CROP PRODUCTION

Indian Journal of Agricultural Sciences 65 (9) : 629–35, September 1995

Effect of yield potential, drought escape and drought tolerance on yield of pearl millet (*Pennisetum glaucum*) in different stress environments

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Received: 1 December 1993

ABSTRACT

An experiment was conducted during the rainy season of 1988 and 1989 and the dry season of 1989 and 1990 to study the effect of yield potential, drought escape and tolerance on the grain yield of pearl millet [*Pennisetum glaucum* (L.) R. Br. emend. Stuntz] under stress. Different types of drought and heat stress occurred, viz moderate and severe post-flowering drought and severe pre-flowering drought, combined with either high or low temperature during grain filling. Yield potential was only related to yield under stress when pre-flowering drought was combined with low temperatures. Escape was the predominant factor if temperature was high, except if combined with pre-flowering drought, in which case tolerance became more important. These results show that for stressed environments, selection for yield potential is of limited use. The importance of escape and tolerance, however, depends on the timing and intensity of stress occurrence. If pearl millet-growing regions can be characterized based on occurrence of abiotic stress, breeders can select more efficiently for plant traits that enhance stress adaptation in specific target environments.

Yield under stress can be considered as a function of yield potential, stress escape and stress tolerance. Yield potential is often only a minor determinant of yield in arid zones, because plant ideotypes that are successful in unfavourable environments differ from those that perform well under stress (Ceccarelli *et al.* 1992, van Oosterom and Ceccarelli 1993). Simultaneous selection for yield potential and yield under stress, however, is effective in regions where both favourable and unfavourable conditions occur (Nachit 1989,

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Zavala-Garcia *et al.* 1992). The effects of escape and tolerance on yield under stress depend on both the timing (Bidinger *et al.* 1987) and intensity (Nachit and Ouassou 1988) of stress occurrence. This indicates that genotype X environment interactions in unfavourable environments are related to the differential effects of yield potential and stress escape and tolerance on yield under stress. A quantification of the importance of these effects on yield in different types of stress environments can assist breeders in the identification of adaptive plant traits for unfavourable environments.

The aim of this study was to quantify the contribution of yield potential, stress escape and stress tolerance to grain yield of pearl millet [*Pennisetum glaucum* (L.) R. Br. emend. Stuntz], grown in different environments with different timings and intensities of the occurrence of drought and heat stress.

MATERIALS AND METHODS

Plant material and environments

The trials were conducted during the rainy season of 1988 and 1989, and the dry season of 1989 and 1990 at sites in both northern and southern India. Data were obtained from 24 environments (site X year X treatment combinations, Table 1). Out of 16 genotypes used, 14 were common in all trials. The genotypes included both hybrids and open-pollinated varieties and were bred at institutions and universities participating in the All-India Coordinated Pearl Millet Improvement Programme (Table 2).

The trial was laid out in randomized complete block design with 3 or 4 replications. Plots consisted of 4 rows, each 5 m long; the row spacing differed between sites. Phosphorus (before sowing) and nitrogen (split application) were applied at most locations; the rates varied in different environments, according to local recommendations.

The timing and intensity of drought stress were calculated for each environment using a water budget developed by Frère and Popov (1979). This budget calculates a cumulative water satisfaction index, which represents the percentage of the estimated crop water requirement (potential evaporation X crop coefficient) that could be supplied by the available soil water up to a particular moment in the growing season. Srivastava *et al.* (1984) successfully applied the budget to explain seasonal differences in yield of groundnut (*Arachis hypogaea* L.) in Rajkot district.

Based on the values for water satisfaction index at flowering and maturity, 4 groups of environments were distinguished, differing in timing and intensity of drought occurrence, viz without drought stress, with moderate or severe post-flowering drought stress and with severe pre-flowering drought stress. The environments were further subdivided into those with low and high temperatures during grain filling (mean maximum < 34°C and > 34°C respectively). This resulted in 7 groups of environments (Table 1).

At each environment, grain yield and time from sowing to flowering were recorded. Time to flowering was expressed as thermal units, assuming a base, optimum and maximum temperature of 11°C, 33°C and 46°C respectively (Ong and Monteith 1985, Squire 1989).

Estimation of yield potential, drought escape and drought tolerance

Yield under stress can be described as (Nachit and Ouassou 1988):

$$Y_{se} = a + b^{*}Y_p + c^{*}Fl + \varepsilon_1 \quad \ldots (1)$$

where Y_{se}, estimated yield under stress; Y_p, yield potential; Fl, time of flowering; and ε_1, error term. The yield potential and time from sowing to flowering were for each genotype estimated as the average across the 5 environments where drought and temperature stress were absent (Table 1). Stress tolerance (St) was defined as the difference between observed (Y_{so}) and estimated yield under stress:

$$Y_{so} — Y_{se} = St + \varepsilon_2 \qquad ..(2)$$

Stress escape (Se) was calculated as the difference between Y_{so} and the estimated yield under stress, $Y_{s\acute{e}}$ (based on the regression of yield under stress on yield potential) minus the effect of stress tolerance:

$$(Y_{so} — Y_{s\acute{e}}) — St = c' * Se + \varepsilon_3 \qquad ...(3)$$

In these 3 formulae, Y_p, Se and St are orthogonal and together explain 100% of the variation in yield under stress. The input data for yield potential, time to flowering, and yield under stress were obtained from data, which were standardized for each environment to a mean of 0 and a standard deviation of 1. The standardized means were then multiplied by the standard deviation of the unstandardized mean and the product was added to the unstandardized mean.

RESULTS AND DISCUSSION

Environmental and genotypic differences

A division of the environments into 4 groups, based on water satisfaction index at flowering and maturity (Table 1), explained 74.9% of the environmental sum of squares for grain yield. This increased to 80.6% if these groups were subdivided based on temperature. Both groupings reduced the ratio of the genotype x environment (G x E) variance to the genotype variance (Table 3), indicating less G x E interaction within the environment groups than within the complete set of environments. The timing and intensity of drought and heat stress were therefore the major environmental constraints to grain yield.

The genotypes were divided into early, intermediate and late flowering (Table 2). Differences in yield potential between these groups were small. Late-flowering genotypes tended to have the highest yield potential (yield in the absence of stress, Table 2). However, the yield potential of the other 2 groups was relatively low, especially if compared with their yields in environments with only heat stress. There was thus no evidence that yield potential and flowering were associated in this experiment.

Under conditions of post-flowering drought stress, early genotypes were found highest yielding, especially when temperature was high during grain filling (Table 2). If high temperature after flowering was combined with moderate drought stress, the early genotypes on average outyielded the medium ones by 31% and the late ones by 43%; these percentages doubled if drought stress became severe. Earliness therefore became more important if stress during grain filling increased.

If drought stress occurred before flowering, the late-flowering genotypes on average had the highest yields and the early-flowering genotypes the lowest, irrespective of the temperature during grain filling (Table 2). This indicates that in those environments the genotype ranking for grain yield was determined by escape from mid-season drought stress rather than by escape from end-of-season heat stress.

Contribution of yield potential, escape and tolerance to yield under stress

The absolute values of the contribution of yield potential, escape, and tolerance to yield under stress were biased by the material used. Therefore the discussion of these results will focus on the relative importance of the 3 factors.

Yield potential contributed little to yield under stress, except if pre-flowering drought was combined with low temperatures during grain filling (Table 4). The effect of yield

Table 1 Cumulative water satisfaction index (WSI) at flowering and around maturity (used 25 days after flowering), mean maximum temperature during grain filling, and average grain yield of pearl millet for the environments

Environment	WSI		Temperature	Yield
	Flowering	Maturity	(°C)	(g/m²)
		Non-drought stress		
Low temperature				
Patancheru 1989	100	100	28.7	427
Durgapura 1988	100	100	32.4	324
Patancheru 1988	100	100	29.3	313
Anantapur 1988 (early sowing)	100	100	30.7	273
Jamnagar 1988	100	89	32.2	267
High temperature				
Hisar 1988 (irrigated)	100	99	35.2	354
Hisar 1988	100	90	35.5	241
Bawal 1988	100	83	35.7	318
Patancheru dry season 1989 (irrigated†)	99	99	36.5	319
Patancheru dry season 1990 (irrigated†)	97	87	35.9	283
		Moderate post-flowering drought stress		
Low temperature				
Anantapur 1988 (late sowing)	99	62	33.1	192
Patancheru 1989 (rain-out shelter$^{\Psi}$)	97	60	28.8	168
Jamnagar 1989	95	70	32.3	291
Anantapur 1989 (late sowing)	88	62	33.6	183
High temperature				
Jobner 1988	100	71	35.4	63
Patancheru dry season 1989 (stress‡)	99	60	35.7	170
Patancheru dry season 1990 (stress‡)	98	54	35.8	148
Durgapura 1989	97	63	35.5	82
Fatehpur 1988	96	60	34.7	212
		Severe post-flowering drought stress		
High temperature				
Jodhpur 1988	97	46	38.0	63
Mandor 1988	92	40	38.0	91
Mandor 1989	87	50	36.6	124
		Severe pre-flowering drought stress		
Low temperature				
Anantapur 1989 (early sowing)	57	44	32.5	81
High temperature				
Fatehpur 1989	61	32	34.7	47

†Irrigated from sowing until maturity; $^{\Psi}$rain withheld after boot stage via rain-out shelter; ‡irrigated only until average flowering

Table 2 Average grain yield (g/m^2) of 14 pearl millet genotypes, grown in environments differing in the timing (pre- or post-flowering) and intensity (moderate or severe) of drought stress and in the temperature during grain filling (the classification of environments is similar to that of Table 1)

Genotype	Without DS and without HS†	Without DS and with HS	With post-flowering MDS and without HS	With post-flowering MDS and with HS	With post-flowering SDS and without HS	With pre-flowering SDS and without HS	With pre-flowering SDS and with HS
Early flowering							
'HHB 67'	301^{bcd}	361^{a}	225^{ab}	178^{a}	159^{a}	65^{c}	29^{cd}
'RHB 27'	294^{bcd}	313^{abcd}	221^{abc}	171^{ab}	144^{ab}	55^{c}	37^{bcd}
'HHB 68'	309^{bc}	346^{abc}	237^{a}	163^{ab}	121^{abc}	69^{bc}	48^{bc}
Mean	301	340	228	170	141	63	38
Intermediate flowering							
'RHB 23'	301^{bcd}	301^{cde}	221^{abc}	128^{cdef}	89^{cde}	70^{bc}	45^{bc}
'CZDT 46'	250^{d}	249^{e}	175^{c}	113^{def}	76^{de}	54^{c}	49^{b}
'ICMV 88904'	309^{bc}	337^{abc}	220^{abc}	143^{bcd}	75^{de}	60^{c}	44^{bc}
'RHB 28'	317^{bc}	297^{cde}	187^{bc}	119^{cdef}	106^{bcd}	62^{c}	24^{d}
'HHB 60'	329^{bc}	358^{ab}	242^{a}	146^{abc}	92^{cde}	128^{ab}	47^{bc}
Mean	301	308	209	130	88	75	42
Late flowering							
'ICMV 87125'	341^{ab}	301^{bcde}	212^{abc}	130^{cde}	86^{cde}	83^{bc}	48^{bc}
'IHPV 85/1'	324^{bc}	290^{cde}	205^{abc}	121^{cdef}	59^{e}	77^{bc}	71^{a}
'ICMH 84122'	384^{a}	318^{abcd}	236^{a}	140^{bcde}	84^{cde}	162^{a}	49^{b}
'WCC 75'	337^{ab}	255^{e}	182^{bc}	116^{cdef}	63^{e}	75^{bc}	76^{a}
'PSB 1'	278^{cd}	264^{de}	188^{bc}	108^{ef}	75^{de}	86^{bc}	44^{bc}
'ICMV 82113'	330^{abc}	249^{e}	210^{abc}	97^{f}	82^{cde}	93^{bc}	51^{b}
Mean	332	280	205	119	75	96	56

DS, Drought stress; MDS, moderate drought stress; SDS, severe drought stress; HS, heat stress

†Yields in environments without drought and heat stress represent yield potential

Means in the same column followed by the same letter are not significantly different ($P < 0.05$) according to Tukey's test for pair-wise comparisons

potential was strongly reduced by higher temperatures during grain filling. This confirms results for Mediterranean environments where yields of barley (*Hordeum vulgare* L. sensu lato) in favourable environments are not related to those in unfavourable ones (Ceccarelli and Grando 1991, van Oosterom *et al.* 1993). For breeding programmes of pearl millet aiming at unfavourable environments, selection for yield potential is thus of limited use.

Escape by early flowering was a major determinant of grain yield in environments where post-flowering stress (drought, heat)

Table 3 Ratio of the genotype x environment variance to the genotype variance for grain yield of pearl millet in different environments and subsets of environments

Drought environment	Temperature environment		
	Low + high	Low	High
Overall	1.93 (24)	1.48 (10)	0.88 (14)
No drought	1.68 (10)	1.35 (5)	0.24 (5)
Post-flowering drought			
Moderate	0.82 (9)	0.76 (4)	0.74 (5)
Severe	0.63 (3)	(0)	0.63 (3)
Pre-flowering drought			
Severe	6.81 (2)	(1)	(1)

Values in parentheses indicate the number of environments

prevailed (Table 4). Early flowering is a common escape mechanism for end-of-season stress in cereals, viz spring wheat (*Triticum aestivum* L. emend. Fiori & Paol.) (Fischer and Wood 1979, Nachit and Ouassou 1988) and barley (Ceccarelli 1987, van Oosterom and Acevedo 1992). In environments with pre-flowering drought, however, late genotypes had the highest yields (Table 2), although the contribution of escape to yield under stress was relatively small (Table 4). The results indicate the importance of escape as a component of yield under unfavourable conditions, although its effect strongly depends on the timing and intensity of stress occurrence.

The contribution of stress tolerance to yield under stress was inconsistent across environments (Table 4). It might be expected that those developmental and physiological mechanisms that confer tolerance, differ with the type of stress (Ludlow and Muchow 1988). A genotype that tolerates one type of stress therefore not necessarily tolerates other types.

Implications for breeding

Considering the effect of stress occurrence on the contribution of escape and tolerance, the optimum plant ideotype and selection strategy vary with the prevalent type of stress in the target region. If favourable and unfavourable seasons alternate, a simultaneous selection for yield potential and yield under stress should ensure responsiveness to favourable conditions, which will result in higher mean yields across seasons. If unfavourable conditions are likely, selection for yield can best be done under stress, because of the limited contribution of yield potential. In case the timing of stress is predictable, phenology will be an efficient selection criterion to improve yields. However, if stress is likely to occur, but its timing and nature are unpredictable, selection for tillering capacity,

Table 4 Contribution (%) of yield potential, stress escape and stress tolerance to yield in environments with contrasting timing and intensity of drought stress and contrasting temperature during grain filling

Drought stress	Low temperature			High temperature		
	Yield potential	Stress escape	Stress tolerance	Yield potential	Stress escape	Stress tolerance
None	100.0	0	0	4.5	58.8**	36.7*
Moderate post-flowering	14.5	37.7*	47.7**	0.4	81.4***	18.2
Severe post-flowering				4.2	72.8***	23.0+
Severe pre-flowering	56.7**	3.9	39.9*	9.3	23.0+	67.7***

+P < 0.10; *P < 0.05; **P < 0.01; ***P < 0.001

which increases asynchrony in flowering, is recommended to enhance the probability of escape (Ludlow and Muchow 1988). A characterization of the major pearl millet-growing areas in the country in terms of patterns of stress occurrence, can therefore be very useful to breeders for identifying plant traits that enhance adaptation to stress.

ACKNOWLEDGMENTS

The critical comments of Dr F R Bidinger and Dr D E Byth, ICRISAT, Patancheru, on the manuscript are highly appreciated.

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