rainy season of 1987 at the ICRISAT Patancheru farm. Selection was based on purity of the landrace (no contamination by non-landrace plant types), on proper classification into local landrace variety groups, and on limiting the number of accessions of several groups which were over-represented. Seed of the selected landraces was produced by sib-mating at least 50 plants per accession. This seed increase was necessary to have sufficient seed for the multi-location trial and to reduce any possible effects of inbreeding that might have occurred during previous regenerations of these accessions (carried out as part of routine genebank operations). The exact number of panicles originally collected for an accession is not known; hence, differences in the level of inbreeding between landraces cannot be ruled out completely.

2.2. Experiments

Experiments were conducted during the rainy seasons (June–September) of 1988 and 1989 in the arid zone of NW India at the Rajasthan Agricultural University in Fatehpur-Shekawati (27.28°N, 81.22°E) and the Central Arid Zone Research Institute in Jodhpur (26.30°N, 73.00°E), and under more favourable conditions in NW India at the Haryana Agricultural University in Hisar (29.02°N, 75.73°E). The experiments at Fatehpur and Jodhpur were rainfed. Those at Hisar were planted with an irrigation in each year, and the 1989 experiment received approximately 150 mm of irrigation prior to flowering because of an unusually dry season (Table 1). A second set of experiments was conducted in south India at ICRISAT in Patancheru (17.45°N, 78.47°E) during the rainy seasons of 1988 and 1989, during the dry seasons (January–April) of 1989 and 1990 under fully irrigated conditions, and during the dry seasons of 1990 and 1991 under managed post-flowering drought stress (Table 1). Irrigation at Patancheru was through overhead sprinklers for approximately the first 5 weeks after sowing, and by furrows thereafter. The four experiments conducted at Patancheru without drought stress will be referred to as the control experiments (Table 1).

At Jodhpur and Fatehpur, experiments were sown on sandy soils (Psamment) and at Hisar on a silt loam soil. Plot size was two rows of 4 m length; row spacing varied from 0.75 m at Hisar, to 0.60 m at Fatehpur and Jodhpur 1989, and 0.50 m at Jodhpur 1988. Experiments received a pre-sowing basal application of 20 kg N and 45 kg P_2O_5 ha^{-1} (100 kg ha^{-1} diammonium phosphate) and a top dressing of 22–44 kg N ha^{-1} (50–100 kg ha^{-1} urea) at Hisar, Fatehpur 1988, and Jodhpur 1989. At Patancheru, experiments were sown on a red alfisol (clayey-skeletal mixed isohyperthermic Udic Rhodustalf) on ridges 60–75 cm apart. Plot size was two rows of 4 m length. Fertiliser was applied at a rate of 42 kg N and 42 kg P_2O_5 ha^{-1} (150 kg ha^{-1} 28:28:0) before sowing, supplemented by a top dressing of 45 kg N ha^{-1} (100 kg ha^{-1} urea) at the start of rapid canopy growth. At each location, the crop was oversown and thinned to the final density (5–10 plants m^{-2}, depending on location) approximately 2 weeks after emergence. Prior to sowing at Patancheru, seeds were treated with metalaxyl (Ridomil) against downy mildew. No such treatment was done for the experiments in NW India, because of the generally low disease pressure. Weeds were controlled manually and no significant outbreak of any pest or disease occurred in any of the experiments.

The experimental layout was a 13 × 13 triple lattice design in the five experiments sown before June 1989 and a 11 × 11 triple lattice design in the seven experiments sown thereafter. Each experiment included six commercially available checks, five of which were repeated three times. Consequently, the first five experiments included 153 landraces and the last seven experiments a subset of 105 of these.

Table 1
Sowing date, latitude, mean daylength during 3 weeks after emergence, thermal time from emergence to flowering, grain yield, harvest index, plant density, mean maximum and minimum temperatures from emergence to 4 weeks after flowering, and total rainfall from 5 days prior to sowing until flowering and for the 4 weeks after flowering for each experiment

Experiment	Sowing date	Latitude	Daylength (h)	Time to flowering[a] (°C d)	Grain yield[a] (g m^{-2})	Harvest index[a]	Plant density (m^{-2})	Temp. Maximum (°C)	Temp. Minimum (°C)	Rainfall[b] Pre (mm)	Rainfall[b] Post (mm)
North India—arid zone											
Fatehpur 1988	26 June 1988	27.28	14.0	1006 (5.5)	174 (24.5)	0.17 (23.9)	10.2	34.9	27.9	284	42
Fatehpur 1989	05 July 1989	27.28	13.9	1146 (4.6)	14 (54.4)	0.09 (35.3)		35.4	24.5	110	2
Jodhpur 1988	12 July 1988	26.30	13.8	929 (7.4)	48 (50.9)	0.11 (44.9)	9.3	35.3	26.0	182	47
Jodhpur 1989	18 July 1989	26.30	13.8		133 (48.9)	0.27 (18.3)	7.2	35.4	24.0	192	7
North India—favourable											
Hisar 1988	06 July 1988	29.02	14.0	972 (3.7)	155 (24.5)	0.14 (32.0)	9.1	34.2	25.3	300	313
Hisar 1989	16 July 1989	29.02	13.9	1002 (3.5)	149 (23.4)	0.19 (20.7)	4.6	35.9	23.6	97 + 150	4
Patancheru—post-flowering drought stress											
Dry season drought stress 1990	18 January 1990	17.45	11.5	823 (3.3)	85 (21.9)	0.22 (15.8)	5.0	33.8	17.7	6 + 180	2
Dry season drought stress 1991	23 January 1991	17.45	11.6	760 (3.7)	156 (18.1)	0.22 (13.5)	8.3	34.0	19.1	4 + 200	35 + 50
Patancheru—no drought stress (control experiments)											
Rainy season 1988	28 June 1988	17.45	13.3	697 (3.4)	133 (20.3)	0.25 (12.7)	7.2	29.3	22.7	329	331
Rainy season 1989	01 July 1989	17.45	13.3	710 (3.1)	134 (26.7)	0.31 (8.2)	6.3	29.1	22.1	520	247
Dry season fully irrigated 1989	23 January 1989	17.45	11.6	743 (5.9)	139 (18.6)	0.29 (9.5)	7.0	33.3	17.2	68 + 236	8 + 250
Dry season fully irrigated 1990	18 January 1990	17.45	11.5	830 (4.4)	142 (22.2)	0.24 (13.8)	5.4	33.8	17.7	6 + 180	2 + 200

Coefficients of variation (CV) are added in parentheses.

[a] Means based on all entries in experiment. CV (in parentheses) calculated from means of individual BLUE's and residual from ANOVA.

[b] Second value is approximate amount of irrigation.

2.3. Observations

Flowering was recorded for each plot in non-stressed environments as the date when stigmas were visible on 50% of the main stem panicles. In severely stressed environments, where flowering was delayed in many plants, flowering was recorded when stigmas were visible on the main stem panicle of the first three plants. At Jodhpur in 1988, some later flowering entries did not reach 50% flowering until after a late shower during harvest and harvest date was used as 50% flowering date for these entries. Time from emergence to flowering was expressed in thermal time, using cardinal temperatures of 10 °C, 33 °C, and 47 °C for the base, optimum, and maximum temperature, respectively, and assuming linear interpolations between these temperatures (Garcia-Huidobro et al., 1982; Ong, 1983).

At maturity, panicles were cut from all plants in a plot, except in the dry season at Patancheru, where two rows of 3-m length were harvested. All panicles with filled grain were harvested, counted, and either sun dried for approximately 1 week (north India) or oven dried for at least 2 days at 80 °C (Patancheru). After weighing, panicles were threshed and grain yield per plot determined. Individual grain mass was obtained from two samples of 100 grains; a third sample was counted if the first two samples differed by more than 0.05 g. Stover dry mass was obtained from the fresh stover mass of the entire plot, and the fresh and dry mass of a chopped sub sample (800–1200 g). In north India, sub sample stover dry mass was obtained after 1–2 weeks of sun drying, followed by an overnight oven drying, whereas at Patancheru sub samples were oven dried.

2.4. Analyses

For each trait in each experiment, an analysis of variance was carried out using PROC MIXED in SAS (Version 8) with the REML method to estimate the covariance parameters. Genotypes (landraces and checks) were made fixed effects and the resulting best linear unbiased estimates (BLUE's) were used for subsequent analyses. For most analyses, only BLUE's for the 105 landraces common across all experiments were used, as the 48 landraces that were excluded in the later experiments were predominantly low-tillering late ones.

2.4.1. Clustering of landraces for phenology and yield architecture under optimum conditions

Clustering of landraces was based on time to flowering, panicle number m^{-2} (grain-bearing panicles only), structural panicle mass per panicle, grain number per unit SPM, and individual grain mass across the four control experiments at Patancheru. However, individual

grain mass (and hence grain number per unit SPM) was only measured in the two 1989 experiments. In addition, time to flowering showed small but consistent interactions between plant type and season, and only data for the rainy season were used. Because the means for individual traits differed across experiments, BLUE's for the 105 landraces for each trait in each experiment were standardised to a mean of zero and a standard deviation of one. These standardised data were averaged over experiments and again standardised.

The standardised means were used in a correlation and a clustering analysis. Clustering was conducted in SAS, using Ward's minimum variance technique (SAS, 1999). Differences between clusters for the average value of each yield component were analysed with PROC TTEST in SAS, using the pooled method for comparisons between clusters with equal variances and Satterthwaite's approximation for the calculation of effective degrees of freedom for comparisons between clusters with unequal variances.

2.4.2. Effect of clustering on grain yield across experiments

The average grain yield of each cluster in each experiment was analysed using PROC MIXED in SAS. Least square means per cluster were calculated with the LSMEANS statement, and the CONTRAST statement was used to test whether these means were significantly different for pairs of clusters. As the clustering of the landraces was based on data from only the four control experiments at Patancheru, the mean grain yields per cluster for all other experiments were independent of the input data of the cluster analysis.

3. Results and discussion

3.1. Environmental effects on grain yield

In the six experiments conducted in north India, biomass at maturity was strongly correlated with pre-flowering rainfall (Fig. 1). This indicates that insufficient rainfall per se was a major constraint to biomass production, in addition to the effects of uneven rainfall distribution on grain yield. The favourable location of Hisar received well-distributed rainfall in 1988 (Table 1). The 1989 season, by contrast, was extremely dry and the crop received several irrigations before flowering. This ensured sufficient water availability until at least early grain filling. In the arid zones, Fatehpur 1988 received well-distributed rainfall until early grain filling (Table 1) and drought stress was unlikely to have developed until well into grain filling. In 1989, however, Fatehpur experienced severe pre- and post-flowering drought stress. The two experiments at Jodhpur received similar total rainfall, but with different distribution, as 1988 experienced a dry period and high evaporation rates around flowering (data not shown).
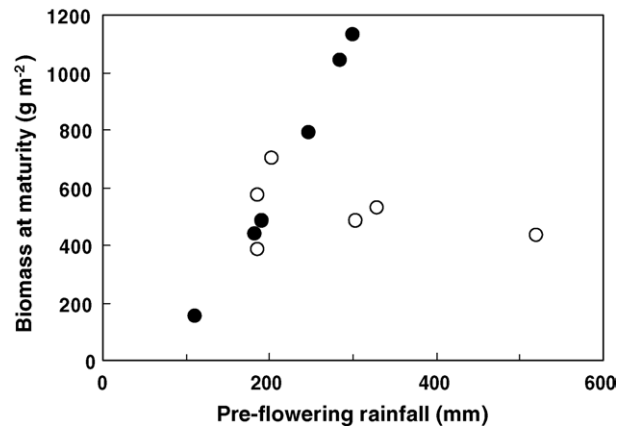

Fig. 1. Above ground biomass at maturity as a function of pre-flowering rainfall for experiments conducted in north (●) and south (○) India.

At Patancheru, biomass at maturity was not related to pre-flowering rainfall (Fig. 1), confirming that in all but the terminal stress environments, biomass accumulation was not limited by rainfall. The lower biomass at Patancheru compared to north India (Table 1) was a consequence of the shorter daylength which accelerates phenology (van Oosterom et al., 2001). Mean temperatures at Patancheru were similar in the rainy season and dry season experiments, but the dry season had a wider daily temperature amplitude (Table 1).

3.2. Grain yield architecture under optimum growing conditions at Patancheru

Correlations between the standardised data showed that high-tillering landraces with small panicles tended to flower earlier than their low-tillering counterparts with large panicles (Table 2). This association accounted for the low stover mass of these high-tillering, small-panicled landraces, as later landraces tended to have a higher stover biomass, an association commonly observed under optimum growing conditions (Bidinger et al., 1994). Phenology was associated neither with SPM m^{-2} (potential sink size), nor with grain yield per unit SPM (the ability of the crop to realise this potential), nor its components (grain number per unit SPM and individual grain mass).

Panicle number m^{-2} and SPM per panicle were significantly negatively correlated (Table 2). This relationship was accentuated by the presence of small nodal tiller panicles in some of the high-tillering landraces, but it likely reflects the competition for resources between the main shoot and basal tillers. A strong, causal relationship between main shoot size (and hence panicle size) and tiller prolificacy exists (van Oosterom et al., 2003), as tiller survival during stem elongation is strongly negatively associated with main shoot leaf area index in both pearl millet (van Oosterom et al., 2001) and sorghum (Lafarge and Hammer, 2002a).

Panicle number m^{-2} was not related to SPM m^{-2} (Table 2). In cereals, SPM is determined by the panicle

Table 2
Correlation between yield components of 105 landraces, based on standardised data, obtained from BLUE's of control experiments at Patancheru (Table 1)

Trait	Panicle number m⁻²	SPM per panicle	SPM m⁻²	Tillering-PC1	Grain number per SPM[b]	Individual grain mass[b]	Grain yield per unit SPM	Grain number m⁻²	Stover mass m⁻²
Time to flowering[a]	−0.67***	0.60***	−0.06 ns	−0.66***	0.18 ns	0.01 ns	0.14 ns	0.15 ns	0.69***
Panicle number m⁻²		−0.86***	0.00 ns	0.97***	−0.31**	−0.24*	−0.51***	−0.30**	−0.28**
SPM per panicle			0.33***	−0.97***	0.23*	0.36***	0.46***	0.44***	0.25*
SPM m⁻²				−0.17 ns	−0.12 ns	0.30**	−0.02 ns	0.47***	0.07 ns
Tillering-PC1					−0.28 ns	−0.31**	−0.50***	−0.38***	−0.27**
Grain number per unit SPM[b]						−0.32***	0.65***	0.68***	−0.10 ns
Individual grain mass[b]							0.36***	−0.06 ns	0.05 ns
Grain yield per unit SPM								0.53***	−0.10 ns
Grain number m⁻²ᵇ									0.05 ns

[a] Based on two rainy season experiments only.
[b] Based on data from 1989 only.
ns: not significant ($P > 0.05$).
* Significant at $P < 0.05$.
** Significant at $P < 0.01$.
*** Significant at $P < 0.001$.

growth rate (and hence crop growth rate) between flag leaf appearance and the start of grain filling (Kirby, 1988; Craufurd and Bidinger, 1988a; Vega et al., 2001; van Oosterom and Hammer, 2006). Under optimum conditions, this growth rate is a function of intercepted radiation and radiation use efficiency (RUE) (Sinclair and Horie, 1989). Our results are therefore consistent with the observation for both pearl millet (van Oosterom et al., 2002) and sorghum (Lafarge and Hammer, 2002b) showing that tillering does not affect RUE and the light extinction coefficient. Under optimum conditions, the various tillering patterns were therefore equally able to produce a certain potential sink size per unit area.

However, panicle number and size (SPM per panicle) were significantly correlated with grain yield per unit SPM under optimal conditions (Table 2). The efficiency with which the potential sink size was realised was lowest in high-tillering, small-panicled landraces. Therefore, genotypic differences in grain yield under optimum conditions were predominantly a consequence of differences in dry matter partitioning, rather than resource capture.

The reduced ability of high-tillering, small-panicled landraces to realise their potential sink size (grain yield per unit SPM) was associated with a lower grain number and a lower individual grain mass per unit SPM (Table 2), consistent with previous results for pearl millet (van Oosterom et al., 2002, 2003; vom Brocke et al., 2003). However, high-tillering per se does not invariably result in a low grain number per unit SPM (vom Brocke et al., 2003) or per m² (van Oosterom et al., 2003). Rather, the low grain yield per unit SPM of the high-tillering landraces was due to a poor grain filling ability, i.e. a low individual grain mass relative to the grain number per unit SPM (Fig. 2). The low correlation between these two yield components (Table 2) also indicated only minor compensation between them.

Individual grain mass in cereals is determined early in the grain filling period by endosperm cell division, number and size (Jenner et al., 1991; Blum, 2004). In pearl millet, this period coincides with the first appearance of nodal tillers (van Oosterom et al., 2003). Profuse nodal tillering under optimum conditions is a common characteristic of high-tillering landraces (van Oosterom et al., 2002; vom Brocke et al., 2003). This is possibly due to assimilate surplus, associated with a slow grain growth rate (van Oosterom et al., 2002, 2003), which could be due to a low endosperm cell number and hence a small sink demand, as observed in barley (Tuberosa et al., 1992) and maize (Lemcoff and Loomis, 1994). This would support the hypothesis that nodal tiller production is a consequence of a low grain yield per unit SPM and is largely dependent upon the (unused) assimilation capacity of the parent basal stem. The (genetic)
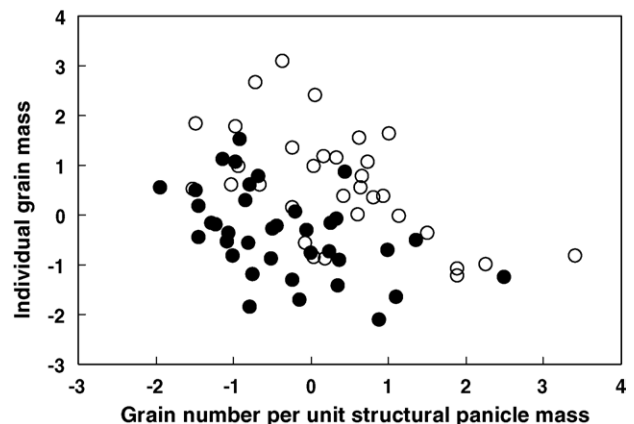

Fig. 2. Individual grain mass as a function of grain number per unit structural panicle mass for high-tillering (tillering-PC1 > 0.5, ●) and low-tillering (tillering-PC1 < −0.5, ○) landraces, averaged across four favourable environments at Patancheru using standardised data.

ability to produce nodal tillers could thus provide a useful mechanism to compensate for reduced grain numbers in the basal shoot panicles due to drought stress at or before flowering. As mid-season drought is common in environments where the high-tillering landraces evolved (van Oosterom et al., 1996), it is possible that the low grain yield per unit SPM of these landraces represents an evolutionary adaptation mechanism to minimise the effects of unpredictable drought stress on grain number and grain filling.

3.3. Grouping of landraces for plant type under optimum growing conditions at Patancheru

Because phenology was significantly correlated with panicle number and size, landraces were first grouped into three phenology classes, based on the standardised mean time to flowering (fl) across two rainy season experiments: early (E, fl < -0.5), medium (M, $-0.5 \leq$ fl≤ 0.5), and late (L, fl > 0.5). Also, panicle number m^{-2} and SPM per panicle, which were strongly negatively correlated, were combined into a principal component (PC1). PC1 explained 93% of the variation present in the two input variables and will be referred to as tillering-PC1, with a high value representing many but small panicles. Within each phenology class, landraces were clustered for tillering-PC1, grain number per unit SPM, and individual grain mass. Although the input parameters for the cluster analysis were significantly correlated, correlations were small in absolute terms (Table 2). Clustering was truncated at the 3- or 4-group level (Fig. 3).

Within a phenology class, clusters generally had a similar phenology, despite significant differences in tillering-PC1 (Table 3). Similar to Table 2, clusters differed little in SPM
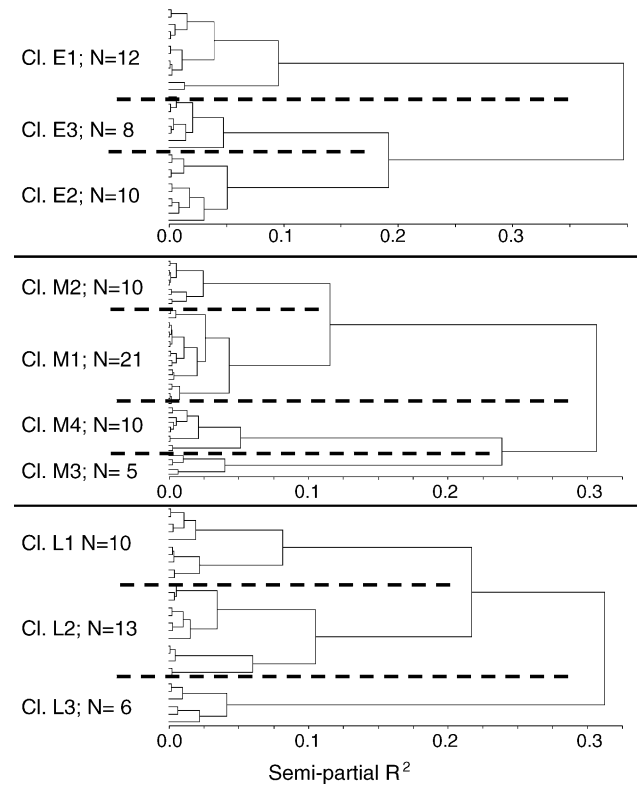

Fig. 3. Dendrogram depicting the clustering of early (E), medium (M), and late (L) flowering landraces.

m^{-2}, but those with a low-tillering-PC1 value (E3 and M4) tended to a have higher grain yield per unit SPM than those with a high-tillering-PC1 value in the same phenology class (E1 and M1).

Table 3

Number of landraces and standardized value for phenology, tillering, grain number per unit structural panicle mass (SPM), individual grain mass, panicle number m^{-2}, SPM per panicle, SPM per m^2, grain number m^{-2}, grain yield per unit SPM, and stover mass m^{-2}

Cluster[a]		Traits used in clustering				Other traits					
	N	Phenology	Tillering-PC1[a]	Grain number per SPM	Ind. grain mass	Panicle number m^{-2}	SPM per panicle	SPM m^{-2}	Grain number m^{-2}	Grain yield per unit SPM	Stover mass m^{-2}
Early phenology											
E1	12	−1.12d	1.19a	−1.13g	0.33cde	1.35a	−0.94d	0.08ab	−0.91e	−0.78d	−0.34cd
E2	10	−0.87d	0.69ab	0.59b	−1.19g	0.65ab	−0.68cd	−0.05ab	0.51abc	−0.27cd	−0.70d
E3	8	−1.01d	0.25bcd	0.36bc	0.45cd	0.19bc	−0.30bc	0.12ab	0.02cd	0.61ab	−0.97d
Medium phenology											
M1	21	−0.13c	0.49bc	−0.23d	−0.75f	0.36b	−0.59c	−0.26b	−0.38de	−0.61cd	−0.03c
M2	10	0.05c	0.22cd	−0.77ef	0.62bc	0.18bc	−0.24bc	0.25ab	−0.54de	−0.48cd	0.24bc
M3	5	−0.16c	−0.01bcde	2.27a	−0.94fg	−0.08bcd	−0.06bcd	−0.51b	1.48a	1.31a	−0.51cd
M4	10	−0.11c	−1.08f	0.41bc	1.25ab	−0.90d	1.19a	0.69a	0.85ab	1.26a	−0.37cd
Late phenology											
L1	10	0.75b	0.03d	−0.20cde	−0.19e	−0.16c	−0.22b	−0.39b	−0.21cd	−0.18bcd	0.97a
L2	13	1.67a	−1.29ef	0.78b	−0.04de	−1.21d	1.27a	−0.25b	0.42abc	0.52ab	0.84ab
L3	6	0.84b	−1.39f	−1.04fg	1.39a	−1.13d	1.55a	0.73a	−0.02bcd	0.11bc	0.46abc

Standardised values are averages over four experiments, conducted under non-drought conditions at Patancheru. For standardisation and description of yield components, see Section 2. Within phenology classes, clusters are ranked for tillering-PC1. Means in a column followed by the same letter are not significantly different at $P < 0.05$ according to a t-test.

[a] Principal component of panicle number m^{-2} and structural mass per panicle.

Clusters E1 and M1 combined a high-tillering-PC1 with low grain number per unit SPM (hereafter referred to as seed set) and very low grain yield per unit SPM (Table 3). Cluster M2 represented a less extreme example of this phenotype. These clusters putatively represent a plant type adapted to unpredictable occurrence of drought stress (van Oosterom et al., 2003). By contrast, Clusters E2 and E3 had a significantly higher seed set, even though tillering-PC1 was not significantly different from that of M1. This resulted in a higher grain yield per unit SPM, which for E3 was significantly higher than either E1 or M1. Clusters E2 and E3 thus represent a yield architecture that could be the selection objective of a breeding program aimed at improving grain yield of landraces adapted to short season arid zones.

Clusters M4 and L2 combined a low-tillering-PC1 with good seed set, resulting in high grain yield per unit SPM under optimal conditions. These clusters represent the yield architecture that is putatively adapted to well-watered conditions and environments with predicable post-flowering drought stress (van Oosterom et al., 1996).

3.4. Grain yield per cluster in individual experiments

In the control experiments at Patancheru, the cluster with the lowest tillering-PC1 within a phenology class consistently yielded more grain than the cluster with the highest tillering-PC1 and in most cases, the difference was significant (Table 4). In general, Cluster M4 had the highest grain yield, whereas Cluster M1 was amongst the lowest. This was consistent with the high SPM m^{-2} and high grain

yield per unit SPM of M4, whereas M1 had significantly lower values for both these yield components (Table 3).

In the favourable environments of Hisar, grain yield was generally slightly higher than in the control experiments at Patancheru. This is consistent with results of Craufurd and Bidinger (1988a,b) that under long days, pearl millet increases the internode number and growth rate of its stem, rather than panicle, resulting in a low harvest index and only small changes in grain yield compared to short days. The relative yield performance of clusters at Hisar was comparable to Patancheru. In the medium phenology class, M4 (low-tillering-PC1) yielded significantly more grain than M1 (high-tillering-PC1) in both years. Similar results were obtained for the early phenology class in 1988 (E3 versus E1). The control experiments at Patancheru were thus representative of favourable north Indian environments in terms of the effect of tillering habit on grain yield.

In the arid zones, however, results were different. In the two high-yielding experiments (Fatehpur 1988, Jodhpur 1989), differences in grain yield between clusters within phenology classes were mostly non-significant (Table 4). In the two low-yielding experiments (Fatehpur 1989, Jodhpur 1988), M1 yielded significantly more than M4 and similar results were obtained for the late phenology class at Jodhpur 1988 (L1 versus L3). No effect of tillering-PC1 on grain yield was observed in the early phenology class. The results for M1 versus M4 represent a significant crossover interaction for grain yield between favourable conditions (Patancheru, Hisar) and the extreme drought conditions in the arid zone.

This crossover interaction for grain yield was not simply a consequence of the yield level of an environment. In the

Table 4
Mean grain yield (g m^{-2}) per cluster in each experiment

Cluster	N	North India						South India					
		Arid zone				Favourable environment		Post-flowering drought stress		Control experiments (no drought)[b]			
		Fatehpur		Jodhpur		Hisar		Patancheru dry season		Patancheru rainy season		Patancheru dry season	
		1988	1989[a]	1988	1989	1988	1989	1990	1991	1988	1989	1989	1990
Early flowering													
E1	12	200ab	18ab	73a	113a	156c	143bcd	83bcd	145cd	125b	110d	129ef	129cde
E2	10	203ab	21a	70ab	127a	191b	131cd	86bc	150cd	133b	124cde	136def	125cde
E3	8	223a	19ab	77a	141a	220a	150bc	103a	170b	156a	128bcd	152bc	154b
Intermediate flowering													
M1	21	177cd	16b	61bc	121a	147c	127d	70f	139d	124b	113de	126f	124de
M2	10	187bc	11c	51cd	133a	142c	152b	78cde	149cd	129b	128ce	133def	126cde
M3	5	181bcd	11c	49cd	145a	158c	158ab	92ab	160bc	131b	144abc	158ab	163ab
M4	10	187bc	9c	40de	132a	198b	176a	100a	188a	164a	162a	173a	174a
Late flowering													
L1	10	163d	10c	57c	134a	147c	144bc	79bcde	140d	122b	126cde	133def	120e
L2	13	140e	9c	25f	144a	145c	151b	75def	137d	128b	146ab	141cde	137cd
L3	6	166cd	9c	27ef	123a	144c	151bc	80bcdef	143cd	158a	154a	147bcd	144bc

Within phenology classes, clusters are ranked for tillering-PC1. For each location, values followed by a same letter are not significantly different at $P < 0.05$ for a t-test type analysis in PROC MIXED, using all entries in the experiment.

[a] Cluster L3 has two landraces for which all three reps were missing.

[b] Four experiments used for the clustering.

managed post-flowering drought environments at Patan-cheru (dry seasons of 1990, 1991), clusters with a low-tillering-PC1 in the medium and late phenology classes consistently outyielded those with a high-tillering-PC1 in the same class, similar to the results obtained under favourable conditions at Patancheru and Hisar. This was not due to differences in drought escape. For pairs of clusters with similar phenology in the managed stress environments (E1–E3, M4–E2, M1–M3), the cluster with the lower tillering-PC1 consistently had a significantly higher grain yield than the one with the higher tillering-PC1 in both managed drought stress experiments (Table 4). This difference with the results from the arid zones in north India was likely due to a different timing of stress (Table 1), as severe pre-anthesis drought stress occurred in the arid zone but not at Patancheru. This interaction pattern is consistent with the perception of farmers in Western Rajasthan, who prefer high-tillering, small-panicled land-races in environments where timing and intensity of drought stress are unpredictable, whereas large-panicled, low-tillering ones are preferred in locations where drought

occurs predominantly post-flowering (Kelley et al., 1996; van Oosterom et al., 1996; Christinck, 2002). Similarly, the drought tolerant but low-tillering *Iniadi* pearl millet landrace (Andrews and Anand Kumar, 1996) evolved in West-African environments where drought stress is more likely to occur after flowering (Sivakumar, 1992). Our results thus support an earlier hypothesis (van Oosterom et al., 2003) that high-tillering genotypes with thin stems are better adapted to environments where mid-season drought stress is likely to occur, whereas low-tillering genotypes with thick stems are better suited to environments where post-flowering drought is more prevalent.

3.5. Physiological causes for the observed GE interactions for grain yield

3.5.1. Maintenance of potential sink size under extreme drought

High grain yield under extreme stress was significantly related to early flowering at both Fatehpur 1989 ($R^2 = 0.61$, $P < 0.001$) and Jodhpur 1988 ($R^2 = 0.30$, $P < 0.001$). Early

Table 5

Mean value for yield components for 105 landraces, grown at Fatehpur 1989 and Jodhpur 1988 and clustered for phenology and yield architecture

Cluster	Panicle number (m^{-2})	Panicle number ($plant^{-1}$)	SPM[a] per panicle (g)	Grain number (m^{-2})	Grain number per unit SPM (g^{-1})	Individual grain mass (mg)	SPM ($g\ m^{-2}$)	Grain yield per unit SPM ($g\ g^{-1}$)	Biomass ($g\ m^{-2}$)	HI
Fatehpur 1989										
Early flowering										
E1	5.62a	0.98ab	2.68c	248ab	3341bc	5.2a	14.0ab	1.29a	141b	0.13a
E2	5.72a	1.10a	3.11bc	260ab	4182a	4.9abc	16.6a	1.24ab	154ab	0.13a
E3	4.72b	0.87b	3.11bc	264ab	3770ab	5.0abc	14.5ab	1.29a	149ab	0.13a
Intermediate flowering										
M1	4.45b	0.88b	2.96bc	280a	3504ab	4.7ce	12.9b	1.26a	164a	0.09b
M2	3.20c	0.58c	3.22b	238b	2303d	4.7cd	9.4c	1.10abc	150ab	0.07c
M3	2.90cd	0.54cd	3.25bc	260ab	2544cd	4.0f	9.6c	1.08abc	164a	0.07c
M4	2.16de	0.41d	4.31a	232b	2188d	4.4def	10.0c	1.00c	149ab	0.06c
Late flowering										
L1	2.75cd	0.51cd	3.29b	226b	2042d	5.1ab	8.7c	1.09abc	151ab	0.06c
L2	1.72e	0.35d	4.30a	243ab	1886d	4.2df	7.3c	1.10abc	160ab	0.05c
L3	1.93de	0.39cd	4.09a	212b	1929d	4.7bcd	8.2c	1.01bc	152ab	0.06c
Jodhpur 1988										
Early flowering										
E1	16.16a	1.83a	1.35d	–	–	–	21.2b	4.96a	372e	0.20a
E2	14.30bc	1.48bc	1.56cd	–	–	–	20.8b	4.64a	389de	0.19a
E3	14.72ab	1.62ab	1.93bcd	–	–	–	27.9a	4.06abc	419bcde	0.18a
Intermediate flowering										
M1	12.94c	1.40c	1.64cd	–	–	–	20.2b	3.99abc	411cde	0.15b
M2	10.76d	1.17d	1.91bcd	–	–	–	19.5bc	3.15bc	468b	0.11cd
M3	9.34d	1.05d	2.17abc	–	–	–	19.4abc	3.46abc	381de	0.12bcd
M4	6.55e	0.73e	2.72a	–	–	–	17.9bc	2.97c	432bcd	0.09d
Late flowering										
L1	10.98d	1.16d	1.58cd	–	–	–	15.7bc	4.51ab	449bc	0.13bc
L2	4.42f	0.51f	2.33ab	–	–	–	9.3d	2.87c	540a	0.05e
L3	4.92ef	0.52ef	2.23abc	–	–	–	12.1cd	3.45abc	538a	0.05e

Within phenology classes, clusters are ranked for tillering-PC1. For each trait in a location, values followed by a same letter are not significantly different at $P < 0.05$ for a *t*-test type analysis in PROC MIXED, using all entries in the experiment.

[a] SPM, structural panicle mass.

flowering clusters consistently had a higher SPM m^{-2} (a measure of yield potential) than late flowering ones (Table 5), even though SPM m^{-2} was not associated with earliness under optimum conditions (Table 3). Panicle exertion depends on stem extension and hence the stem dry matter accumulation rate (Squire, 1989). Our results thus indicate that early flowering landraces experienced less stress at the critical moment of stem elongation than late flowering ones and that growth rates for landraces in these clusters were above the threshold required for panicle exertion. Consistent with this hypothesis, there were no consistent differences among the three early-flowering clusters (E1–E3) in panicle number per plant and SPM m^{-2} in these two environments (Table 5). In the presence of partial drought escape, a higher tillering-PC1 had no comparative advantage, which would explain the lack of differences in grain yield among the three early flowering clusters in the two extreme drought environments, similar to the results of more favourable arid zone environments (Table 4).

Plant type, however, had a significant effect on grain yield in the intermediate phenology group, with M1 yielding significantly more grain than M4 at both Fatehpur 1989 and Jodhpur 1988 (Table 4). In both experiments, M1 had a higher SPM m^{-2} than M4 (Table 5), despite having a significantly lower SPM m^{-2} under optimum conditions (Table 3). Although M1 flowered slightly earlier than M4 in the extreme stress environments, the difference in SPM was not associated with an inherently earlier flowering under the long days of north India, as flowering times were similar at Hisar (data not shown). Rather, >50% of plants in M4 failed to produce a fertile main shoot panicle at Fatehpur 1989, compared to <20% of plants in M1 (Table 5). Similar results were obtained at Jodhpur 1988, where panicle number per plant was <1 for M4, but >1 for M1. Low-tillering germplasm generally has a thick stem and high SPM per panicle (vom Brocke et al., 2003), and is thus likely to require a higher dry matter accumulation rate per stem to achieve a given stem elongation rate than does high-tillering germplasm. Thicker stems could therefore have a higher threshold assimilate requirement below which stem elongation ceases, in which case a reduced crop growth rate under drought could have a disproportionately large effect on stem elongation in low-tillering germplasm. This could explain the delayed flowering in pearl millet following pre-flowering drought stress (Squire et al., 1986; Bidinger et al., 1987), in particular in germplasm with a low-tillering-PC1 (Mahalakshmi and Bidinger, 1985; van Oosterom et al., 2003; vom Brocke et al., 2003). The contrast between M1 and M4 indicates that under extreme, unrelieved drought, exertion and flowering of the main shoot panicle can be indefinitely delayed in large-panicled types. A similar effect of tillering type on grain yield was observed for Cluster L1 versus Cluster L3 at Jodhpur (Table 4), but not at Fatehpur, presumably because yield levels there were too low to distinguish these clusters. In more favourable arid zone

experiments (Fatehpur 1988, Jodhpur 1989), tillering type had no effect on grain yield in both the M and the L clusters. Overall, our results support the hypothesis that if extreme stress occurs just prior to panicle emergence, a large panicle size can have a detrimental effect on panicle exertion, which in turn can negatively affect potential sink size m^{-2}. The prospects for manipulating genetically the traits controlling sink potential in pearl millet under severe pre-flowering stress conditions seem very good, as the range of genetic diversity for panicle number m^{-2} and SPM per panicle is large (Craufurd and Bidinger, 1988b; Bidinger and Raju, 2000; vom Brocke et al., 2003).

3.5.2. Maintenance of efficiency realising the potential sink size under extreme stress

The crossover interaction for grain yield was also associated with a superior ability of small-paniced landraces to realise their potential sink size under extreme stress. At both Fatehpur 1989 and Jodhpur 1988, grain yield per unit SPM of clusters with the highest tillering-PC1 tended to be higher than of those with the lowest tillering-PC1 in the same phenology class (Table 5). Under optimum conditions at Patancheru, by contrast, grain yield per unit SPM was lowest for the highest tillering cluster in each phenology class (Table 3). This relatively higher efficiency with which high-tillering landraces realised their potential grain yield under extreme stress was associated with a smaller response of individual grain mass to reduced resource availability as stress increased; high-tillering landraces better maintained their non-stressed individual grain mass under the extreme conditions at Fatehpur 1989, where overall individual grain mass was low (Fig. 4).

Presumably, insufficient assimilate was available under severe stress to allow low-tillering landraces to achieve as high a grain growth rate as under favourable conditions (van Oosterom et al., 2002). The better ability of high-tillering pearl millet to maintain individual grain mass across environments has been reported before (Bidinger and Raju,
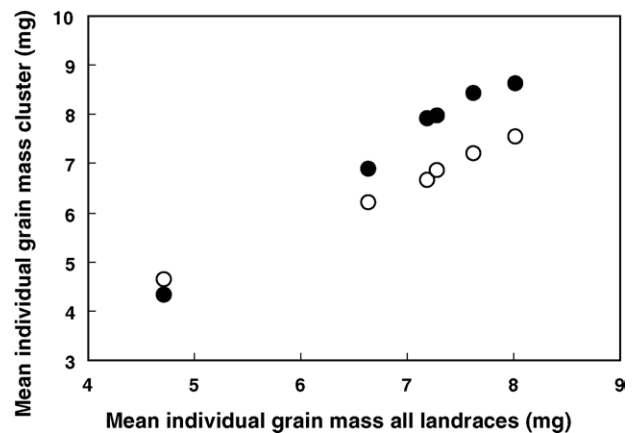

Fig. 4. Mean individual grain mass per cluster as a function of mean individual grain mass of all 105 landraces in six experiments for Clusters M1 (○) and M4 (●).

2000; van Oosterom et al., 2003; vom Brocke et al., 2003). This ability minimises the risk of extremely low individual grain mass, which reduces not only harvestable yield, but also the value of the seed as a source for next year's crop (Dhamotharan et al., 1997), as small grain size can adversely affect early growth vigour and seedling survival (Manga and Yadav, 1995; López-Castañeda et al., 1996). Maintenance of individual grain mass under adverse conditions is thus an important adaptation mechanism in arid environments. The higher grain yield per unit SPM of the high-tillering genotypes could indicate a lower assimilate flux threshold for grain growth, similar to the lower threshold assimilate requirement for stem growth. This provides additional support for the hypothesis that grain yield differences in extremely stressed environments are mainly associated with resource partitioning, rather than resource capture.

3.6. Implications for crop improvement programs targeting stress environments

Breeding for improved productivity for the arid zones of NW India remains a challenge for plant breeders. Performance of new varieties under highly adverse conditions is the key selection criteria, but selection progress is hampered by very large annual variation in environmental conditions (Sharma and Pareek, 1993; van Oosterom et al., 1996). A selection strategy to identify adaptation to long-term environmental conditions that is less reliant on random rainfall conditions for germplasm testing could enhance the efficiency of breeding programs targeting arid zones (Chapman et al., 2002). This is particularly the case in early generations of a selection program, when selection decisions have to be made every season. It is thus

highly advantageous for a selection program to identify indirect selection criteria which are expressed under good conditions, but do contribute significantly to improved adaptation to adverse conditions.

Our analyses identified germplasm with differential adaptation to arid zones, by using the expression of yield components under optimum conditions. To test the possibility of using such trait expression to guide selection for arid zones, we conducted a simulated selection exercise, in which two schemes for direct selection for grain yield were compared with schemes for trait selection, using all 105 landraces. Grain yield selection was done either across the four control experiments at Patancheru (Scheme 1), or across all 12 experiments (Scheme 2), using averaged standardised data across the selection environments. Trait selection was done for plant type (high-tillering plus small panicle size, Scheme 3) or phenology (Scheme 4), using the same standardised data from the four control experiments at Patancheru as employed in the clustering (Section 3.3). Each selection scheme identified six superior landraces, with some of them selected in multiple schemes (Table 6).

Selection Scheme 1 identified low-tillering landraces with average phenology, high potential sink size (SPM m^{-2}) and good ability to achieve this potential (grain yield per unit SPM). These selections had high grain yield in most environments, except those with severe stress, where grain yield of the selected landraces was less than the mean of all 105 landraces (Table 6). This is consistent with the hypothesis that the low-tillering plant type is particularly adapted to environments where pre-flowering drought is unlikely to occur and supports the conclusion of Simmonds (1991) and Ceccarelli (1996) that selection in favourable environments is unsuitable if a high proportion of the target

Table 6
Phenology, yield architecture, and grain yield of four groups of six landraces, selected for (1) high grain yield across four control experiments at Patancheru, (2) high grain yield across all experiments, (3) high panicle number and small panicle size across four control experiments at Patancheru, and (4) early flowering across two rainy season control experiments at Patancheru

	Mean standardised value				Grain yield (g m^{-2})							
	Phenology	Tillering-PC1	Structural panicle mass (m^{-2})	Grain yield per unit SPM	North India arid zone						North India		Managed post-flowering drought	
					Severe stress		Mid stress		Favourable			Patancheru 1990	Patancheru 1991
					Fatehpur 1989	Jodhpur 1988	Fatehpur 1988	Jodhpur 1989	Hisar 1988	Hisar 1989			
Selection schemes for grain yield													
1. Four control experiments	−0.31a	−1.29c	0.86ab	1.51a	9c	40cd	191b	142a	196abc	181a	103ab	200a
2. All 12 experiments	−1.13b	−0.14b	0.75a	0.96a	17abc	62ac	246a	140ab	207ab	167a	117a	198a
Selection schemes for physiological traits													
3. Tillering	−1.00ab	1.89a	−0.32c	−0.81b	23ab	69ab	184b	109c	149c	127c	73d	122b
4. Phenology	−1.86b	1.21a	0.07abc	−0.12b	22a	78a	241a	111abc	212a	145bc	98bc	160ab
Mean across 105 landraces					14bc	54bd	181b	130bc	162bc	145ab	82c	150b

All selections were done on standardised data, averaged across selection environments. Groups 1 and 2 had two landraces in common. Groups 2 and 3 had two landraces in common. Groups 3 and 4 had one landrace in common. Means in a column followed by the same letter are not significantly different at $P < 0.05$ according to a *t*-test.

environments experience severe stress. Landraces selected in Scheme 2 had a slightly higher (albeit non-significant) grain yield under severe stress than those selected in Scheme 1, likely because this scheme selected germplasm with significantly earlier phenology. Grain yield in the other environment types was not consistently different.

Selection for high-tillering (Scheme 3) identified landraces with a significantly lower SPM m^{-2} and grain yield per unit SPM than those selected in Schemes 1 and 2. This resulted in a lower grain yield in most environment types, except the severely stressed ones (Table 6). By contrast, landraces selected for earliness (Scheme 4) yielded significantly less than those selected in Scheme 2 in only two experiments, but significantly more than the mean across all 105 landraces in three of the four arid zone experiments. Under severely stressed conditions, grain yields of landraces selected in Schemes 3 and 4 were as high as those selected for grain yield across all 12 experiments (Scheme 2). But as trait selection was based on only the favourable environments, it identified germplasm that yielded well under extreme stress more effectively than did direct grain yield selection. Therefore, favourable environments can be used to identify germplasm with high yield under severely stressed conditions, provided selection is done for targeted traits, rather than grain yield per se. However, the poor grain yield of the landraces selected for tillering (Scheme 3) in all other experiments indicates that this scheme selected germplasm, unable to capitalise on additional resource availability in more favourable years. Therefore, individual traits selection, without complete understanding of the underlying physiology, may be ineffective in identifying adapted germplasm.

To assess the value of more detailed physiological knowledge in the selection of adapted germplasm, we conducted a divergent selection exercise, where we selected for high versus low grain yield per unit SPM in addition to high panicle number/small size versus low panicle number/ large size, as measured in the control environments. To avoid confounding effects with phenology, we included only the 46 medium phenology landraces of Clusters M1–M4. Using averaged standardised data from the four control experiments at Patancheru, we first selected landraces with extreme standardised values for panicle number and size (<-0.5 or >0.5). This gave two main groups of landraces, one having many but small panicles and one having few but large panicles. Within each group, we subsequently selected for extreme grain yield per unit SPM (<-0.5 or >0.5). The number of selections per group ranged from 2 to 9 (Table 7). We also selected for high grain yield in either the four control experiments at Patancheru, or across all 12 experiments. The top 10 landraces in these two selection schemes had 8 landraces in common, 6 of which were in common with the 9 landraces selected for low-tillering, large panicles, and high grain yield per unit SPM. Therefore, we used that selection scheme to represent direct selection for grain yield.

Selection under optimum conditions for many but small panicles had a positive effect on grain yield under severe stress, no effect under mild stress, but a negative effect under both favourable conditions and post-flowering drought stress, compared with selection for few but large panicles, i.e. direct selection for grain yield (Table 7). This is consistent with the hypothesis that high-tillering and small panicle size are likely to result in a higher SPM m^{-2} (and hence grain yield) only under conditions where the growth rate per axis prior to anthesis (when grain number is determined) is below the threshold of larger panicled landraces. Subsequent selection, within the high-tillering group, for high standardised grain yield per unit SPM did not affect grain yield under severe stress, but consistently increased grain yield (compared with selection for low grain yield per unit SPM) in the other environment types, although the difference was significant in only 1 of the 2 years (Table 7). Selection for seed set (grain yield per unit SPM), in addition to high-tillering, thus identified germplasm that is capable of increasing grain yield if the required assimilates are available, without necessarily compromising yield in severely stressed seasons. More importantly, it identified germplasm with higher grain yield under severe stress than selection for low-tillering, large panicles and high grain yield per unit SPM (i.e. direct selection for grain yield), without compromising grain yield under mild stress in the arid zones (Table 7). Selection for yield components, based on a physiological dissection of grain yield under favourable conditions, was thus superior to direct selection for grain yield in identifying germplasm with adaptation to arid zones.

Our results illustrate how basic physiological understanding of the response of yield components to environmental conditions can be used to identify, under optimum conditions, germplasm with adaptation to arid zones. The expression of some of these yield components (in particular panicle number and size), as well as phenology, was very consistent across environments, suggesting a high heritability. We therefore propose a selection strategy for a variety development program targeting arid zones, in which early generations are used to indirectly select for adaptation to arid zones, by selecting for the above traits under optimum conditions. This could significantly reduce direct yield testing of early generations in uncertain, low-yielding environments (which often have a low heritability) and allow more resources to be focussed on unstressed or managed stress environments. To assess the importance of selection for these traits, it is vital to not only acquire a sound understanding of their responses to different patterns of abiotic stress, but also to characterise the frequency of occurrence of these stress patterns in the target population of environments (van Oosterom et al., 1996; Chapman et al., 2002). The optimum selection index would depend on the prevalent stress patterns in the target environment. Potentially adapted plant types that are selected in early generations under optimum conditions can subsequently be

Table 7
Grain yield of four groups of landraces, selected for plant type at Patancheru under optimum conditions using a two-stage selection procedure (In section A, selection was done for high panicle number and low structural panicle mass (SPM) per panicle, or low panicle number and high SPM per panicle. In section B, landraces within these two groups were further divided into high or low grain yield per unit SPM.)

	Mean standardised value				Grain yield (g m^{-2})							
	Phenology	Tillering-PC1	Structural panicle mass (m^{-2})	Grain yield per unit SPM	North India arid zone				North India		Managed post-flowering drought	
					Severe stress		Mid stress		Favourable		Patancheru 1990	Patancheru 1991
					Fatehpur 1989	Jodhpur 1988	Fatehpur 1988	Jodhpur 1989	Hisar 1988	Hisar 1989		
A												
High-tillering, small panicles (9)					16	62	179	125	131	131	68	137
Low-tillering, large panicles (11)					9[**]	37[***]	181 ns	145 ns	192[***]	177[***]	98[***]	186[***]
B												
Selection for high-tillering, small panicles												
High yield per SPM (3)	−0.29	0.93	−0.02	0.83	16a	55a	207a	131a	183a	145b	87a	144c
Low yield per SPM (6)	−0.07	0.95	−0.70	−1.15	15a	66a	166b	122a	105b	124b	58b	134c
Selection for low-tillering, large panicles												
High yield per SPM (9)[a]	−0.05	−1.24	0.11	1.63	10ab	36b	185ab	144a	195a	182a	98a	181b
Low yield per SPM (2)	0.13	−1.10	2.13	−0.61	5b	42ab	164ab	149a	179a	153ab	96a	209a
Mean across 46 landraces					13	53	181	128	158	146	80	154

Number of landraces in each group given in brackets. Only 46 landraces with intermediate phenology (Clusters M1-M4) were considered and mean grain yield across all 46 landraces added for comparison.
Section A:
ns, not significant ($P > 0.05$).
[**]Significant at $P < 0.01$.
[***]Significant at $P < 0.001$.
Section B:
[a]This group represents direct selection for grain yield (see text).
Values followed by the same letter are not significantly different ($P < 0.05$) for a *t*-test type analysis done in PROC MIXED in SAS.

tested in multi-environment trials to select the best performing varieties under low-yielding environments. Although our results are specific to adaptation of pearl millet to arid zones of NW India, they adequately illustrate the potential for using physiological understanding to break a complex trait down into component traits, which can then be used as indirect selection criteria to select for the complex trait itself (Richards et al., 2002; Hammer et al., 2005). This should improve the efficiency of selection programs targeting arid zones.

4. Conclusion

An analysis of grain yield components that determine either the potential sink size or the ability to realise this potential, showed that the crossover GE interaction for grain yield of pearl millet landraces with contrasting yield architecture was predominantly due to differences in resource allocation pattern, rather than in resource capture per se. Selection under optimum conditions for yield components representing a resource allocation pattern favouring high yield under severe drought stress, combined with a capability to increase grain yield if assimilates are available, was more effective than direct selection for grain yield in identifying germplasm that performed well in severely stressed environments, without significantly compromising yield in more favourable arid zone environments. This approach will reduce reliance on selection in random stress environments and can improve the efficiency of selection for grain yield in millet breeding program targeting arid zones.

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