Breeding for Adaptation to Environmental Stress?

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Abstract

Although breeding for adaptation to environmental stresses is a more complicated problem than breeding for adaptation to biotic stresses, the basic procedure is virtually identical. Initial steps include understanding the specific problems, and establishing methods to identify better-adapted materials. This is followed by determining if useful genetic variability for adaptation exists, and if so, deciding upon the best means to select for improved adaptation in a breeding program. The results of these steps then allow a rational decision on whether breeding for better adaptation is justified.

This procedure is illustrated using two different environmental stress problems in pearl millet: failure of stand establishment and drought stress during grain filling. Useful progress has been made on understanding the problems involved and developing screening and selection methods. Current efforts center on assessing the genetic variability for these traits and evaluating the response to direct selection for adaptation.

Résumé

Sélection pour l'adaptation aux stress environnementaux : *La sélection visant à l'adaptation aux stress environnementaux s'avère plus compliquée que celle pour l'adaptation aux stress biotiques. Cependant le processus de base pour ces deux types de sélection reste pratiquement le même. On commence par l'examen des problèmes particuliers et l'établissement des méthodes d'identification du matériel mieux adapté. Ensuite, il faut déterminer s'il existe une variabilité génétique intéressante et définir les moyens les plus efficaces de sélectionner ce matériel en vue d'améliorer son adaptabilité. Les résultats obtenus permettront d'établir dans quelle mesure la sélection pour l'adaptation se justifie.*

Ce processus est explicité à l'aide de deux exemples des problèmes de stress environnementaux : l'échec de l'établissement des plantules et la sécheresse advenant pendant la formation des grains. L'étude des problèmes donnés et la mise au point des méthodes de criblage et de sélection sont déjà bien avancées. L'évaluation de la variabilité génétique et de la réponse à la sélection directe est actuellement en cours.

Introduction

title of this paper has been deliberately phrased as a question because there has traditionally been considerable skepticism about breeding for 'resistance' to environmental stresses. Selection for tolerance to certain stresses—such as freezing temperatures, low pH, and aluminium-toxic soils—has been effective (Blum 1985), but plant breeders have been far more willing to devote resources to breeding for disease and insect pest resistances than to breeding for adaptation to environmental stress.

Research on environmental stress is admittedly more complex than research on biotic stress. While

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biotic stresses exist as discrete entities—individual species, races, or biotypes—variation in environmental stress is continuous. Usually, biotic stress is also easier to manage experimentally. Finally, immunity, and possibly even true resistance to environmental stress, is not possible. The choice is among degrees of tolerance or adaptation. Nonetheless, breeding for adaptation to environmental stress is still a conventional scientific problem, to be attempted by conventional scientific methods. Plant breeders have, in the past, produced genetic materials with a wide range of traits using such standard methods. It is the contention of the authors that a similar approach is equally appropriate to increased tolerance to environmental stresses.

General Framework

There are two parts to the question of breeding for adaptation to environmental stress. (1) What methodology to use, and (2) what evidence is there to justify the investment of resources? Although there have been a number of reviews of this topic recently, particularly on breeding for drought resistance (Blum 1985, IRRI 1982, Christiansen and Lewis 1982), the literature does not provide a consensus on either methodology or probability of success. Many reviews, in fact are little more than a discussion of possibilities. These are specified (Table 1) following Khalfaoui (1985). The steps themselves involve first understanding exactly what the problem is (I and II), establishing the basic requirements to employ plant breeding as a solution (III and IV), and finally, deciding whether breeding for improvement is a realistic solution (V and VI). The remainder of this paper covers each of these in turn, using two particular problem areas for pearl millet as examples: poor crop establishment and drought stress during grain filling. In most cases, illustrations presented are from work by the authors.

Table 1. A logical framework to consider breeding for adaptation to environmental stress.

I. What is the specific stress for which improved adaptation is needed?

II. What factors are responsible for observed differences among cultivars under this stress?

III. How can systematic screening for genetic differences in adaptation be done?

IV. Is there useful genetic variation for adaptation in breeding materials?

V. How can the breeder best select for improved adaptation?

VI. Is breeding for adaptation justified?

Concrete Definition of the Problem

Failure of Crop Establishment

Pearl millet is particularly subject to poor stand establishment. The seed has limited reserves for early growth, and is generally grown in harsh climates by farmers who have limited land preparation and sowing methods. Failure of stand establishment, however, can occur for a wide variety of reasons: seed quality, sowing methods, seedbed environment, and the subsequent seedling environ

Comparative studies of reasons for stand . in India and Niger (Soman et al. 1984b; P. Soman and L.K. Fussell, ICRISAT, personal communication), illustrate differences between areas. In both countries the emergence of seedlings as a percentage of seeds sown was low (<25%) (Fig. 1). In Niamey Department, Niger, where sowing is done in hills, initial stands on a hill basis (at least one emerged plant per hill), averaged 80% of those hills sown. By 12 d after emergence however, hill populations were reduced by >50% and hill stands were poor; due to very high soil surface temperatures (>50°C at midday) which occurred in the absence of rain following emergence. In contrast, in Sikar district, India, where sowing is done in rows and desired plant population are higher, initial plant populations were very poor (<10% of seed sown in most fields), because low seedbed moisture and high seedbed temperature killed most seedlings before they emerged. Breeding to improve the stand establishment capability in these two situations would ther involve breeding for tolerance to different conditi

Drought Stress

Drought stress is notorious for the near-infinite number of combinations of timing, duration, and intensity in which it can occur. Adaptation to drought stress (as measured by grain yield), depends on different traits, responses, etc., for the different times and intensities of its occurrence. An attempt to breed for improved adaptation to stress makes sense only if the stress is reasonably well defined.

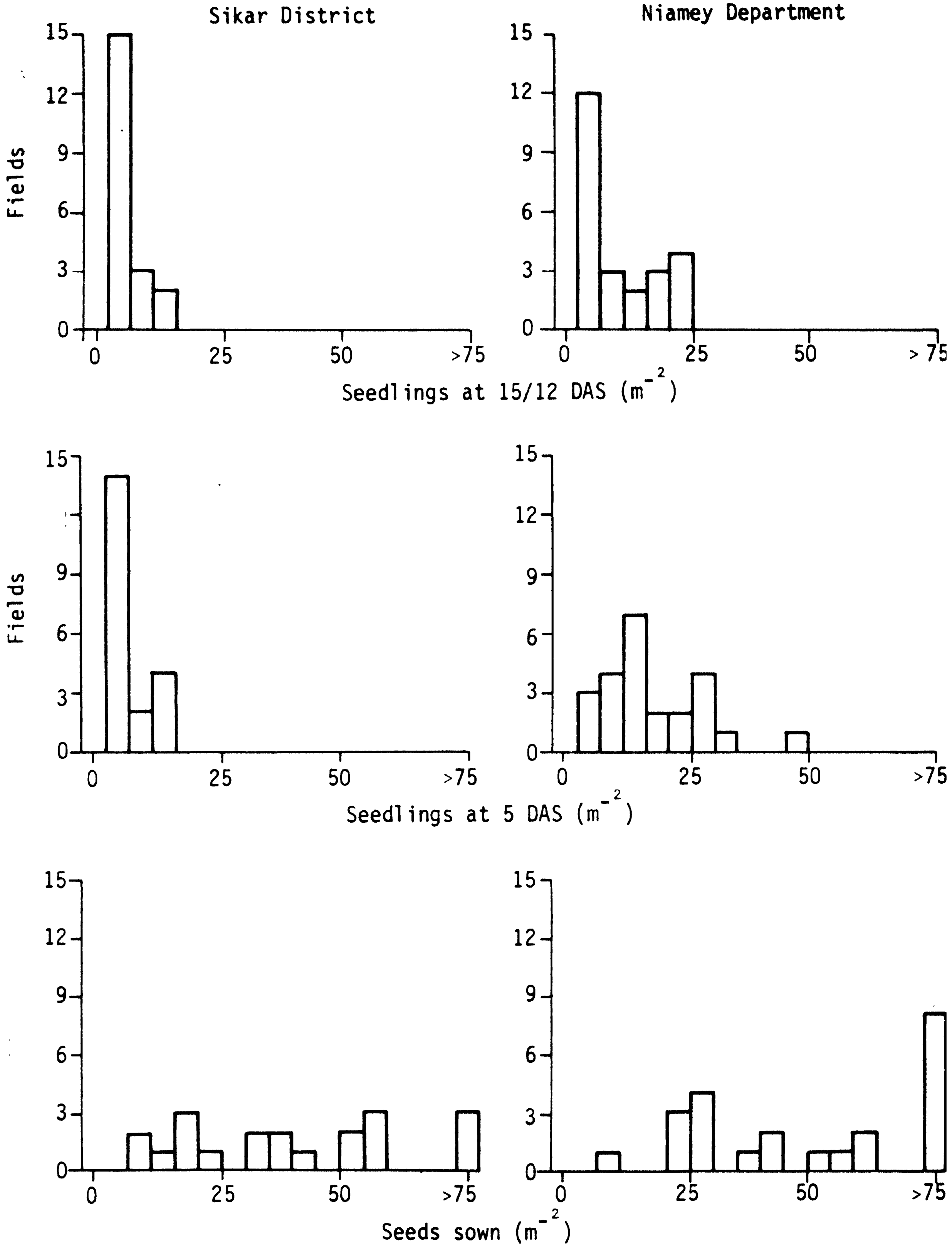

Figure 1. Distribution of seeds sown (bottom), emerged seedlings (center), and surviving seedling (top) in farmers' fields in Dhandhan village, Siher District, Rajasthan, India in 1983, and in Niamey Department, Niger in 1985. (Source: Soman et al. 1984 and Soman and Fussell, ICRISAT, Personal Communication).

Analysis of climatic data for occurrence of drought periods can be complex when done at the soil water balance level, but useful information is available from long-term rainfall probability analyses. Across an east-west (Alwar- Bikaner) transect in the state of Rajasthan, India, based on long-term rainfall records, total rainfall not only decreases markedly, but the probability of adequate rainfall from flowering onwards falls precipitously (from 117, to 55, to 19 mm at a 50% level of probability) (Fig. 2). Whereas some adjustment for the generally lower rainfall level in the west is possible through crop management, little can be done to compensate for lack of rainfall during grain filling. Given that stress at this time is the most damaging to yield (Mahalakshmi et al. 1987), drought tolerance during grain filling is clearly the main objective for a breeder working in western Rajasthan.

Analysis of Factors Affecting Genotype Performance During Stress

Drought Stress During Grain Filling

A 'successful' genotype in case of drought stress during grain filling is one which produces an acceptable level of grain yield. While it is possible to select for grain yield under conditions of terminal st it may be much more useful for the plant bree to know more about why a successful genotype is successful. There are complex hypotheses (e.g., Paleg and Aspinall 1981), but again, a simple framework of analysis is useful. Repeated, large-scale comparisons of cultivars under terminal drought conditions (Bidinger et al. 1987a) have indicated that the largest factor in yield differences among cultivars is drought escape, due to time to flowering differences relative to the beginning of the stress (Fig. 3). In comparisons over a number of years, drought escape has accounted for nearly 50% of the total variation in grain yields in severe terminal stress, a much greater proportion than either differences in yield potential or drought resistances among cultivars (Table 2).

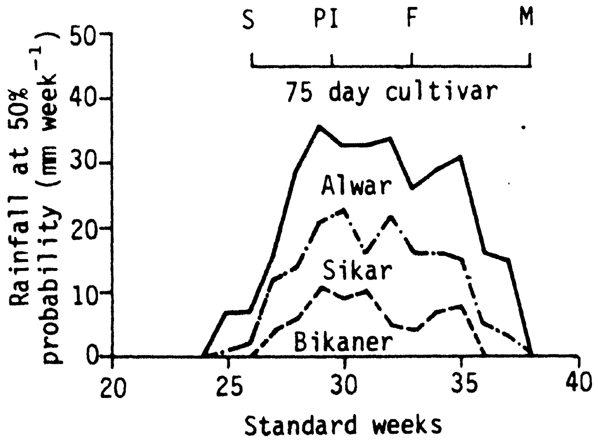

Figure 2. Experimental weekly rainfall during the growing season, at a 50% level of probability for Alwar, Sikar, and Bikaner, Rajasthan, India. The duration of a typical 75 day variety is indicated in the figure, where S = sowing, PI = panicle initiation, F = flowering, and M = maturity. The sowing week (week 26) is June 25 to July 1. (Source: Biswas et al. 1982).

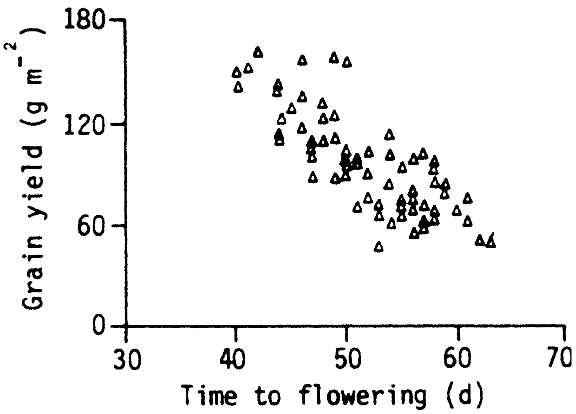

Figure 3. Cultivar grain yield under conditions of terminal drought stress in relation to time of flowering (Source: Bidinger, Mahalakshmi, and Rao 1987a).

Any attempts to improve cultivar adaptation to terminal drought must obviously consider drought escape, either by capitalizing on it to breed shorter-duration cultivars, or by excluding it, if drought resistance or tolerance is the objective of selection. These alternatives will be discussed in more

Failure of Crop Establishment

A 'successful' genotype in this case is simply one that establishes well under a variety of conditions. A knowledge of why genotypes differ in their capacity to establish would obviously help when selecting for improved establishment. Although differences for such factors as high temperature tolerance during germination are undoubtedly at the metabolic level, understanding these may or may not simplify the

Table 2. Percentage of variation in cultivar grain yield under terminal stress due to variation in yield potential, time to flowering (drought escape), and drought response index (drought adaptation). (Data from Bidinger, Mahalakshmi, and Prasada Rao 1986b; and Mahalakshmi and Bidinger, personal communication).

	Percentage variation in yield[1] due to:			
Year	No. of cultivars	Yield potential	Time to flowering	Drought response index
1981	72	1	64	30
1982	72	4	40	50
1983	72	1	65	29
1984	54	0	56	40
1985	90	14	25	54
Mean	72	4	50	41

[1] From the following regression model.
$Ys = a + bYp + CTF + DRI$
Where: Ys = yield in the stress TF = time to flowering
Yp = yield potential DRI = drought response index

ıg process. Very little research has been done on the reasons for differences in crop establishment capability in millet, partly because direct screening for differences usually appears to be relatively simple and economical.

Screening Techniques for Evaluating Genotype Differences in Adaptation

Screening techniques for adaptation to stress are similar to those for resistance to biotic stresses: they must be capable of applying uniform and repeatable selection pressure, and able to economically screen relatively large numbers of breeding lines. This obviously implies an ability to exercise some control over temperature and water, either by the selection of seasons and locations where these factors are at the desired level (or absent in the case of rainfall, wing control of water availability by irrigation), lse through the use of controlled environment facilities. The particular response or parameter measured in such screening must also be directly related to field performance (often yield differences under stress conditions), and be as free from the influences of confounding factors as possible.

Crop Establishment Ability

Screening for crop establishment ability is not too difficult. Success or failure is obvious, and the screening procedures require relatively little land and time. Techniques are available to screen for ability of pearl millet to emerge through a crusted soil surface (Fig. 4, and Soman et al. 1984a), and to germinate and emerge in high temperature conditions (Soman and Peacock 1985). Techniques to screen for the ability to emerge under conditions of low seedbed moisture (P. Soman, ICRISAT, personal communication), and for seedling survival under low moisture and high temperature (L.K. Fussell, ICRISAT Sahelian Center, personal communication) have progressed to the point where they are being used to evaluate genetic materials. Not all of these techniques are adaptable to screening as large a number of lines as desired, but all produce repeatable evaluations of genetic differences.

Adaptation to Drought Stress During Grain Filling

Screening for adaptation to stress during grain filling is a much more complex problem than screening for seedling establishment. Neither the choice of a criterion for relative success or failure, or its measurement are as simple. The use of grain yield as a criterion is not adequate because it depends on factors other than adaptation to drought, assuming that adaptation rather than escape is the objective of the breeding program (Table 2).

It is possible to derive an estimate of genotypic drought response (adaptation) based on the unex-

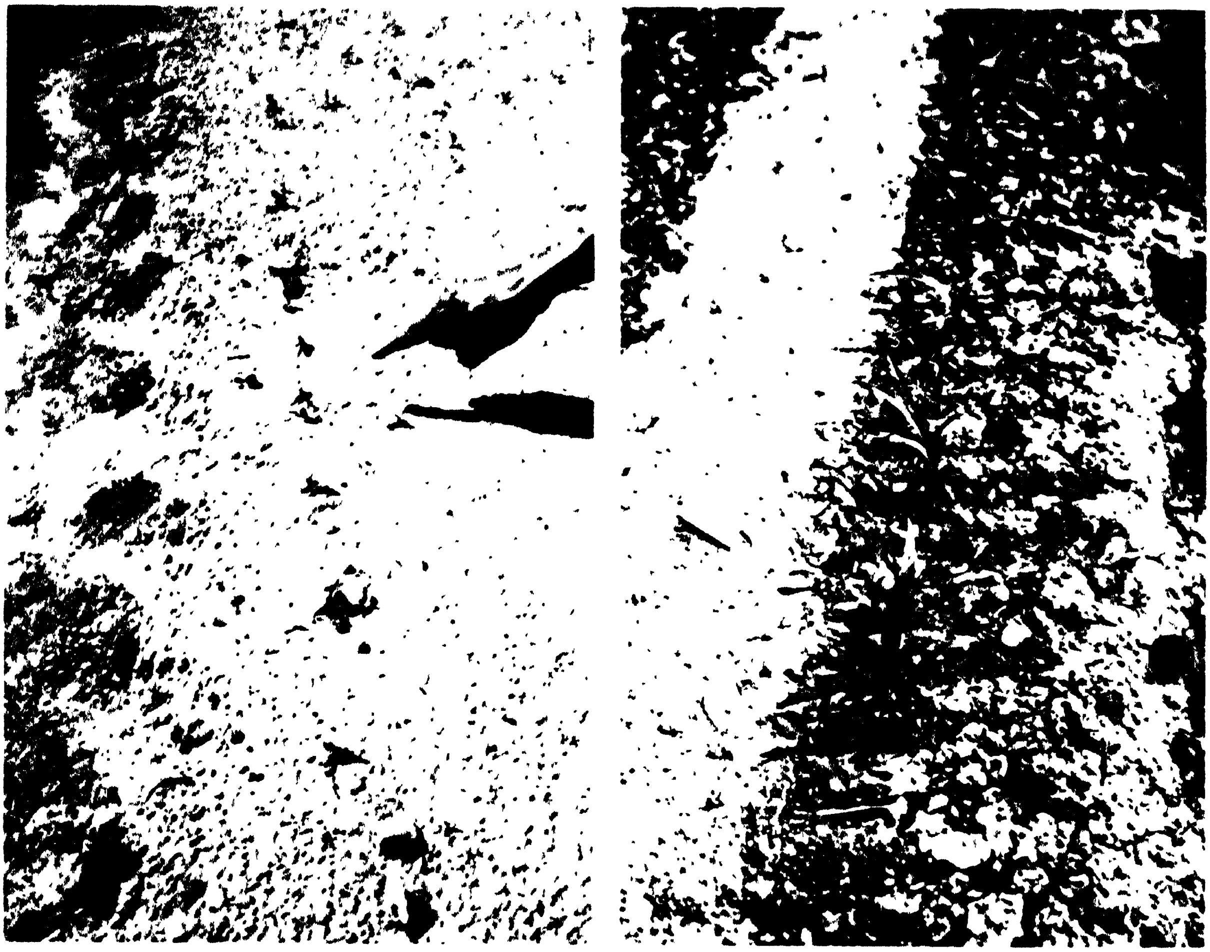

Figure 4. Screening for ability to emerge under crusted soil surface conditions (a) in which the crust was broken before emergence and (b) in which the crust remains intact.

plained variability in grain yield once the effects of drought escape and yield potential differences are removed (Bidinger et al. 1987b). This procedure involves three steps, using data from paired irrigated and drought-stressed plantings during the dry season:

1. Establishing the relationship of yield in the stress to time to flowering (drought escape) and yield potential (yield in the same test environment but in the absence of stress). These two factors generally account for 50-60% of the grain yield variation in the stressed planting (Table 2).
2. Using this relationship to establish an expected grain yield based on the above two factors for each genotype.
3. Comparing the differences between the expected yield in the stressed planting for each genotype, and the actual measured yield. If this difference is less than the experimental error, the genotype is considered to have no specific response to stress. If this difference is greater than the experimental error, the entry has a stress response (drought response index) that is either positive (measured yield $>$ predicted yield) or negative (meas yield $<$ predicted yield).

This index of drought response is significantly, positively correlated to grain yield in the stressed planting, but is independent of the effects of both drought escape and irrigated yield potential (Table 3). It thus provides an indication of drought adaptation, although adaptation is only one contributing factor to actual yield. However, the other two factors, yield potential and drought escape, are characteristics which can be assessed without using a specific drought screening methodology.

Table 3. Correlation of the drought response index (DRI) with yield potential, time to flowering (drought escape), and grain yield in the terminal stress. (Data from Bidinger, Mahalakshmi and Prasada Rao, 1986b; and Mahalakshmi and Bidinger, personal communication).

	Correlation of DRI with:		
Year	Yield potential	Drought escape	Yield in stress
1981	0.05	0.00	0.55***
1982	0.05	-0.05	0.72***
1983	0.06	-0.01	0.54***
1984	-0.07	0.06	0.65***
1985	0.00	-0.10	0.74***

*** $P < 0.001$

ence for the Existence of Genetic Variability for Adaptation to Stress

The existence of genetic variability for adaptation to stress—statistical, repeatable differences among genotypes—is obviously essential to the possibility of breeding for adaptation to stress. Unfortunately, there has not been sufficient research done on pearl millet to assess whether sufficient variability exists in this species. This is therefore the key question to be answered in deciding on the feasibility of breeding for adaptation.

Adaptation to Drought Stress During Grain Filling

Several control cultivars used in dry season drought nurseries habitually rank among the best entries in he trial, but the reason is inevitably their earlier urity, i.e., escape from drought rather than ught tolerance.

There has been interest, recently, in the possible drought tolerance in the Iniadi germplasm from northern areas of Togo and Ghana. Representatives of this landrace that have been tested frequently yield well in severe terminal stress situations (Mahaakshmi and Bidinger, ICRISAT, personal communication), but it has not been clear if this advanage is simply a function of their earliness or if they do in fact possess some adaptation to stress. Experments in which the drought escape factor was emoved by comparing only materials of similar early maturity have indicated a possible additional advantage to the Iniadi types. The five Iniadi entries improved their basic yield advantage by 4% of the trial mean (from 108% to 112%), in two trials conducted under terminal stress, due to a combination of their ability to maintain their considerably larger grain mass (125% of the trial mean) while actually filling relatively more grains per panicle than in the nonstressed control (Table 4). While the advantages indicated are not large, there is the possibility that specific selection within Iniadi types might further reinforce these differences. These data also clearly show how a useful yield difference under stress (12%) is possible from a combination of an initial yield advantage (8%), plus some degree of adaptation to the stress condition.

Crop Establishment Ability

There is better evidence for genetic differences in adaptation to stress during emergence and establishment than for adaptation to drought stress during grain filling. This evidence is primarily repeatable differences among control cultivars employed in the development and subsequent use of various screening techniques. An illustration is the different emergence percentage between two commercial Indian hybrids when evaluated across a range of low-moisture, high-temperature seedbeds (Fig. 5). Emergence of these two hybrids differed little under favorable seedbed conditions but MBH 110 was considerably more tolerant to stress conditions than BJ 104. If differences of this magnitude exist in breeding materials, the scope for improvement of emergence ability should be large.

Table 4. Mean of five Togo varieties as a percentage of 25 entry trial mean under nonstressed (ICRISAT, dry season 1985) and stressed conditions (ICRISAT, dry season 1985, and Anantapur, rainy season 1985) (Data from Bidinger and Mahalakshmi, personal communication).

	Non-stressed	Terminal stress	
Variables	ICRISAT	ICRISAT	Anantapur
Grain yield	1.08	1.11	1.13
Panicle m^{-2}	0.87	0.86	0.84
Grain mass $panicle^{-1}$	1.23	1.25	1.28
Grains $panicle^{-1}$	0.97	1.03	1.05
Grain mass	1.25	1.23	1.21

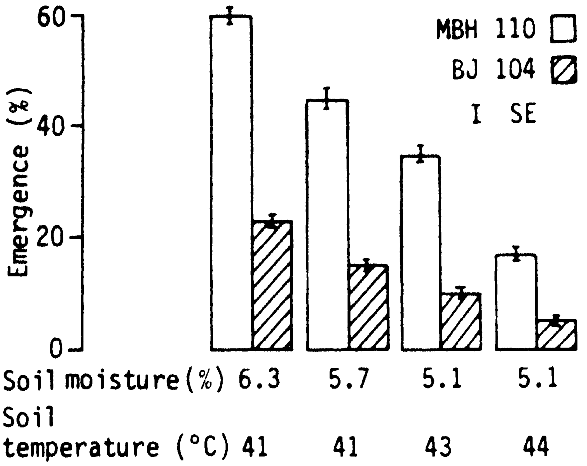

Figure 5. Emergence of control cultivars MBH 110 and BJ 104 from seedbeds with below-optimum seedbed and temperature conditions, measured at midday on the day following sowing. (Source: Soman, ICRISAT personal communication).

Selection Methodology to Breed for Adaptation to Stress

Crop Establishment Ability

Direct selection for emergence and survival using the screening methods described above should be adequate to breed for crop establishment ability. These techniques fulfill the requirements outlined in the section on screening methodology and, as they are generally conducted during the dry season (when temperatures are high and rainfall absent), they can be readily integrated into a breeding program. In fact, such methods can be useful as initial selection criteria to reduce large numbers of progenies to more manageable numbers. The selected progenies can then be evaluated for characters such as yield and disease resistance, which are more expensive to screen for than seedling emergence. The large numbers of seed produced by individual millet plants allow replicated selection for crop establishment ability without depleting seed quantities needed for subsequent evaluations.

Adaptation to Drought Stress During Grain Filling

The use of the procedure described above to estimate genotype drought response is not practical as a selection procedure because it requires replicated yield trials in both stressed and nonstressed environments. Two alternatives are possible: direct selection for performance under terminal drought conditions (in a managed drought nursery) with control of drought escape, and selection for a positive drought index by selection for a response or trait correlated to the index.

Selection for yield with control of escape. Selection for grain yield under terminal stress, with elimination of drought escape (by either rigorous blocking of materials by time to flowering in the field, or statistical adjustment for the effects of time to flowering), is effectively selection for a combination of higher yield potential and adaptation to terminal drought. These are both desirable characteristics. Such a procedure has been used experimentally to select among inbred lines derived by selfing good but variable pollinators (B.S. Talukdar, ICRISA1 sonal communication). One hybrid made us pollinator selected in such a procedure performed well in a number of trials conducted under terminal drought conditions (Fig. 6). This procedure is being tested to reselect several high-yielding, open-pollinated varieties for better adaptation to terminal stress.

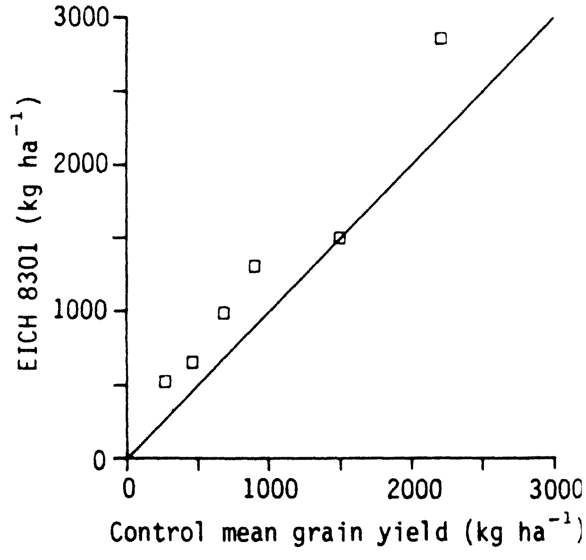

Figure 6. Grain yield EICH 8301 in relation to the yield of two standard control varieties (WC-C75 and ICMS 7703) in five trials conducted under varying levels of drought stress during grain filling. (Source: Talukdar and Mahalakshmi, ICRISAT. personal communication).

Selection for Traits Correlated to Drought Adaptation. Correlation studies with the drought response index described above indicate that grain yield per panicle in terminal stress could potentially serve as a selection criterion for adaptation to terminal drought (Bidinger et al 1987b) The relationship of these two parameters is not exceptionally strong, from r = 0 28 (P<0 05) to r = 0 72 (P<0 001), over 5 years However, selecting entries with grain mass per panicle greater than the population mean is generally effective to identify entries with a positive drought response index (Fig 7) Where selection intensity for adaptation to drought is to be applied regularly, for example, in a population breeding program, selection of the best 50% of the entries based on grain yield per panicle in the stress should be an effective procedure to gradually improve adaptation to terminal drought

Justification to Breed for Adaptation to Environmental Stress

Whether or not the investment of resources to breed for adaptation to environmental stress is justified depends on the answers to questions specific to individual breeding programs Adding additional selection criteria or breeding objectives to any breeding program will be at the expense of other efforts and therefore must be justified First, the relative importance of environmental stress problems as factors in low pearl millet production must be established How do these compare to the problems from diseases or pests, on which the breeder might also concentrate? How do the limitations on production caused by environmental stress compare to those due to poor management, lack of inputs, markets, etc ? The second, and perhaps most pertinent question, is whether or not there are other, simpler solutions to improve production in areas where it is limited by environmental stresses Could crop establishment be improved by better land preparation or sowing methods? Could production in drought areas be increased by shorter-duration cultivars, or by the use of management techniques which improve rainfall use efficiency? The third and final question is whether or not the breeder can expect sufficient progress in breeding for environmental stress tolerance to justify the resource allocation Will this produce varieties with higher yields on farmers' fields? Or more critically, will it produce varieties that will survive in national variety testing systems, which frequently emphasize yield potential rather than adaptation to stress environments?

The answers to these questions will ultimately determine whether or not breeding is attempted as a solution to environmental stress problems The authors believe that not only is there a logical framework, but that there has been considerable success in developing screening and selection methods. There is some evidence of genetic variability in responses to at least some of the environmental stresses facing pearl millet Not enough work has been done however, to estimate the progress that might be made As indicated in the introduction, immunity to environmental stress does not exist, only relative degrees of adaptation Evidence from screening genetic resources accessions and breeding lines for adaptation to these stresses suggests that differences are large enough to be of real value, if they can be incorporated with otherwise elite materials

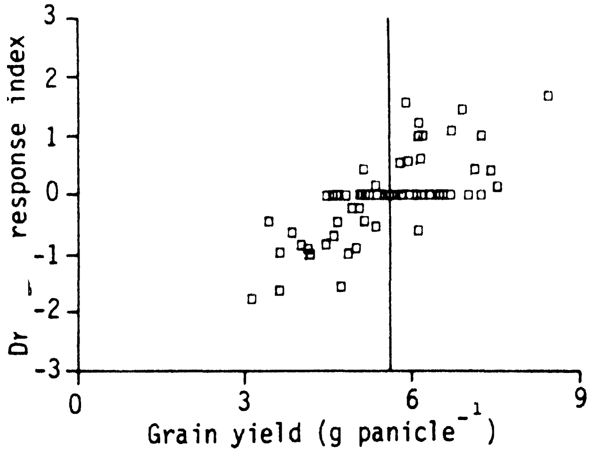

Figure 7. Relationship of drought response index (drought adaptation) and grain mass per individual panicle (r = 0.58, P < 0.001), based on a replicated evaluation of 72 genotypes under terminal stress in 1982. The vertical line represents the mean grain mass per panicle (Source: Bidinger, Mahalakshmi, and Rao, 1987b).

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