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Crop physiology and breeding for drought tolerance: research and development

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ABSTRACT

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This paper presents an example of the research and development function of a physiology group within a cereal breeding program: an evaluation of the possibility of incorporating selection for tolerance to drought stress during the flowering and grain-filling period in pearl millet. It includes a review of the problem and possible solutions, and a report of two experiments conducted to identify phenotypic characteristics associated with yield differences under stress which could be used as selection criteria in breeding for tolerance.

Differences among genotypes in yield under stress during flowering and grain-filling were partitioned into differences in yield potential, drought escape, and drought tolerance; the drought response accounted for more than 40% of the observed yield differences. Phenotypic traits related to yield under stress were divided into those reflecting drought escape and those reflecting drought tolerance. Drought tolerance was found to be primarily expressed in traits relating to the ability to maintain grain numbers under stress (grain number per panicle and per unit area, and grain yield per panicle). Drought escape, in contrast, was expressed in terms of greater grain biomass and higher harvest index. However, the field data also indicated that considerable progress in yield under stress should be possible by selection for earlier flowering and improved yield potential alone.

INTRODUCTION

Plant or crop physiology, as a component of a crop improvement program, differs markedly from plant physiology as a basic research discipline. Research objectives for the physiologist in a crop improvement program are set by the overall objectives of the program, and most often are solutions to problems or evaluations of new selection criteria, plant traits, etc. The final outcome is as much new procedures and products as it is new knowledge. In contrast, the basic research physiologist is more free to determine his own specific avenues of research, and the new knowledge generated in the investigation of basic processes is usually sufficient justification for undertaking the work.

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A crop improvement program has been compared to an industrial process (Blum, 1985). Raw materials (in the form of crop genetic resources) are fed into the process, and products in the form of varieties, hybrid parents, etc., are produced at the end of the process. Success is measured in terms of volume of production and quality and marketability of the product; therefore both innovation and efficiency are necessary in the process. This analogy is conveniently extended to a physiology unit within a crop improvement program, in terms of an industrial Research and Development (R & D) unit within the overall process. Thus, the physiologist may be asked to examine a part of the breeding process which is not productive or is comparatively inefficient, to evaluate the possibility of adding a new feature to a present product, or to determine if a new product is feasible. Pathology, entomology, etc., units serve similar functions in their particular areas of specialization.

This paper presents an example of the R & D function of a physiology group within a cereal breeding program. The problem considered is the possibility of incorporating selection for tolerance to drought stress during the flowering and grain-filling period into a breeding program on pearl millet (*Pennisetum glaucum* (L.) R. Br.) in the Sahelian Zone of West Africa. The R & D exercise consisted of an assessment of the problem and the solutions to it available in the literature, and field experimentation to identify basic crop parameters (yield components and phenology) which were correlated to drought tolerance and drought escape, and which could potentially be used as selection criteria. This initial 'physiology' input into the breeding program involved mainly a systematic analyses of a problem and possible solutions to it, rather than detailed studies of the physiology of either drought effects on the crop or the crop itself.

DEFINING THE PROBLEM

The need for drought tolerance

Rainfall in the Sahelian zone (300–600 mm) of West Africa is characteristically variable and undependable. The coefficient of variation of annual rainfall ranges between 15 and 30% (Sivakumar, 1986) and is inversely related to average annual rainfall (Cochème and Franquin, 1967). More importantly, annual rainfall has been persistently less favourable across the zone since the late 1960's (Forest, 1982; Sivakumar, 1987). For example, Sivakumar (1989) has shown, for Niger, that the standard deviation for the onset and ending of rains has increased during the period, and that the length of the growing-season itself has been reduced by 5 to 20 days. Most importantly, rainfall during the month of August, when the soil profile normally fills, providing stored water for grain-filling during September/October, has declined by as much as 40% (Sivakumar, 1989). Thus, the frequency of drought stress during the grain-filling period has increased both because the rains have ended earlier and because the amounts of stored soil moisture at the end of the rains have declined.

Yields of pearl millet, the dominant cereal crop in the Sahelian agroclimatic zone, have declined over the last two decades because of these changes. New millet varieties need to be of somewhat shorter cycle, to adjust to the shorter rainy period, and to possess tolerance to stress during the grain-filling period to adjust to the probability of reduced amounts of stored soil moisture at the end of the season.

Selection for tolerance

Breeding for adaptation to drought has been the subject of a great deal of discussion and advocacy in the literature in the past two decades (cf. Blum, 1985). Several points emerged from a review of this literature which seemed relevant to establishing a practical breeding program for improving the adaptation of pearl millet to changing rainfall pattern in the Sahel.

(1) While grain-yield (mean and variance) is the ultimate touch-stone of adaptation to drought stress, direct selection for yield under natural drought conditions is not likely to be the most effective way of improving actual yields in stress conditions. Naturally occurring stress environments are notoriously variable and unrepeatable, and the precision of measurement of genotypic differences is often poor and therefore heritability is low (Blum, 1985).

(2) Grain-yield achieved in a stress environment is also not necessarily a good measure of stress tolerance per se, as genotype differences in yield potential and drought escape have large effects on yields under stress as well (Fischer and Maurer, 1978; Bidinger et al., 1987a). Breeding for adaptation to drought environments involves breeding for more than stress tolerance (in a physiological sense) alone.

(3) The approach outlined by Blum (1983) which combines selection for yield potential (and presumably an appropriate phenology) in favorable conditions, with selection under stress conditions for the expression of traits thought to be associated with drought tolerance, seems most appropriate. It requires specific research to identify the most appropriate traits to use for selection for drought tolerance, however (e.g., Fischer and Wood, 1979); and, if possible, the creation of controlled, repeatable stress environments for effective selection.

(4) The number of traits proposed as responsible for, or as indicators of, drought tolerance are large (cf. reviews by Turner, 1979; Ludlow and Muchow, 1988). Few of these traits have been critically evaluated, however (Ludlow and Muchow, 1988), and the necessary evidence to support their use as selection criteria is often lacking (Bidinger and Witcombe, 1989).

(5) It is likely that whole-plant/crop responses to stress (sometimes called

'integrated traits') will be more effective as selection criteria, at least initially, than will individual physiological or biochemical mechanisms of drought avoidance or tolerance. Such whole-plant responses are more easily measured, and are more likely to be related to crop performance than are individual resistance mechanisms (Bolanos and Edmeades, 1988).

(6) To identify responses to stress that could be used as selection criteria for stress tolerance, their relationship to genotype tolerance or susceptibility to stress needs to be assessed in field experiments. To do this, some estimate of genotype tolerance of, or susceptibility to, stress (as distinct from genotype yield) of the type proposed by Fischer and Maurer (1978) or Bidinger et al. (1987b) is essential.

(7) Once such potential selection criteria are identified from field experiments, the degree of genetic variability which exists for them, their heritability, the response to selection for them (in terms of yield improvement) and the cost of adding them to a breeding program, need to be assessed before a final decision on their use is made. Such assessments, however, can be done in a pilot-scale breeding program, so that materials produced in these assessments can be directly used, if selection is useful.

Field research needs

The above review of the literature led to the design of the experiments described below, which were intended to:

(1) verify that there were useful yield differences among pearl-millet genotypes of Sahelian origin under flowering/grain-filling drought-stress conditions;

(2) determine if the expression of grain-yield under stress was correlated to the expression of particular basic components of crop growth or crop yield, (e.g., Ludlow and Muchow, 1988); and to determine if these correlations under stress differed from those in the absence of stress;

(3) separate these components/traits, etc., which are correlated to grain-yield under stress conditions, into expressions of the effects of yield potential, drought escape, or drought tolerance; and

(4) select one or more specific yield components/traits to evaluate as selection criteria for tolerance to stress, i.e. to evaluate for available genetic variability, heritability and response to selection.

EXPERIMENTAL MATERIALS AND METHODS

Experimental design and treatments

Two field experiments were conducted at the ICRISAT Sahelian Center, Sadoré (13°N, 2°E) in Niger during the dry season (February–May) in 1988

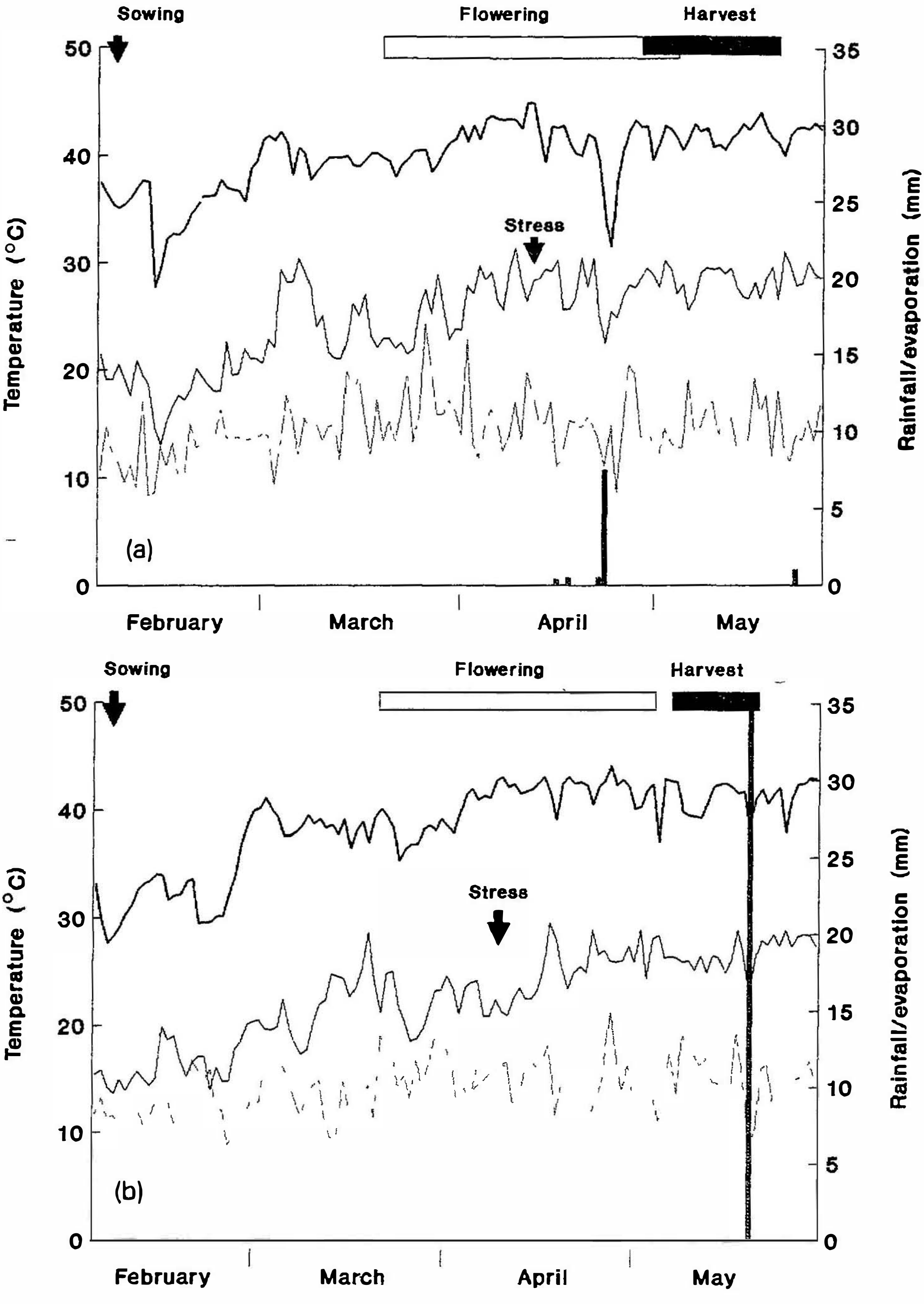

Fig. 1. Daily maximum (—) and minimum (—) temperatures, pan evaporation (.........) and rainfall (bars) during the crops' development (indicated by upper horizontal lines) in (a) 1988 and (b) 1989.

and 1989. This period is characterized as rain-free, with high mean air temperatures, and large vapor-pressure deficits which result in high potential evaporation rates (Fig. 1).

The experimental design was a modified split plot, with main plots (irrigation treatments) replicated three times and sub-plots (genotypes) repeated twice within each main plot. Irrigation treatments consisted of a well-irrigated control and a flowering/grain-filling drought-stress, in which irrigation was discontinued when 50% of the genotypes reached 50% flowering, simulating an early ending of the rains. Both treatments received regular sprinkler irrigation on a 4–7-day cycle (30 mm per irrigation in 1988 and 38 mm in 1989). Subplots were four rows (3.0 m) by 5.6 m (in 1988) and 4.8 m (in 1989), of which two rows by 2.4 m (3.6 m^2) in 1988 and 2.0 m (3.0 m^2) in 1989 were harvested at maturity. The remaining length of the plots was used in a grain-growth study, not reported here. A total of 42 (in 1988) and 45 (in 1989) genotypes were included in the experiments. However, only 34 entries were included in the final analysis in both years, as certain genotypes were dropped because of high disease incidence and extremes in flowering date. The range in flowering date of the 34 included in the analysis was limited to ten days. This interval was considered the likely maximum range in flowering among breeding materials intended for a specific environment. The genetic materials grown in these experiments were advanced breeding lines, released varieties, and local landraces from the Sahelian countries of Senegal, Mali, Burkina Faso, Niger and Nigeria. The entry composition of the experiments varied between years.

Crop management

The experiments were conducted on a sandy loam soil of more than 3 m in depth (Alfisol, Labucheri series after West et al., 1984) containing a sand fraction of more than 90%. Farmyard manure and fertilizer were broadcast and incorporated with a tractor-drawn tyned cultivator, at the rate of 10 t manure ha^{-1} and 45 kg each of N, P_2O_5, and K_2O ha^{-1}. A side-dressing of 26 kg N ha^{-1} was incorporated 18 days after sowing (DAS). Carbofuran was applied at the rate of 4 kg a.i. ha^{-1} at the time of sowing. Seeds were sown by machine on ridges 0.75 m apart and thinned to three plants per hill, 0.4 m apart at 11–13 DAS. The resultant high plant population (100 000 plants ha^{-1}) hastened and enhanced drought stress after termination of irrigation. Apart from birdscaring, no other disease or pest control was required after planting. Weeds were controlled by mechanical cultivation and one hand-weeding.

Observations and data analysis

Time to flowering (plot basis) was determined when stigmas had emerged on 50% of all main-shoot inflorescences. At harvest, the number of plants and panicles, grain-yield, and above-ground crop biomass were recorded per plot, and 100-grain biomass (from triplicate samples of 100 grains taken at random from the bulk plot harvest) was determined. All crop and grain samples were oven dried at 70°C for 24 h before weighing. Number of grains per panicle and per unit area, as well as threshing percentage (ratio of grain biomass to total panicle biomass, on a plot basis), were derived from the primary data.

The drought tolerance/susceptibility of the trial entries was assessed according to a Drought Response Index (DRI; Bidinger et al., 1987b). It is based on the assumption that the grain yield of the *i*th genotype under stress conditions ($Y_{\mathrm{s}i}$) is a function of potential yield under irrigated conditions ($Y_{\mathrm{p}i}$), time to flowering (FL_i) and a drought response (DR_i):

$$Y_{\mathrm{s}i}=a+bY_{\mathrm{p}i}+c\,\mathrm{FL}_i+\mathrm{DR}_i+E \qquad (1)$$

where E is random error with zero mean and variance δ. The DRI value for an individual genotype is the difference of the actual yield under stress and the regression-estimated yield under stress ($\hat{Y}_{\mathrm{s}i}$) by equation (1), divided by an estimate of E, with the prevision that if $(\hat{Y}_{\mathrm{s}i}-Y_{\mathrm{s}i})\leq E$, then $\mathrm{DRI}=0$. This model can be applied to any stress situation in which a significant portion of the variation in measured grain-yields is due to variation in genotype yield potential and/or time to flowering.

Yield-component traits, biomass, threshing percentage, etc., measured in both the stressed and non-stressed treatments, were correlated across entry means to grain-yields measured in the stressed treatment, to determine patterns of association between yielding ability and the expression of the various traits. Associations of yield under stress with traits measured in the absence of stress were assumed to be constitutive (independent of the effects of stress) where associations with traits only when measured in the stress were assumed to be adaptive (reflecting the response of genotypes to stress).

Those traits whose expression was correlated to yield differences in the stress were correlated, across entry means, to both time to flowering and to DRI, to try to separate those relationships which were expressions of drought escape (correlated to time to flowering) from those which were expressions of drought response per se (correlated to DRI).

RESULTS

Yield under stress

Grain-yields were reduced, on average, by 45% in 1988 and 49% in 1989 in the stress, mainly due to a reduction in grain-yield per panicle (37% and 42%), rather than to a reduction in panicle number (13% and 12%; Table 1). This was consistent with the timing of the initiation of the stress — about the middle of the flowering period — so that only the latest tillers failed to produce

TABLE 1

Means and *F*-ratios (genotype) for flowering and growth-and-yield components in the irrigated control and drought-stressed treatments

Variable	1988		1989	
	Mean	*F*[a]	Mean	*F*[a]
Irrigated control				
Flowering (days)	64	6.11***	66	5.75***
Biomass (g m^{-2})	635	3.68***	856	2.09**
Stover (g m^{-2})	406	3.82***	480	2.21***
Panicle (g m^{-2})	229	3.07***	378	2.11**
Grain-yield (g m^{-2})	161	2.80***	271	1.87**
Panicle m^{-2}	9.8	1.75*	11.5	4.73***
Yield panicle^{-1} (g)	16.4	4.56***	23.7	4.15***
Grains panicle^{-1}	2470	4.68***	3080	4.05***
1000-grain mass (g)	6.73	10.57***	7.70	0.80
Grains m^{-2} ($\times 10^{-3}$)	24.1	3.69***	35.2	2.19***
Harvest index (%)	25.6	4.24***	32.1	4.17***
Threshing percentage	70.0	4.32***	71.6	1.88**
Drought-stressed				
Flowering	62	6.01***	65	5.99***
Biomass (g m^{-2})	453	3.54***	585	3.25***
Stover (g m^{-2})	308	4.93***	358	4.37***
Panicle (g m^{-2})	146	3.67***	228	2.19***
Grain yield (g m^{-2})	88	4.44***	139	2.64***
Panicles m^{-2}	8.5	2.61***	10.1	2.33***
Yield panicle^{-1} (g)	10.4	4.65***	13.7	3.23***
Grains panicle^{-1}	1920	2.48***	2300	3.16***
1000-grain mass (g)	5.41	9.61***	5.99	2.17**
Grains m^{-2} ($\times 10^{-3}$)	16.4	3.43***	23.3	2.43***
Harvest index (%)	19.5	7.49***	24.1	4.34***
Threshing percentage	59.8	5.14***	60.3	3.75***

[a] *F* statistic for genotype; *$P<0.05$; **$P<0.01$; ***$P<0.001$.

panicles. Reduction in yield per panicle was due to an approximately equal reduction in grain number per panicle and in individual grain biomass in both years. The onset of stress about mid-flowering obviously resulted in either the failure of late florets or in the abortion of some embryos following fertilization, as well as in a reduction in grain size.

The range in grain-yield among varieties in the stress treatment was very broad (560–1360 kg ha^{-1} in 1988 and 970–1910 kg ha^{-1} in 1989), indicating that there were considerable differences among the varieties tested in their ability to produce a yield under this type of drought stress. Although there was a slight increase in the coefficient of variation in the stress treatment (from 14.6% to 17.6% as an average of all variables in 1988, and 12.8%–18.0% in 1989), the significance of genotype differences, as judged by the *F*-

ratio from the analyses of variance, was as great in the stress treatment as in the irrigated control for all variables analyzed (Table 1).

The relative contributions of yield potential (yield in the nonstressed treatment), drought escape (assessed by time to flowering) and drought susceptibility or tolerance (assessed by the DRI) to measured yields in the stress, were evaluated by multiple regression of measured grain-yield in the stress on these three variables. The contribution of each was assessed as the percentage of the regression sums of squares it accounted for. Yield in the absence of stress accounted for 4% and 23% of the variability in yield under stress in 1988 and 1989, respectively, time to flowering accounted for 37% and 23%, respectively, and DRI for 41% and 47%, respectively. Drought-response index was significantly ($P < 0.001$) positively correlated to stress grain-yield in both years ($r = 0.65$ and 0.66) and was independent of both time to flowering or yield potential ($|r| < 0.10$), according to definition.

Phenotype/yield relationships

Patterns of association of grain-yield and various crop traits differed considerably in the two treatments (Table 2). For example, in the irrigated treatment, grain-yield was as, or more, closely associated with biomass than with harvest index. In the stress treatment, biomass and grain-yield were only marginally related ($r = 0.33$, $P < 0.05$), but harvest index, reflecting more the growth made during the stress, was very closely related ($r = 0.87$ and 0.69;

TABLE 2

Correlation of measured variables with grain yield in the irrigated control and stressed treatments

Correlate	Correlation coefficient			
	Control		Stress	
	1988	1989	1988	1989
Time to flowering	0.07	−0.27	−0.50**	−0.35*
Biomass	0.76***	0.49**	0.33*	0.33*
Stover	0.64***	0.18	−0.12	−0.01
Panicle	0.93***	0.90***	0.75***	0.95***
Panicles m^{-2}	−0.08	0.35*	0.75***	0.51**
Yield panicle^{-1} (g)	0.90***	0.51**	0.87***	0.87***
Grains panicle^{-1}	0.65***	0.41*	0.51**	0.61***
Individual grain biomass (mg)	0.47**	0.01	0.59***	0.53***
Grains m^{-2} ($\times 10^3$)	0.58***	0.77***	0.79***	0.86***
Harvest index	0.24	0.44**	0.87***	0.69***
Threshing %	0.39*	0.45**	0.77***	0.80***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

TABLE 3

Analyses of the constitutive or adaptive nature of the relationship[a] of grain-yield and selected traits in the stress

Trait	Correlation to yield in the stress		Genotype × treatment F value	
	1988	1989	1988	1989
Time to flowering	−0.61***	−0.50**	1.21	1.38^{+}
Harvest index	0.74***	0.29	2.24**	1.23
Panicles m^{-2}	0.25	0.18	1.26	1.21
Yield $panicle^{-1}$ (g)	0.04	0.26	1.23	1.89**
Grains m^{-2} ($\times 10^3$)	0.00	0.38*	1.19	0.97
Individual grain mass (mg)	0.18	0.11	0.93	1.11
Grains $panicle^{-1}$	−0.10	0.17	1.51*	1.34^{+}
Threshing %	0.58***	0.49**	2.28**	0.82

$^{+}P<0.10$, $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

[a] Data are correlations of the traits measured in the abscence of stress to yield in the stress and the genotype × treatment F values from the across treatment analysis of variance.

$P<0.001$) to yield in both years (Table 2). Several yield components were similarly related to yield in both control and stress, e.g., grain numbers per panicle and per unit area, but there were several yield components which were more strongly correlated to yield in the stress than in the control, i.e. time to flowering, panicle number, grain biomass, and threshing percentage.

The relationships of grain-yield and yield components in the stress treatment were re-examined to determine if these were constitutive or adaptive: (1) by comparing the relationship of yield in the stress to the yield components when the latter were measured in the control compared with when measured in the stress treatment; and (2) by testing for the presence of genotype × treatment interactions in the analysis of variance for the traits across treatments. Only time-to-flowering and threshing percentage were equally well correlated to yield in the stress whether measured in the stress treatment (Table 2) or in the control treatment (Table 3) in both years; all other traits were associated with yield in the stress only when they were measured in the stress. F values from the genotype × treatment analysis of variance were generally >1, but were generally not statistically significant, or F values for traits which were significant in one year were not in the other year (Table 3). Only for grain number $panicle^{-1}$ did the analysis of variance support the hypothesis that the relationship to grain-yield in the stress represented an adaptive response. For the other traits, the correlation data indicated that they were not constitutive indicators of stress tolerance, but clear evidence of g × e interactions was lacking.

Escape vs. tolerance in yield differences

Initial analyses of the data indicated that both time-to-flowering and DRI contributed significantly to the differences in grain-yield among the 34 genotypes. Individual phenotype characteristics which were related to grain-yield in the stress treatment (Table 2) could therefore be reflections of genotype differences in either time-to-flowering (drought escape) or DRI (drought-treatment susceptibility). This was investigated by correlating those traits measured in the stress treatment to both time-to-flowering and the drought index. High values of harvest index and individual grain biomass were clearly associated with drought escape (Table 4). Using these as selection criteria may thus identify many of the same genotypes as would be identified by using early flowering as a selection criterion. In contrast, grain number, both per unit area and per panicle (and consequently grain-yield per panicle), were associated with drought tolerance/susceptibility (drought response index), and not related to flowering. These results suggest that tolerance of drought during flowering and grain-filling is in some way related to the ability of a genotype to maintain grain numbers under these conditions.

The relationship of maintenance of grain numbers under stress to the DRI and grain-yield was examined in greater detail. Grain numbers in the stress were expressed as a percentage of the control values (=percentage maintenance of control values), to adjust for inherent differences among genotypes in grain number. Percentage maintenance of grain number per panicle was

TABLE 4

Correlation of yield and yield-related variables in the stress treatment to flowering (drought escape) and drought-response index (tolerance/susceptibility)

Correlate	Correlation coefficient			
	Flowering		Drought-response index	
	1988	1989	1988	1989
Biomass	0.48**	0.47**	0.52**	0.59***
Stover	0.73***	0.51**	0.23	0.39*
Panicle	−0.35**	−0.39*	0.68***	0.68***
Grain-yield	−0.61***	−0.51**	0.65***	0.66***
Panicles m^{-2}	−0.55***	−0.59***	0.51**	0.12
Yield panicle^{-1}	−0.31	−0.24	0.56***	0.73***
Grains panicle^{-1}	0.04	0.12	0.42*	0.57***
Individual grain mass	−0.46**	−0.56***	0.29	0.38*
Grains m^{-2} ($\times 10^3$)	−0.27	−0.26	0.61***	0.57***
Harvest index	−0.78***	−0.68***	0.39*	0.20
Threshing %	−0.62***	−0.60***	0.41*	0.44**

*$P<0.05$, **$P<0.01$, ***$P<0.001$.

TABLE 5

Correlation of percentage (of control) maintenance of grain numbers in the stress treatments to grain-yield, drought-response index, and phenotype

Correlated variable	Per panicle		Per unit area	
	1988	1989	1988	1989
Yield in stress	0.63***	0.57***	0.82***	0.66***
Time to flowering	−0.47**	−0.44**	−0.52**	−0.22
Drought-response index	0.44**	0.45**	0.68***	0.73***
Control phenotype:				
Grains panicle^{-1}	−0.51**	−0.36*	−0.32	−0.11
Grains unit area^{-1}	−0.36*	−0.11	−0.29	−0.24
Stress phenotype:				
Grains panicle^{-1}	0.41*	0.46**	0.42*	0.48**
Grains unit area^{-1}	0.53***	0.53***	0.76***	0.67***
Individual grain biomass	0.31	0.29	0.32	0.27
Yield panicle^{-1}	0.57***	0.55***	0.60***	0.56***
Threshing %	0.74***	0.58***	0.66***	0.50**

*$P<0.05$, **$P<0.01$, ***$P<0.001$.

negatively correlated to time-to-flowering (i.e. positively correlated to drought escape) and positively correlated to DRI in equal measure (Table 5). Percentage maintenance of grain number on a unit-area basis was more closely correlated to drought response. Both estimates were very highly positively correlated ($P<0.001$) to grain-yield in the stress.

Genotypes which suffered greater reductions in grain numbers had (as expected) lower grain numbers, grain-yields per panicle, and a lower threshing percentage in the stress (Table 5). Thus, at least a part of the correlation of these three variables to yield in the stress (Table 2) and to the DRI (Table 4) can be explained by differences among genotypes in the ability to maintain grain numbers in the stress.

DISCUSSION

Phenotype-yield relationships

The broad range in grain-yield differences as a result of flowering/grain-filling drought stress of genotypes of Sahelian origin was similar to those reported for pearl millet genotypes of largely Indian genetic backgrounds (Bidinger et al., 1987a). With approximately similar F values for grain-yield and yield-related variables in the irrigated control and the stressed treatments, the ability to distinguish statistical differences among varieties was not necessarily poorer in the stress treatment than it was in the irrigated control treatment. Therefore the first objective of the field trials — to determine if there were genetic differences among the lines tested — was met.

Patterns of association of grain-yield and certain crop traits (e.g. time-to-flowering, panicle number per unit area, harvest index, individual grain biomass) differed between treatments, but were generally similar between years, confirming the hypotheses that grain-yielding ability is dependent upon different traits (or expressed in different ways) in the presence and in the absence of flowering/grain-filling drought stress. The evaluation of breeding materials should thus focus on different sets of traits in these two environments, an approach similar to that of Blum (1983). Furthermore, the poor correlations between grain-yield in the stress treatment and most yield-related variables when those variables were measured in the control treatment suggested that these correlations represented the expression of an adaptive response to stress. There was no consistant evidence of genotype × treatment interactions for any of these variables, however, with the exception of grain number panicle^{-1}.

The results therefore support the hypothesis that selection for stress tolerance based on selection for traits related to tolerance should be done under stress conditions, but do not support the hypothesis that the association of yield in the stress and these traits represents genotype × treatment interactions, or true adaptive responses to stress, with the possible exception of grain number panicle^{-1}.

Stress tolerance (positive DRI), drought escape (early flowering) and, to a lesser extent, yield potential all played a role in determining grain-yield of the pearl millet genotypes measured in the stress environment, as has been found in other studies (Bidinger et al., 1987b) and crops (Fischer and Maurer, 1978; Acevedo et al., 1989). Separating yield correlates into expressions of the first two of these factors provided an indication of which traits are most useful as selection criteria for drought tolerance (vs. drought escape) under a stress environment. Traits such as higher grain number — both per panicle and per unit area — and grain-yield per panicle were consistently correlated with DRI and not time-to-flowering. Harvest index and individual grain biomass, although strongly related to stress yield, would not be useful traits to select for drought tolerance, as these traits are highly correlated to time-to-flowering, which can be directly selected for.

The finding that better tolerance of flowering/grain-filling drought stress was consistently expressed by higher grain number, both per panicle and per unit area, and grain-yield per panicle, are consistent with findings for Indian genetic materials (Bidinger et al., 1987b), suggesting that this may be a general pattern for pearl millet. All three are to some degree expressions of the same phenomenon, the ability to maintain grain numbers under stress. A recent summary of breeding for drought tolerance in maize suggested that a higher rate of partitioning of assimilates to the reproductive structures was the reason for higher grain numbers and grain-yield under stress (Edmeades et al., 1989). A similar phenomenon may be occurring in millet, which would explain the correlations of DRI and grain-number maintenance.

Selection criteria for drought tolerance

The literature on breeding for improved adaptation to drought suggests that the most efficient approach should be concurrent selection for the various factors affecting crop yields under stress: i.e., selection, in the absence of stress, for yield potential and appropriate crop duration to maximize drought escape, plus selection for traits or responses to stress which are related to tolerance of stress, done under stress conditions. Such an approach is particularly well suited to a recurrent selection program, in which progeny can be assessed for traits associated with tolerance to drought in especially created 'drought nurseries', as a part of the normal multi-environment evaluation of progenies in each cycle.

To do this successfully, the heritabilities of the traits selected as indicators of drought tolerance need to be high, and the correlated response to selection (in terms of drought response) should be large. This latter point is particularly important if selection for the drought-tolerance-related traits is to be done in an off-season drought nursery, where the probability of confounding genotype × season interaction may be substantial.

This dataset did not permit the assessment of correlated response to selection, but the broad-sense heritabilities were assessed for the traits measured in the trial (Table 6). These appeared to be sufficiently high for most of the traits of interest, at least when measured under controlled stress conditions. Additional experimentation is needed to determine the realized heritabilities and response to selection in terms of DRI and grain-yield.

TABLE 6

Broad-sense heritabilities for selected traits correlated to grain-yield in the stress treatments

	Heritability[a]	
	1988	1989
Biomass	0.72	0.69
Harvest Index	0.87	0.77
Grain yield panicle^{-1}	0.78	0.69
Grain number panicle^{-1}	0.61	0.68
Grain number m^{-2}	0.71	0.59
Individual grain mass	0.90	0.54
Threshing percentage	0.81	0.73
Grain-yield	0.77	0.62

[a] Ratio of the genetic to the error variance from the analysis of variance of the stress treatment.

The importance of drought escape

In spite of the focus on drought tolerance in the analysis, drought escape and yield potential accounted for as much of the variation in stress yield in both the experiments, as did drought response. Given that a part of the current problem is the reduced season length (Sivakumar, 1989), breeding for higher-yielding, shorter-cycled pearl millet genotypes for the Sahelian zone may be as productive a strategy as breeding for drought tolerance per se, for stabilizing and increasing yields under such conditions. Short-duration varieties that escape end-of-season drought stress can easily be bred as the heritability of time-to-flowering is high, and the character is easily assessed. Earliness in millet can be associated with reduced yield potential (Bidinger et al., 1987a), and care may be needed not to reduce the cycle length too much, and/or effort made to offset increased earliness with an increased harvest index. For the range of flowering of the genotypes used in the analysis, earliness was not associated with low yield potential (Table 2), and was strongly related ($r > 0.60$, $P < 0.001$) to improved harvest index. A potential disadvantage of choosing earliness as a strategy to offset an apparently changed climatic pattern and high frequency of end-of-season drought is that, in a season with early drought stress, short-duration varieties are more seriously affected as they initiate reproductive growth earlier (Mahalakshmi and Bidinger, 1985). However, the Sahelian genotypes used in this study are strongly photoperiod-sensitive, and the earliest line has a much longer vegetative period that those of the short duration Indian varieties used in those studies (Craufurd and Bidinger, 1988). Other potential problems with earlier varieties (especially increased problems with panicle insects and diseases) would need to be carefully evaluated before such a decision was taken, however.

SUMMARY

This paper describes an R & D effort by a physiology program on the possibility of adding selection for tolerance to drought stress to a breeding program for the Sahelian zone of Africa. The exercise included an assessment of the need for stress tolerance, a review of the literature on selection for tolerance, and a two-year-field experiment to test the conclusions drawn from the literature review and to identify potential selection criteria. Experimental results confirmed that there is variation for grain-yield among pearl millet genotypes of Sahelian origin under flowering/grain-filling drought stress, and that a significant proportion (>40%) of this variation is due to differences in drought tolerance/susceptibility. Several grain-number-related traits were closely related to these differences in drought response, and appear to be useful indicators of drought tolerance. Heritabilities of these traits under controlled stress conditions were high, but their usefulness will finally depend

upon the correlated response to selection for them under controlled conditions, in terms of drought tolerance under naturally occurring stress conditions. The results of the experiment also indicated, however, that improvements in yield potential and in earliness may have as large an effect on yields under stress as will improvement in drought tolerance, for the type of stress experienced in these experiments.

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