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Assessment of Drought Resistance in Pearl Millet [*Pennisetum americanum* (L.) Leeke]. II* Estimation of Genotype Response to Stress

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Abstract

The finding that the more than 50% of the variation in grain yield of pearl millet breeding lines in two different drought stress treatments could be attributed to variation in yield potential and time of flowering was used to develop a drought-response index (DRI) based on the residual variation in grain yield, adjusted for experimental error. DRI was positively correlated to measured yield in the drought treatments, and independent of both yield potential and time to flowering.

DRI in both midseason and terminal stress treatments was unrelated to yield component structure in the irrigated control treatment, indicating that selection for plant type under non-stressed conditions will not influence drought response. DRI was correlated to both grain number per panicle, and grain yield per panicle in both stress treatments, suggesting differential ability to maintain normal grain number, and/or that grain yield per panicle was an important factor in response to stress. Maintenance of panicle number did not seem to be important for maintenance of yield under drought stress. The correlation of DRI and individual panicle yield was of sufficient magnitude for the latter to serve as a selection index in terminal stress. The use of a DRI as a component of breeding for better adaptation to stress is discussed.

Introduction

In the previous paper of this series, it was argued that a retrospective analysis of the reasons for genotype yield differences in a drought-stressed environment (black box analysis, Fischer 1981) is a useful initial step in developing a breeding program to produce improved genotypes for drought environments (Bidinger *et al.* 1987). Such an analysis demonstrated very marked, although contrasting, effects of phenology in midseason and terminal stress conditions in pearl millet [*Pennisetum americanum* (L) Leeke]. These included both direct effects on grain yield — drought escape — and associations between phenology and yield component structure that largely determined the relationship of yield components and grain yield under stress conditions. The combined effects of phenology and yield potential accounted for more than 50% of the observed variation in grain yield among the test entries in both stress treatments.

If drought resistance is considered to be a consequence of advantages conferred by one or more physiological or morphological characteristics (Turner 1982) and is to be manipulated in a breeding program as an independent genetic character (Blum 1979; Richards 1982; Quisenberry 1982), then the assessment of drought resistance should be free from the confounding effects of yield potential and phenology. Yield potential improvement is a universal breeding objective, and

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phenology can be easily manipulated where it offers opportunities to increase or stabilize yields in stress conditions. A procedure for assessing drought resistance should identify genotypes whose performance under stress is better than that predicted from the combined effects of their yield potential and phenology. This is particularly true if such assessments are to be used to identify plant characteristics that confer advantages in stress conditions (Fischer and Wood 1979), otherwise correlation analyses using drought-resistance estimates may identify yield potential- or phenology-related characteristics rather than ones related to drought resistance.

Fischer and Maurer (1978) defined an index of drought susceptibility (*S*) based on the relationship of the change in relative yield (yield in drought/yield in the absence of drought) of an individual cultivar to the change in mean relative yield, across a range of stress intensities, of all cultivars in the comparison. Yields measured in the drought were adjusted for differences in phenology before *S* was calculated. This approach was successful in combining data from multiple-drought treatments to obtain an estimate of genotypic response to a range of stress intensities, and in removing the effects of phenology, but the *S* calculated in this fashion was not independent of yield potential (Fischer and Maurer 1978). As a consequence, *S* was found to be positively correlated to traits associated with high yield potential in the material studied in the trials (Fischer and Wood 1979).

This paper presents a different approach to the calculation of a drought response index (DRI), and examines correlations of this index and yield components in advanced breeding lines of pearl millet. The index presented here is independent of both yield potential and phenology effects. As used here, it is based on a single comparison between stress and nonstress treatments and as such is of limited value for assessment of individual genotypes. It is of use, however, for assessing the effects of specific physiological or morphological characters on response to drought, if the number and diversity of the genotypes tested are sufficiently large. As the objective of the experiments was to examine the variation in drought response, and the factors associated with it, in the current ICRISAT pearl millet breeding program, this index was quite suitable for this purpose.

Materials and Methods

Field Experiments

The field experiments on which this analysis of drought resistance are based are described fully in the previous paper (Bidinger *et al.* 1987). Briefly, they consisted of 3 years of advanced breeding trials grown in two drought environments, and a fully irrigated control environment, during the dry season (February-May). The drought environments were a midseason stress — from floral initiation to flowering — and a terminal stress — begun at flowering and not rewatered. The irrigated control environment was used to measure the expression of potential yield, and yield components for comparative purposes.

The effects of the stress treatments, the relationship of yield and yield components in each stress treatment, and the role of phenology in each, were presented in the previous paper.

Estimation of Drought Resistance

Based on the results of the previous paper, grain yield in a specific stress condition (Y_s) can be considered as a function of yield potential (Y_p), time to flowering (FL), and drought response (DR) such that the yield of a genotype can be expressed as follows:

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

where E is random error with zero mean and variance σ.

Results of analyses in the previous paper indicated that approximately half of the variation in grain yield in each stress treatment could be attributed to variation in yield potential and time to flowering, measured in the fully irrigated treatment. Therefore, if the parameters a, b and c of equation (1) are estimated by minimizing residuals (E + DR_i), yield in the stress can be estimated:

$$\hat{Y}_{si} = a + bY_{pi} + c\mathrm{FL}_i. \qquad (2)$$

The difference between the actual and estimated yields under stress is then a measure of the remaining terms in equation (1):

$$(Y_{si} - \hat{Y}_{si}) = \mathrm{DR}_i + E. \qquad (3)$$

A test for the significance of drought response (DR_i) can be derived by considering the following:

$$Z = | Y_{si} - \hat{Y}_{si} | / \sigma, \qquad (4)$$

where σ is the standard error $\hat{Y}_{si}$.

In practice, if Z is $< 1 \cdot 3$, DR_i is considered to be zero. That is, if the absolute value of the difference between the measured yield in the stress (Y_{si}) and the yield predicted ($\hat{Y}_{si}$) from the time of flowering and yield potential was less than $1 \cdot 3$ times the standard error of $\hat{Y}_{si}$, then the genotype is considered to have no specific response to drought ($\mathrm{DR}_i = 0$). The threshold value of Z of $1 \cdot 3$ was chosen, as it selects those genotypes in the upper and lower 10% of the normal distribution of Y_s.

In the above derivation (equation 1), the estimate of E, σ, will be affected in those cases where $\mathrm{DR}_i \neq 0$. A more robust estimate of E (E') can be obtained using only those genotypes for which $Z < 1 \cdot 3$, i.e., for which $\mathrm{DR}_i = 0$:

$$\hat{Y}_{si}' = a + bY_{pi} + c\mathrm{FL}_i + E'. \qquad (5)$$

DR_i can now be estimated by substituting E' in equation (3), where E' is estimated by σ' (standard error of $\hat{Y}_{si}'$).

The drought response index (DRI) is based on DR and is defined as follows:

(i) if $| Y_{si} - \hat{Y}_{si} | \leq \sigma'$, then $\mathrm{DRI}_i = 0$

(ii) if $| Y_{si} - \hat{Y}_{si} | > \sigma'$, then $\mathrm{DRI}_i = (Y_{si} - \hat{Y}_{si})/\sigma'$.

That is, DR_i is expressed as a multiple of σ' and may have a positive or negative value.

Thus, the response of a genotype to a particular stress (DRI) is zero, if the predicted yield in the stress is within the limits of experimental error as defined above, or has a real (non-zero) value if the difference between predicted and measured yields exceeds the expected error. This method of calculation of DRI can be applied to any stress situation in which a significant portion of variation in measured grain yields is due to variation in genotype yield potential, and/or time to flowering.

Correlation with DRI

The drought response index calculated for each genotype in the midseason and terminal stress treatments in each year was correlated to yield component data to identify traits related to positive DRI values which might be used as selection criteria for DRI. These included the expression of these traits in the non-stressed control, in the stressed treatment, and the relative (to the control) expression in the stress (Fischer and Wood 1979). All values (including the zero values) of DRI were used in the correlations, giving 70 d.f. for each correlation.

Results

The Drought Response Index

Drought response indices were calculated for the terminal stress treatment using linear terms for both yield potential and time to flowering. For the midseason stress treatment, time to flowering was a second order rather than linear effect, so the equation for calculating DRI contained both linear and squared terms for time to flowering.

Because of the way in which DRI was determined, its distribution is symmetric with a positive kurtosis and a mean of 0. Fifty to sixty per cent of the individual genotypes in each stress treatment had a DRI = 0, indicating that their measured yield in the stress was adequately estimated by their yield potential and time to flowering. The remaining entries had non-zero (real) values of DRI, indicating that relative to the other varieties in the trial, they had a different response to the stress at the probability level used in the definition of the DRI.

DRI was designed to provide an estimate of genotypic response to drought stress that is independent of the effects of time to flowering and yield potential. How well it fulfilled these criteria was tested by determining the relationship between DRI and grain yield in the stress treatments, and between DRI and non-stressed yield and time of flowering (Table 1). DRI was significantly positively correlated to grain yield in all years and stress treatments (r = 0·46 to 0·72, $P < 0{\cdot}001$). DRI was not related to yield potential or time to flowering (r = −0·05 to + 0·08), confirming that its relationship to grain yield in stress is independent of the effects of these factors.

Table 1. Correlations of drought response index (DRI) with time to flowering and grain yields measured in the fully irrigated (control) treatment, the stress treatment, and the stress treatment as a percentage of the irrigated control (stress/control). Advanced trials 1981, 1982 and 1983

	1981	1982	1983
Midseason stress DRI			
Control flowering	0·06	0·08	0·02
Control yield	0·06	0·06	−0·01
Stress yield	0·67***	0·58***	0·49***
Stress/control yield	0·47***	0·46***	0·54***
Terminal stress DRI			
Control flowering	0·00	−0·05	−0·01
Control yield	0·05	0·05	0·06
Stress yield	0·55***	0·72***	0·54***
Stress/control yield	0·55***	0·61***	0·46***

*** $P < 0{\cdot}001$.

Grain yields measured in the two stress treatments were simultaneously regressed on yield potential, time to flowering and DRI to evaluate the individual contributions of these three factors to explaining the variation in grain yield under stress. Time to flowering was the major factor in both stress treatments, explaining an average of 46% of the variation in yield in the midseason stress treatment and 56% in the terminal stress treatment (Table 2). DRI explained approximately 35% of the variation in yield in each of the two stress treatments, despite the fact that more than half of the genotypes had DRI values of zero. Yield potential generally made a negligible contribution. In the terminal stress treatment this was probably a result of the severity of the stress which greatly favoured early-flowering genotypes. In the midseason stress, yield was apparently more related to the ability to recover from stress than to yield potential, as growth was virtually stopped by the end of the stress period. The three factors combined predicted an average of 92% of the variability for grain yield in the midseason, and 94% of the variability in the terminal stress treatments (Table 2). This method of analysis is thus an effective integrator/estimator of the major factors that determine yield in the two stress conditions used.

Individual genotype drought response indices (and individual genotype grain yields) were not correlated in the two stress treatments (data not presented), indicating that genotype response to stress was specific to the particular stress treatment. DRI is therefore specific to a given type of stress pattern and not an index of universal response to drought.

Table 2. Estimated contribution (% of SS[A]) of yield potential (Y_p), time to flowering (FL) and drought response index (DRI) to grain yield under stress (Y_s). Advanced trials 1981, 1982 and 1983

	Yield potential	Time to flowering	Drought response index
Midseason stress			
1981	7	19	59
1982	4	63	28
1983	25	55	15
Mean	12	46	34
Terminal stress			
1981	1	64	30
1982	4	40	50
1983	1	65	29
Mean	2	56	36

[A] From the following regression models (see text):
Midseason stress: $Y_{si} = a + bY_{pi} + c\mathrm{FL}_i + d\mathrm{FL}_i^2 + \mathrm{DRI}_i$.
Terminal stress: $Y_{si} = a + bY_{pi} + b\mathrm{FL}_i + \mathrm{DRI}_i$.

Table 3. Ranges in time to flowering, grain yield and yield components in the irrigated control treatment, and in the drought response index among entries. Advanced trials 1981, 1982 and 1983

	1981	1982	1983
Time to flowering (days)	40–64	33–59	40–63
Grain yield (g m^{-2})	154–307	192–309	202–376
10^{-3} × grains (m^{-2})	28–52	27–57	33–79
Plants (m^{-2})	11–16	11–16	9–14
Panicles ($plant^{-1}$)	1·3–3·3	1·3–3·0	1·6–6·9
Grains ($panicle^{-1}$)	850–2230	900–2490	740–2430
Individual grain mass (mg)	5·2–8·8	4·9–9·4	4·6–10·7
DRI			
Midseason stress	−1·73–+2·51	−2·67–+2·31	−3·10–+2·44
Terminal stress	−1·77–+1·71	−2·05–+2·12	−1·88–+2·57

Correlations of DRI and Yield Components

There was considerable variation in yield component expression among the 72 entries grown in each year (Table 3). Also individual cultivar DRI values varied from less than −2·0 to more than +2·0 (Table 3). This provided an opportunity to test for associations between DRI and yield components, to determine whether certain yield structures were more advantageous under stress than others. If this were the case, selection for genotypes adapted to stress would be considerably simplified.

There were no significant associations between DRI and yield component structure measured in the irrigated control treatment, for either stress treatment, or for any year (data not presented). This was a somewhat unexpected finding: although DRI (by definition) was independent of non-stress grain yield, it was not assumed that different yield structures (e.g. high panicle number, or large panicle size) would not affect response to stress.

When the correlations of DRI and yield components were repeated using the yield structure measured in the appropriate stress treatments, a number of significant relationships emerged (Table 4). DRI was generally better correlated to grain number per unit area than to grain mass in both the midseason and terminal stress treatments. The component of grain number per unit area most closely related to DRI was clearly grain number per panicle, indicating that the ability to produce a large number of grains per panicle under stress was the best predictor of a low sensitivity to stress. The strength of this relationship was slightly greater in the terminal stress than in the midseason stress (Table 4).

Table 4. Prediction of DRI from the stress phenotype: correlations of drought response index (DRI) and yield components measured in the stress. Advanced trials 1981, 1982 and 1983

	1981	1982	1983
	Midseason stress		
DRI versus			
Grains m^{-2}	0·39***	0·49***	0·41***
Plants m^{-2}	0·03	0·28*	0·14
Panicles $plant^{-1}$	0·08	−0·19	−0·02
Grains $panicle^{-1}$	0·26*	0·31**	0·24*
Individual grain mass	0·10	0·32**	0·22
Panicles m^{-2}	0·07	0·18	0·13
Grain yield $panicle^{-1}$	0·24*	0·34**	0·27*
	Terminal stress		
DRI versus			
Grains m^{-2}	0·46***	0·45***	0·58***
Plants m^{-2}	−0·12	−0·04	0·07
Panicles $plant^{-1}$	0·10	0·07	0·30***
Grains $panicle^{-1}$	0·53***	0·37**	0·26*
Individual grain mass	0·25*	0·40***	0·01
Panicles m^{-2}	0·10	0·06	0·33**
Grain yield $panicle^{-1}$	0·69***	0·58***	0·25*

***$P \leqslant 0{\cdot}001$; **$P \leqslant 0{\cdot}01$; *$P \leqslant 0{\cdot}05$.

The fact that the correlations of DRI and yield components were significant only in the stress treatments indicated that it was the ability to maintain yield component expression under stress rather than any *a priori* difference in those values that was important. This was confirmed by repeating the correlations of DRI and yield components using relative (stress/control) values of the latter to remove any inherent genotypic differences (Table 5). The ability to maintain grain number under stress was again a better predictor of drought response index than the ability to maintain individual grain mass, and again it was grain number per panicle that was the most important component of grain number per unit area.

The above correlation analyses were repeated in a simpler fashion using only panicle number per unit area (plants per unit area × panicles per plant), and grain yield per panicle (grain number per panicle × individual grain mass) (Tables 4 and 5). Grain yield per panicle was the better predictor of DRI in both stress treatments, although the percentage of the variation in DRI accounted for by grain yield per panicle was small in the midseason stress. Grain yield per panicle was a better predictor of DRI in at least 2 of the 3 years in the terminal stress.

Table 5. Prediction of DRI from the maintenance of normal yield component expression on the stess: correlations of drought response index (DRI) and yield components in the two stress treatments as proportion of the value in the irrigated control. Advanced trials 1981, 1982 and 1983

	1981	1982	1983
	Midseason stress		
DRI versus relative:			
Grains m^{-2}	0·30*	0·42***	0·58***
Plants m^{-2}	−0·08	0·77**	0·18
Panicles $plant^{-1}$	0·21	−0·04	0·02
Grains $panicle^{-1}$	0·11	0·31**	0·34**
Individual grain mass	0·19	0·28*	0·14
Panicles m^{-2}	0·21	0·50***	0·19
Grain yield $panicle^{-1}$	0·23	0·32**	0·38***
	Terminal stress		
DRI versus relative:			
Grains m^{-2}	0·52***	0·57***	0·49***
Plants m^{-2}	−0·07	0·15	−0·03
Panicles $plant^{-1}$	0·15	0·14	0·36**
Grains $panicle^{-1}$	0·34**	0·47***	0·29*
Individual grain mass	0·38***	0·38***	0·10
Panicles m^{-2}	0·13	0·16	0·41***
Grain yield $panicle^{-1}$	0·44***	0·51***	0·28*

***$P \leqslant 0·001$; **$P \leqslant 0·01$; *$P \leqslant 0·05$.

Discussion

Drought Response Index

The method used to estimate experimental error in the derivation of DRI (based on a s.e. of estimated yield under stress derived after removing genotypes whose DR $\neq$ 0) was not as rigorous as normally used criteria for establishing yield differences [$P < 0·20$ for a significant DRI (two-tailed test) v. $P < 0·05$ for significant yield differences]. It was chosen, however, for the purpose of identifying the best and poorest lines at a 10% selection intensity level. Other levels of probability could also be used if desired.

The DRI for an individual variety has both a sign (indicating susceptibility or resistance to the stress in question) and a magnitude. For at least half of the varieties in the trials, the DRI was zero, indicating that within the limits of experimental error, they had no specific response to stress. Such varieties are similar to those in other reports with average drought susceptibility (Fischer and Maurer 1978) or average responsiveness across a range of moisture environments (Laing and Fischer 1977; Keim and Kronstad 1979).

Although our estimate of DRI was based on a single drought exposure, the method could be adapted to the results of a sequence of drought treatments, by adjusting regression-derived estimates of genotype responsiveness for the effects of both yield potential and drought escape. Positive relationships between regression coefficients (*b* values calculated according to Eberhardt and Russell 1966) and yield potential are common in data sets from drought environments (Laing and Fischer 1977; Fischer and Maurer 1978; Keim and Kronstad 1979), indicating a need to adjust for yield potential. Data provided by Fischer and Maurer (1978), Saeed and Francis (1983) and our unpublished data (line source irrigation experiments) suggest that time to flowering can also be strongly enough related to regression coefficient to require adjustment. In such cases, the difference between actual and expected *b* values could serve as a measure of response to drought in a manner identical to the DRI used here.

DRI and Plant Characters

The range of traits available for correlation to DRI was limited to a few basic yield components, and therefore any attempts to explain the reasons for variation in DRI are only preliminary. Lists of traits proposed as advantageous under drought conditions are long (Turner 1982; Zobel 1983); simultaneously evaluating a significant number of them on a meaningful number of genotypes is a daunting task.

Irrigated control

The consistent absence of significant correlations between DRI and yield components measured in the irrigated control indicated no consistent, *a priori*, advantages of one yield structure over another in either stress treatment. Advantages to particular yield structures under specific stress conditions in winter wheat have been reported by Innes and Blackwell (1981) and Innes *et al.* (1981). Their data suggest that a black box analysis, similar to the one done here, would indicate advantages to lower or smaller values for yield components determined during stress periods (e.g. lower grain number per ear in pre-anthesis drought, or smaller grains in post-anthesis drought). Correlations reported by Fischer and Wood (1979) in a very extensive study of factors affecting grain yield and susceptibility to terminal stress in spring wheat give similar indications. The lack of such correlations in the data presented in this paper indicates that it should be possible to select for any desired combination of yield components in the absence of stress in pearl millet, without necessarily affecting response to a stress environment.

Stress treatments

The stronger correlations of DRI to grain number than to grain mass (Table 4) were not surprising in either treatment. In the midseason stress, grain filling occurred after the termination of the stress in most genotypes, whereas grain number (both panicles per plant and grains per panicle) were determined during or immediately following the stress. Why the relationship to DRI was significant only in the case of grain number per panicle is not clear, as the increase in panicle number was one of most striking effects of the midseason stress (Bidinger *et al.* 1987). In case of the terminal stress Fischer and Wood (1979) have also reported stronger positive correlation of drought resistance with kernel number than with kernel mass in spring wheat, but their correlation was due primarily to variation in ear number as a component of grain number, rather than to variation in grain number per panicle, as found in pearl millet (Table 4). The correlation of DRI and grain number per panicle in the terminal stress treatment apparently represents a better ability of certain genotypes to set grains under stress. Unpublished data of the authors suggest that differences among genotypes for this ability do exist. The lack of a stronger relationship between DRI and panicles per plant in the terminal stress was unexpected in an asynchronously tillering cereal (Mahalakshmi *et al.* 1987).

Relative Stress/Control Values

The correlations of DRI and yield components expressed on a relative basis, indicating effectiveness of maintenance of yield components in the stress, gave essentially the same results as the correlations of DRI to components measured only in the stress (compare Tables 5 and 4). As the investment in resources to measure relative expression of yield components is double that required to measure expression in the stress alone, there is no apparent advantage in using relative yield components to understand drought response. An irrigated control treatment is, however, still required to estimate potential yield.

Breeding for Drought Conditions

The underlying hypothesis of the foregoing analysis is that maximum progress in developing varieties with better yields in drought situations should be made by combining yield potential, an appropriate developmental cycle (drought escape), and characteristics associated with a high, positive DRI (drought resistance).

Although yield potential was generally not a major factor in actual yield in either drought treatment in these experiments (Table 2), in studies with more diverse materials it has been shown to be a significant factor (Bidinger *et al.* 1982). In less severe stress, differences in yield potential also have a larger influence on actual yields in wheat (Laing and Fischer 1977; Fischer and Wood 1979). Although the results reported here may suggest a re-evaluation of the investment of resources in breeding for yield potential *v.* the other factors conditioning pearl millet yields in the drought environments, they are not an argument for ignoring yield potential as a selection criterion for drought areas.

Time to flowering was clearly the most important factor affecting yields under both stress conditions, yet the value of this as a selection criterion depends strongly on the predictability of the timing of stress (Mahalakshmi *et al.* 1987). Drought escape is not an absolute phenomenon, but depends upon the time of flowering relative to the timing of the stress. An early-flowering genotype which has an advantage in a terminal stress may be more seriously affected in a midseason stress than a late genotype would be. The ability to capitalize on drought escape exists only if moisture patterns are repeatable or predictable. A knowledge of the relative probabilities of occurrence of stress at different times in the crop cycle is therefore essential for breeding varieties for stress environments.

Correlations of DRI and yield components did not identify any useful indicators of drought resistance for the midseason stress. Differences among varieties in DRI were obviously due to other, unmeasured differences, probably ones that occurred during the stress period itself, and that influenced recovery ability once the stress was terminated. In the future, the focus should be on genotypic differences during the midseason stress period rather than at harvest.

Correlations of DRI and yield components were more promising for the terminal stress, possibly for the reasons cited above — that final harvest yield components directly reflect events during the terminal stress. In 2 of the 3 years the relationship between DRI and grain yield per panicle in the stress was strong enough to be useful as a selection criterion ($r = 0{\cdot}69$ and $0{\cdot}58$, $P < 0{\cdot}001$). Selection of materials with grain yield per panicle exceeding the population mean value in each of these two years would have identified nearly all of the lines with a positive DRI (Fig. 1*a*). Similar selection in 1983, where the correlation of DRI and grain yield per panicle was weaker ($r = 0{\cdot}25$, $P < 0{\cdot}05$), would still have been effective in identifying the majority of entries with DRI > 0 (Fig. 1*b*). Grain yield per panicle under terminal stress probably represents an integrated evaluation of the ability to both set and fill grains in these conditions. Selection for grain yield per panicle in terminal stress should therefore be an effective procedure for identifying the better pearl millet lines for such stress conditions.

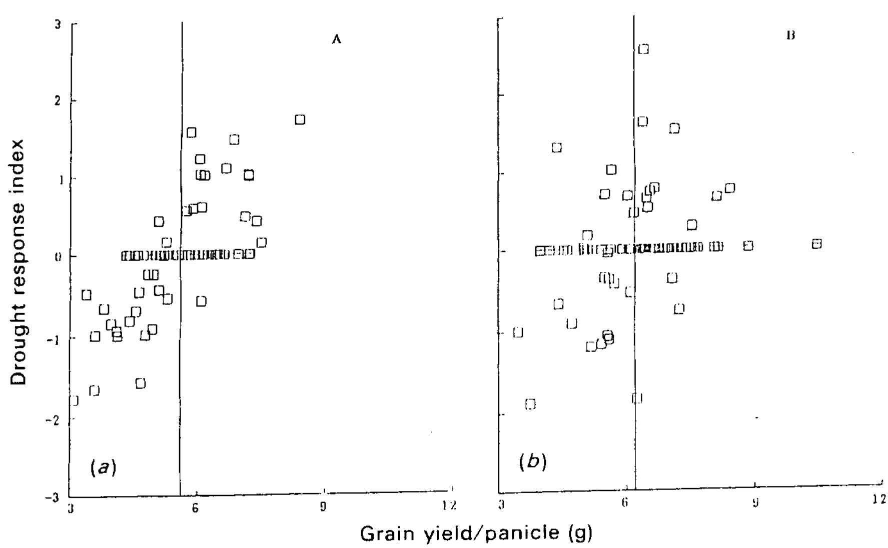

Fig. 1. Drought response index as a function of grain yield per panicle for the (*a*) 1981 and (*b*) 1983 terminal stress treatments. Mean grain yield per panicle for each year is indicated by the vertical line.

Authors' Note

The above analysis of grain yield in the two drought treatments was carried out using normal harvest data obtained in the process of evaluating advanced breeding trials for performance in drought conditions. No special physiological or other measurements were made. The extra cost to perform the black box analysis was only in computer time for the calculation of DRI and for correlation analyses. From these, the authors were able to obtain a very useful understanding of some of the reasons why genotype yields differed under drought (Bidinger *et al.* 1987), and to identify a potential selection criterion for resistance to terminal drought (this paper).

While drought is undeniably one of the most complex problems facing the plant breeder, it can be broken down into understandable causes and effects using an analytical approach of the type used in these papers. As Fischer (1981) has pointed out, much of the data to perform such analyses may already exist, where experiments have included both irrigated and stress treatments.

References

Bidinger, F. R., Mahalakshmi, V., and Rao, G. D. P. (1987). Assessment of drought resistance in pearl millet. I. Factors affecting yields in stress. *Aust. J. Agric. Res.* **38**, 37–48.

Bidinger, F. R., Mahalakshmi, V., Talukdar, B. S., and Alagarswamy, G. (1982). Improvement of drought resistance in pearl millet. In 'Drought Resistance in Crops With Emphasis on Rice'. pp. 357-76. (IRRI: Los Baños, Philippines.)

Blum, A. (1979). Genetic Improvement of drought resistance in crop plants: a case for sorghum. In 'Stress Physiology in Crop Plants'. (Eds H. Mussell and R. C. Staples.) pp. 430–45. (Wiley, Interscience: New York.)

Eberhardt, S. A., and Russell, W. A. (1966). Stability parameters for comparing varieties. *Crop Sci.* **6**, 36–40.

Fischer, R. A. (1981). Optimizing the use of water and nitrogen through breeding crops. *Plant Soil* **58**, 249–78.

Fischer, R. A., and Maurer, R. (1978). Drought resistance in spring wheat cultivars. I. Grain yield response. *Aust J. Agric. Res.* **29**, 897–912.

Fischer, R. A., and Wood, J. T. (1979). Drought resistance in spring wheat cultivars. III. Yield associations with morphophysiological traits. *Aust. J. Agric. Res.* **30**, 1000–20.

Innes, P., and Blackwell, R. D. (1981). The effect of drought on the water use and yield of two spring wheat genotypes. *J. Agric. Sci.* **96**, 603–10.

Innes, P., Blackwell, R. D., Austin, R. B., and Ford, M. A. (1981). The effects of selection for number of ears on the yield and water economy of winter wheat. *J. Agric. Sci.* **97**, 523–32.

Keim, D. L., and Kronstad, W. E. (1979). Drought resistance and dryland adaptation in winter wheat. *Crop Sci.* **19**, 374–76.

Laing, D. R., and Fischer, R. A. (1977). Adaptation of semidwarf wheat cultivars to rainfed conditions. *Euphytica* **26**, 129–39.

Mahalakshmi, V., Bidinger, F. R., and Raju, D. S. (1987). Effect of timing of water deficit in pearl millet [*Pennisetum americanum* (L.) Leeke]. *Field Crops Res.* (in press).

Quisenberry, J. E. (1982). Breeding for drought resistance and plant water use efficiency. In 'Breeding Plants for Less Favourable Environments'. (Eds N. M. Christiansen and C. F. Lewis.) pp. 193-212. (Wiley, Interscience: New York.)

Richards, R. A. (1982). Breeding and selecting for drought resistance in wheat. In 'Drought Resistance in Crop Plants with Emphasis on Rice'. pp. 303–16. (IRRI: Los Baños, Philippines.)

Saeed, M., and Francis, C. A. (1983). Yield stability in relation to maturity in grain sorghum. *Crop Sci.* **23**, 683–87.

Turner, N. C. (1982). The role of shoot characteristics in drought resistance of crop plants. In 'Drought Resistance in Crops with Emphasis on Rice'. pp. 115–34. (IRRI: Los Baños, Philippines.)

Zobel, R. W. (1983). Crop manipulation for efficient use of water: constraints and potential techniques in breeding for efficient water use. In 'Limitations to Efficient Water Use in Crop Production'. (Eds H. M. Taylor, W. R. Jordan, and T. R. Sinclair.) pp. 381–92. (Am. Soc. Agron.: Madison, Wisc.)

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