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ABSTRACT

Yields of pearl millet [*Pennisetum americanum* (L.) Leeke]—a rainfed crop grown mainly on light soils in the semiarid and arid regions—are often reduced by water deficit when rains end early. The comparative response of this crop to varying intensity and timing of water deficit during flowering and grain-filling was investigated in field experiments using a line-source sprinkler system. The soil was an Alfisol (Udic Rhodustalf) with approximately 60 mm of plant-extractable moisture. Genotypes differing in maturity were used to simulate differing timings of terminal stress. Grain yields were linearly reduced with increasing intensity of stress in all genotypes. Yield reduction rate was dependent on the time of stress onset in relation to time of flowering, as earlier-flowering genotypes partially escaped stress. Grain number per unit area and grain size were reduced by intensity of water deficit. Grain yield and grain number, but not grain size, were affected by the time of stress onset at all intensities. Across the entire data set, stress intensity and timing accounted for 75% of the variation in measured grain yield. An advance in time of onset of stress by a day caused a 0.9% reduction in relative grain yield, compared to a 0.7% reduction in relative grain yield for each 1% additional irrigation deficit. Effects of timing of stress increased significantly with increase in stress intensity. The results emphasize the importance of timing and intensity of stress when comparing genotypes of different maturity groups using line-source gradient system, or when selecting genotypes for drought-prone environments.

Additional index words: Line-source sprinkler irrigation, Water stress, Drought stress, *Pennisetum americanum* (L.) Leeke, Irrigation deficit.

PEARL millet is grown almost entirely as a rainfed crop in the arid and semiarid regions of south Asia and sub-Saharan Africa. Productivity of this crop is limited by the low amounts and erratic distribution of rainfall in these regions, compounded by the low water holding capacity or shallow soils on which the crop is frequently grown.

Periods of crop water deficit in such environments vary in timing, intensity, and duration. Each of these factors has different effects on crop growth, and they occur in a myriad of interactions under natural rainfall conditions, making the assessment of specific responses of crops to naturally occurring droughts difficult. In general, crops are more sensitive to water deficits at growth stages when critical steps in reproductive processes occur (Salter and Goode, 1967), but the effects of timing are also dependent on the intensity and duration of the stress period.

In cereals, studies have indicated different responses to intensity and timing of stress at different growth stages, with the most damaging combination being severe water deficits at flowering and during grain-filling (Choudhary and Kumar, 1980, Garrity et al., 1982; Lewis et al., 1974, Mahalakshmi et al., 1987). The importance of timing of stress is evident when genotypes of different maturity groups are subjected to a single terminal water stress treatment beginning at the same time (Fisher and Maurer, 1978, Garrity et al., 1983; Saeed and Francis, 1983; O'Neill et al., 1983). Earlier-maturing genotypes partially escape stress, while later-maturing genotypes suffer stress during critical periods of flowering and grain-filling.

Previous reports on the effects of water stress at different growth stages in pearl millet have identified flowering and grain-filling as the periods most sensitive to water stress (Lahiri and Kharabanda, 1965, Mahalakshmi and Bidinger, 1985), and have shown the importance of time of onset of stress during these periods (Mahalakshmi et al., 1987). These earlier studies addressed the problem only partially by comparing the effects of a single intensity of water deficit at different times of onset of stress. Field studies reported here were conducted using the line-source sprinkler irrigation system (Hanks et al., 1976) to compare the response of pearl millet to an increasing intensity of water deficit at different times of onset of stress during flowering and grain-filling. Genotypes differing in time to maturity were used to simulate different times of onset of stress.

MATERIALS AND METHODS

The experiments were conducted during the 1981 and 1982 dry seasons (January–May) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) (17°30′ N and 78°16′ E). The soil was an Alfisol with approximately 60 mm of plant extractable moisture. Since the dry season is almost rain-free, with high atmospheric evaporative demand (Fig. 1), the crop was irrigated except during the treatment periods.

Sixteen millet genotypes in 1981 and 32 in 1982 were machine-planted in rows on ridges 75 cm apart, and irrigated. In both years the crop emerged on 25 January. Rows were oversown and thinned to 10 cm between plants at 10 d after emergence (DAE). The experimental design in both the years was a modified split-plot (strip) design with the genotypes as the main plot and the nine irrigation deficit

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treatments (created by line-source irrigation) arranged in strips as subplots within the main plot. The subplot unit consisted of two adjacent rows of 4-m length (1981) or 2-m length (1982). The main plots were replicated twice. Nitrogen and P (P_2O_5), each at the rate of 40 kg ha^{-1}, were banded into ridges prior to planting. Additional N at the rate of 40 kg ha^{-1} was side dressed at 15 DAE.

The crop was irrigated to field capacity by flooding the furrows between ridges at weekly intervals from sowing to 45 DAE. Irrigation deficit treatments were imposed from 58 DAE in 1981 and 50 DAE in 1982 (Fig. 1) until maturity, by a single line of sprinklers parallel to the ridges with the replications on either side of the line. Data from the two rows next to the line source were discarded. The irrigation deficit treatments were applied at weekly intervals during the early morning hours when wind speeds were low. The amount of irrigation applied to the treatment nearest to the line source was designed to replace approximately two-thirds of the cumulative class A pan-evaporation for the preceding week. Water was collected in catch cans placed at 1.50, 3.75, 6.00, 8.25, 10.50, 12.75, and 15.00 m from the sprinkler line. Irrigation treatments were expressed as irrigation deficits compared to the nonstressed subplot closest to the line source (1.50 m).

Time to flowering was recorded when stigmas had emerged on the main shoots of 50% of the plants in a plot. At maturity, panicles from two rows of 3-m length (4.5 m^2) in 1981 or 1.5-m length (2.25 m^2) in 1982 were harvested and dried at 60°C; grain yield and its components were determined from the plot sample.

The response of individual genotypes to increasing water deficits was not the object of this study. Genotypes were used merely as a method to vary times of onset of stress relative to flowering. Therefore, to remove the inherent genotypic differences in grain yield potential, relative (to nonstressed control plot) values of grain yield and its components were used. The range in time to flowering of the genotypes in 1981 was 42 to 64 DAE, and 32 to 61 DAE in 1982. Genotypes therefore were at different times from flowering when the line-source treatment was imposed. Timing of onset of stress (from flowering) was determined as the difference between time of starting the irrigation deficit treatments and time to flowering for each genotype. In 1981 the onset of stress ranged from 16 d before flowering to 6 d after flowering, and in 1982 it was 11 d before flowering to 18 d after flowering.

For each genotype the response to irrigation deficit was estimated by linear regression of relative grain yield and its components against irrigation deficit. The linear regression coefficient, the fractional reduction in relative grain yield of each genotype for each 1% additional irrigation deficit [defined as yield reduction ratio (YRR)] reflected the sensitivity of the genotypes to changing intensity of stress.

Multiple linear regression analysis was used to determine the combined effects of intensity and timing of stress on relative grain yield and its components.

RESULTS AND DISCUSSION

Comparison of Years

The range in time to 50% flowering of the genotypes was 22 d (42-64 DAE) in 1981, and 29 d (32-61 DAE) in 1982 (Fig. 1). The line-source irrigation was begun later in 1981 (58 DAE) because of rains between 45 and 52 DAE (total of 76 mm) and later onset of flowering due to cooler mean air temperatures during the panicle development stage. The weather conditions, however, were hot and dry during the treatment period, ensuring a severe water deficit (Fig. 1). A few showers occurred during the treatment period in 1982 (total of 17 mm between 65 and 85 DAE) (Fig. 1), which reduced pan-evaporation, so lesser amounts of water were applied compared to 1981. The total pan-evaporation during the treatment period (beginning of the line-source irrigation to harvest) was 356 mm in 1981, and 325 mm in 1982.

Comparison of Genotypes

Maximum grain yield (yield in the nonstressed subplots) of the genotypes ranged from 138 to 263 g m^{-2} in 1981, and 156 to 286 g m^{-2} in 1982. Differences were significant in both years. These differences resulted in the common problem of negative association between the intercept and regression coefficient found in regression analyses of grain yield on water applied in line-source studies (ICRISAT, 1979) or stability analysis (Fisher and Maurer, 1978). For this reason grain yield and its components were expressed relative to the nonstressed control plots.

Relative grain yields in both years were linearly reduced with increasing water deficit. However, reduction was higher in the later-flowering genotypes than in the earlier-flowering ones (Fig. 2). This finding resulted in significant positive correlations (r = 0.87, P<0.001 in both years) of the YRR with time to flowering in both years (Fig. 3). The lower YRR for earlier-flowering genotypes was attributed to their escaping stress during the critical period of early grain-filling (Mahalakshmi et al., 1987). Similar effects of early maturity have been reported in sorghum [*Sorghum bicolor* (L.) Moench] in both line-source irrigation stud-

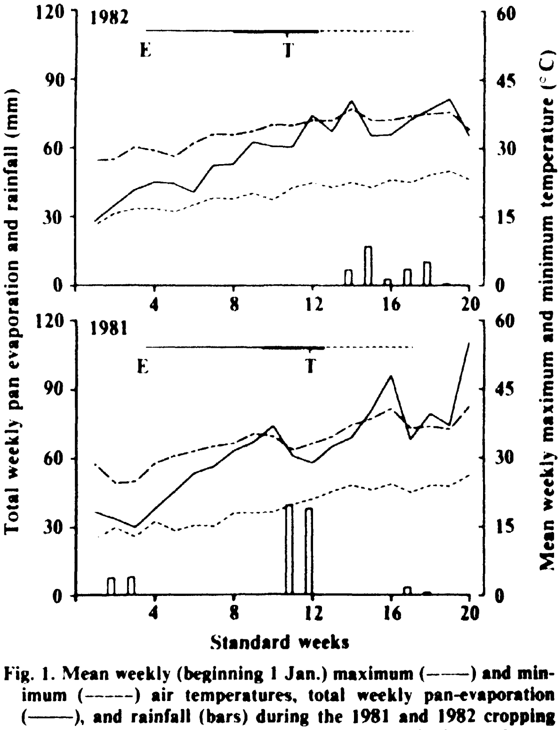

Fig. 1. Mean weekly (beginning 1 Jan.) maximum (——) and minimum (-----) air temperatures, total weekly pan-evaporation (——), and rainfall (bars) during the 1981 and 1982 cropping seasons. The horizontal line above each figure indicates the experimental period. E = crop emergence; bold portion = range in time to flowering; T = initiation of moisture gradient treatments.

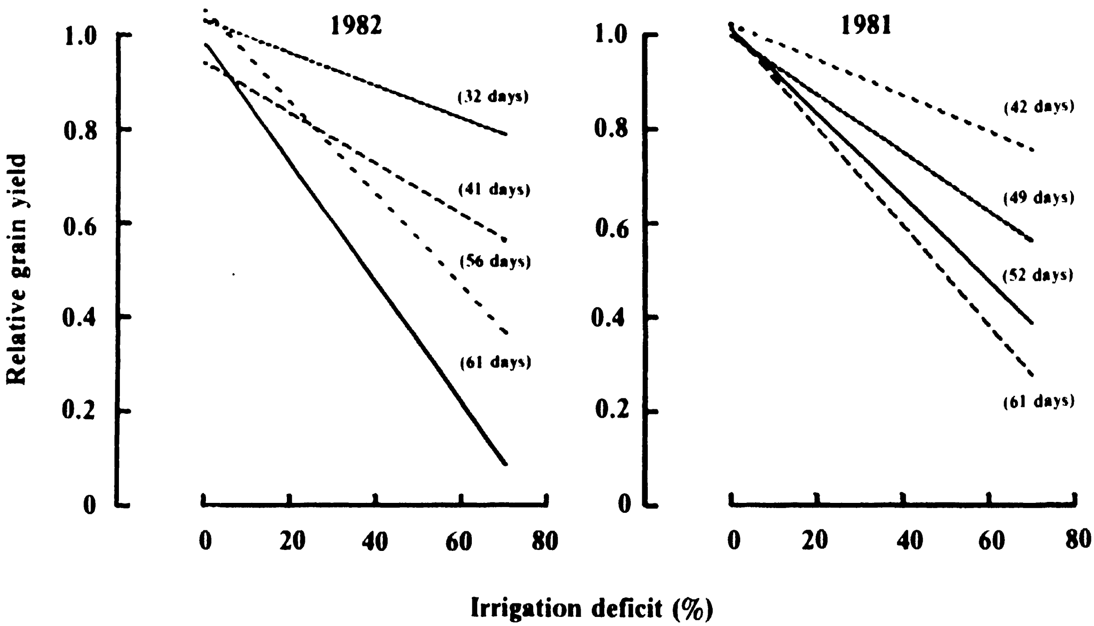

Fig. 2. Relative grain yield at different irrigation deficits for a few selected genotypes of different flowering times in 1981 and 1982. Time to flowering is indicated for each genotype.

ies (Garrity et al., 1983) and in multilocation adaptation testing (Saeed and Francis, 1983), and in wheat (*Triticum aestivum* L.) in genotype comparisons under stress (Fisher and Maurer, 1978).

Intensity of Stress

As the relative grain yields of individual subplots were influenced by both intensity of stress and the time of onset of stress, the data were analyzed in a way that would separate these two factors. Relative yield and relative yield components were regressed against time of onset of stress for each individual irrigation deficit produced by the line-source system. In this comparison, the intercept of the regression represents the effect of intensity of stress beginning at flowering at each irrigation deficit, and the regression coefficient represents the effect of time of onset of stress.

An increase in irrigation deficit (intensity of stress)

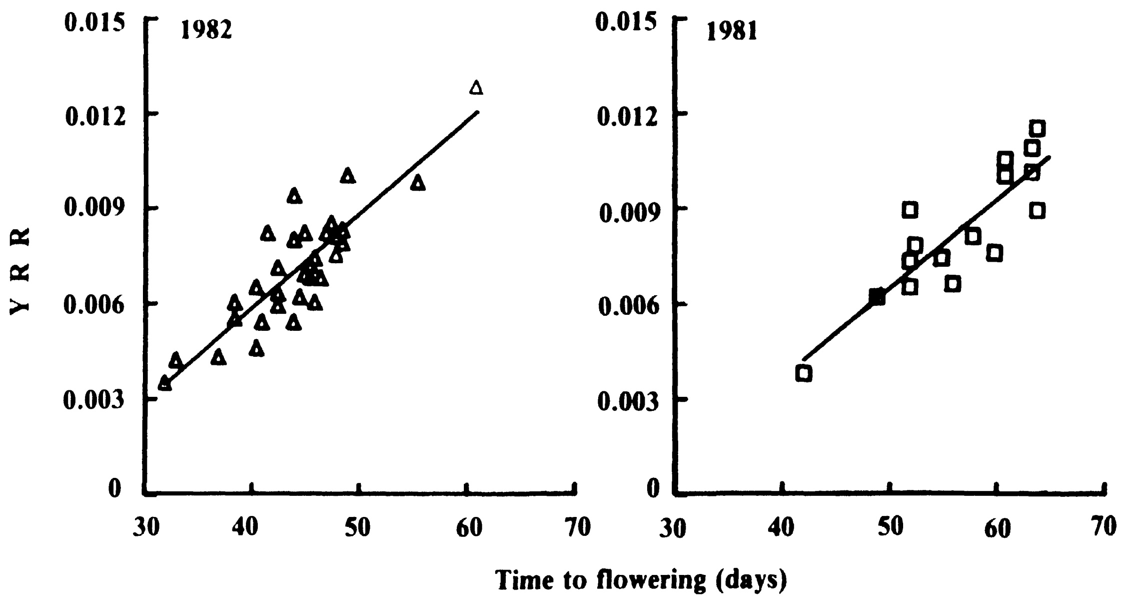

Fig. 3. Relationship between YRR (change in relative grain yield for each percent irrigation deficit) and time to flowering for all genotypes 1981 and 1982.

Table 1. Intercept (a) and regression coefficient for time (in days) of onset of stress from flowering (b_t, relative grain yield per day, relative grains per day, and relative 100-grain size per day) and percent variance accounted for (r^2) at various irrigation water deficiets for relative grain yield and its components in 1981 and 1982.

Irrigation deficit (%)	Relative grain yields m^{-2}			Relative grains m^{-2}			Relative 100-grain size		
	a	b_t	r^2	a	b_t	r^2	a	b_t	r^2
1981									
Mild stress									
10	0.94	0.0044	28*	0.97	0.0007	NS	0.95	0.0031	NS
19	0.88	0.0066	28*	0.90	0.0052	38**	0.95	0.0009	NS
Moderate stress									
27	0.80	0.0107	38**	0.85	0.0114	55**	0.91	0.0008	NS
39	0.71	0.0104	42**	0.75	0.0103	43**	0.91	0.0007	NS
46	0.63	0.0131	47**	0.71	0.0118	37**	0.85	0.0038	NS
Severe stress									
55	0.51	0.0170	73**	0.59	0.0184	71**	0.83	0.0003	NS
63	0.45	0.0195	68**	0.55	0.0217	68**	0.79	0.0020	NS
72	0.37	0.0188	89**	0.46	0.0188	81**	0.77	0.0056	NS
1982									
Mild stress									
8	0.87	0.0008	NS	0.89	−0.0015	NS	0.92	0.0015	NS
17	0.83	0.0083	16*	0.85	0.0081	15*	0.92	−0.0001	NS
26	0.74	0.0060	NS	0.76	0.0072	NS	0.92	−0.0015	NS
Moderate stress									
35	0.72	0.0103	24**	0.77	0.0096	18**	0.88	0.0016	NS
44	0.59	0.0109	36**	0.68	0.0100	26**	0.82	0.0019	NS
Severe stress									
52	0.49	0.0183	52**	0.60	0.0166	35**	0.78	0.0037	NS
61	0.39	0.0194	66**	0.51	0.0187	56**	0.73	0.0057	12*
71	0.28	0.0187	68**	0.41	0.0205	52**	0.69	0.0021	NS

*,** Significant at the 5 and 1% probability levels, respectively. NS = not significant.

resulted in a linear decline in relative grain yield for stress beginning at flowering (intercepts of the regressions, Table 1). In both years we found approximately 0.9% reduction in relative yield for each 1% additional irrigation deficit, with little evidence of departure from linearity, even at low irrigation deficits (Fig. 4). We attributed this latter result to the combination of low soil moisture storage and high evaporation rates. The yield decline was attributable to a decrease in both grain number and size. Individual grain size was less affected by milder stress intensities than grain number, and was less sensitive to increasing irrigation deficits than was grain number. Grain number at severe intensities of stress declined to about 45% of that of the nonstressed control, compared to only 75% of the nonstressed control for individual grain size (Table 1). In cereals, grain size is generally less influenced by water stress during flowering and grain-filling than is grain number (Cruz and O'Toole, 1984; Garrity et al., 1983; Mahalakshmi et al., 1987). This effect may be due to greater amounts of stored carbohydrate being remobilized under stress (Passioura, 1976) or to the reduction in sink size (grain number) under stress.

Timing of Stress

The importance of time of onset of stress was dependent on the severity of the stress (Table 1). Both change in relative yield per day, with change in time of onset of stress (b_t), and the percentage of variation in grain yield explained by the time of onset (r^2) increased with an increasing irrigation deficit. At mild stress levels (< 25% irrigation deficit) the time of onset of stress accounted for 28% of the variation in relative yield in 1981 and was considerably less in 1982. The actual decline in relative yield was approximately 0.5% per day-advance in the onset (Table 1). The variation in yield accounted for by time of onset of stress increased to 30 to 40% for moderate stress (25 to 50% irrigation deficit) and to 60 to 80% for severe stress (>50% irrigation deficit). The rate of decrease in yield per day-advance in onset of stress similarly increased to 1.1% in moderate and 1.9% in severe stress.

The reduction in relative yield with change in time of onset of stress was entirely due to a reduction in grain number, as in only one case was the regression of individual grain size on time of onset of stress sig-

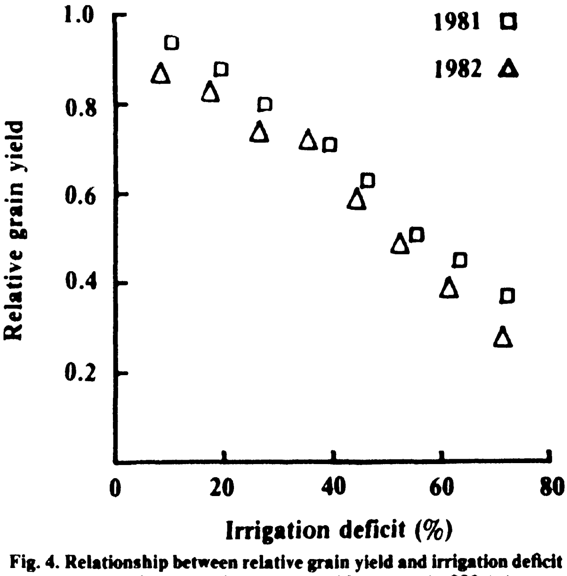

Fig. 4. Relationship between relative grain yield and irrigation deficit for stress beginning at flowering in 1981 (□) and 1982 (△).

Table 2. Intercept (a), regression coefficients for time (in days) of onset (b_t, relative grain yield per day), intensity of stress (b_i, relative grain yield per percent irrigation deficit) and coefficient of determination (R^2) for relative grain yield for 1981 and 1982, and the combined data at the three stress intensities.

Intensity of stress	a	b_t	b_i	R^2
		Across intensities		
1981	0.998	0.01090	-0.00826	0.86**
1982	0.899	0.01023	-0.00709	0.72**
Combined	0.941	0.00873	-0.00746	0.76**
		By intensity		
Mild	0.948	0.00316	-0.00593	0.14**
Moderate	1.092	0.00993	-0.01076	0.48**
Severe	1.013	0.01651	-0.00957	0.69**

** Significant at the 1% probability level.

nificant (Table 1). As the irrigation deficit increased, the reduction, in both relative grain number and relative grain yield, and the amount of variation in both grain number and grain yield explained by time of onset of stress (r^2) were similar (Table 1).

The reduction in grain number per unit area with earlier onset of stress was due to a reduction in both panicle number and grain number per panicle (data not presented). In the mild to moderate stress treatments, the effects of time of onset of stress were mainly on panicle number. Grain number per panicle was not consistently affected by time of onset; but there was some evidence for compensation between the two components of grain number (i.e., if panicle number was not significantly reduced, grain number per panicle would be more affected). Under severe stress, earlier onset of stress affected both components, but generally, grain number per panicle was affected to a greater degree than panicle number.

The lack of a significant effect of time of onset of stress on grain size (in contrast to the marked effect of intensity of stress) may have been due to prior adjustments in grain numbers. With an early onset of stress, particularly under severe stress, the large decline in grain number allowed the remaining grains to fill to a degree equal to those subjected to later stress.

The regression coefficients for the time of onset of stress (b_t) at different irrigation deficits for relative grain yield were similar within the three intensities of stress defined above and in Table 1, although between groups the regression coefficients were different. This finding, in fact, was the basis of an origin~l grouping of stress intensities. Thus, the effects of intensity on the relationship of yield and time of onset of stress could be simplified into three general classes of mild, moderate, and severe stress. The importance of time of onset of stress approximately doubled from one class to another.

Timing and Intensity of Stress

The two factors, timing and intensity of stress, accounted for 70 to 85% of the variation in grain yields (Table 2), both within and across years. Therefore, these factors determined crop productivity in this end-of-season stress environment. Both effects were linear and their interaction was not significant in either year. The magnitudes of the regression coefficients across years were similar, despite the fact that they were for different genotypes in the 2 yr. The combined regression indicated a decrease of 0.9% relative yield per each day-advance in onset of stress from flowering, compared to a 0.7% decrease in relative grain yield for each percent increase in moisture (irrigation) deficit.

When the data sets were separated into the three stress intensity classes described earlier, the absolute and relative importance of timing and intensity of stress were evident (Table 2). At mild intensities of stress, these two factors accounted for only 14% of the variation in relative grain yield. At moderate and severe intensities the percentage of the variation in grain yield explained by the two factors increased significantly. The regression coefficient for timing of stress (change in grain yield per day-change in onset of stress) also increased from mild to severe intensities (Table 2), indicating greater relative grain yield reductions due to earlier onset of stress as the irrigation deficit increased. The regression coefficient for intensity of stress (change in yield per percent change in stress intensity) was greater at moderate and severe intensities than at mild intensities. However, between moderate and severe intensities there was no significant difference.

These results have significance for breeding in drought-prone environments. In environments characterized by water deficits at or after flowering, the benefit of fitting genotypes whose flowering coincides with moisture availability will depend on the intensity of stress. In the present study the absolute gain in relative grain yield for a genotype that flowered a week earlier in the mild (80–90% relative grain yield) stress environments, was only 2%. In the moderate (60–80% relative grain yield) and severe (45–60% grain yield) stress environments, a week-earlier flowering resulted in 7 and 11% absolute increases in relative grain yield, respectively. Therefore, the value of recommending drought escape (appropriate time to flowering) for environments where end-of-season stress is common would depend on the severity of the stress. Only in environments where droughts of moderate to severe intensity during grain-filling are a regular feature, would it be advantageous to fit genotypes whose sensitive periods of flowering and grain-filling coincide with availability of water.

Several reports on the use of the line-source system to compare the relative tolerance of individual genotypes to water stress have indicated that genotype response is dependent, partially at least, on maturity (Garrity et al., 1983; O'Neill et al., 1983; ICRISAT, 1979), suggesting drought escape as an important component of drought response. Our experience with pearl millet suggests that drought escape is in fact a much larger component of drought response than drought tolerance (Bidinger et al., 1987). Clearly this role of drought escape needs to be quantified, or accounted for, if differences in drought tolerance are the objective of the comparison.

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