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IMPROVEMENT OF DROUGHT RESISTANCE IN PEARL MILLET

F. R. BIDINGER, V. MAHALAKSHMI, B. S. TALUKDAR, AND G. ALAGARSWAMY

Pearl millet is grown almost exclusively in arid and semiarid tropical areas characterized by high growing season temperatures, low and frequently erratic rainfall, and shallow or sandy soils. Inadequate moisture is the major limitation to production in most of the areas. The crop appears to adapt to these conditions by a combination of short-duration important developmental periods and considerable development plasticity to maximize its use of short periods of favorable moisture. Little is known of its possible physiological adaptations to stress, although the limited information available suggests a significant heat tolerance.

Efforts to improve performance under drought stress have centered on the development of field and analysis techniques to assess drought resistance as a factor independent of or complementary to yield potential and drought escape in determining cultivar performance under stress. Direct selection for yield ability in a controlled, off-season stress nursery is being evaluated as a breeding tactic for improvement of pearl millet's adaptation to stress. Progress in combining adaptation to at least certain types of stresses and better yield potential is the goal.

Pearl millet *Pennisetum americanum* (L.) Leeke and rice stand at opposite ends of the spectrum of major tropical cereals. Almost entirely a rainfed crop, pearl millet is grown in sandy and often shallow soils in areas of 200-800 mm of rainfall/year. It is entirely a subsistence crop, generally grown without fertilizer or chemical protection. Relatively little research has been done on pearl millet and many farmers grow traditional land race cultivars.

Like rice, pearl millet is the main source of calories and protein for the people

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who depend on it. Most are in arid and semiarid areas where no other major cereal is as well adapted. The ever-present risk of drought in these areas makes yielding ability under drought conditions a major objective for millet improvement programs. Progress in realizing this objective is limited by the general lack of methods to improve drought resistance in crop plants and by the specific lack of knowledge of responses to drought of the millet crop itself.

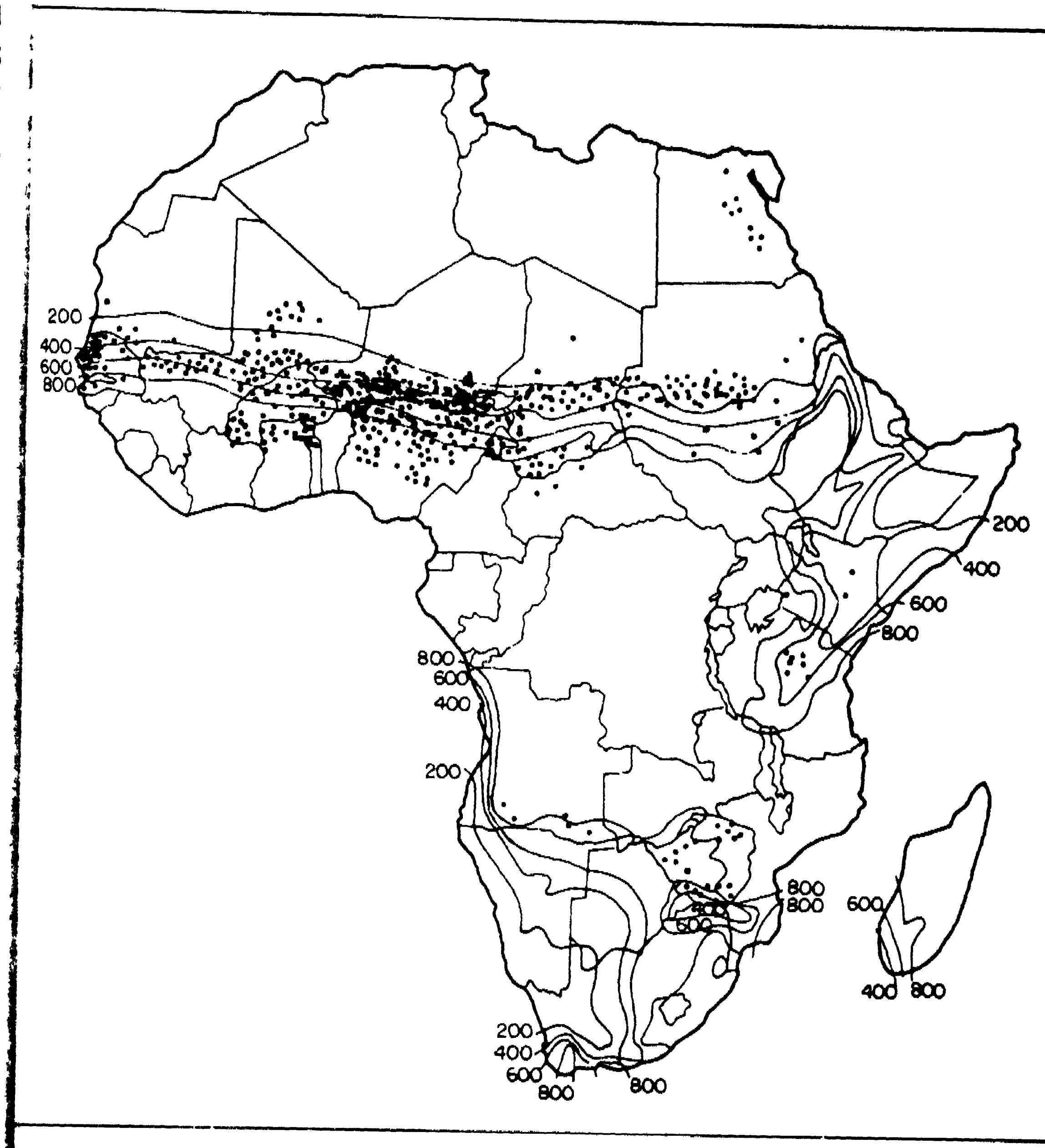
ECOLOGICAL DESCRIPTION OF MILLET GROWING AREAS

More than 95% of the world's millet crop is grown in Africa and South Asia, principally in the Sahelian-Sudanian zones of West Africa and in the semiarid regions east and southeast of the Thar desert in India. The areas of adaptation of the species are clearly defined by the mean annual rainfall isohyets of 200-600 mm in both continents (Fig. 1, 2). These zones are generally characterized by short rainy seasons (2-4 mo), high mean temperatures, high potential evapotranspiration rates, and shallow, sandy soils (Cocheme and Franquin 1967, Kowal and Kassam 1978).

Inter- and intraseasonal variability in available soil moisture is the major hazard to pearl millet production. Rainfall is erratic as well as low and the water-holding capacity of soils is typically low to moderate, limiting the possibilities of buffering rainfall fluctuations with stored soil moisture. To illustrate these conditions, two locations in important millet-growing areas were chosen: Jodhpur in Rajasthan state, northwestern India, and Bambey in Senegal, West Africa. Bambey has a slightly longer rainy season (defined by Virmani et al 1978 as the period during which the ratio of rainfall to potential evapotranspiration exceeds 0.33) and a greater mean weekly total than Jodhpur (Table 1). Average weekly rainfall during the rainy season exceeds potential evapotranspiration at Bambey and the probability of receiving at least 20 mm/week (about 2/3 of the average weekly potential evapotranspiration) is high (Fig. 3). At Jodhpur, mean weekly rainfall is less than the mean potential evapotranspiration and the probability of receiving at least 20 mm of rainfall/week during the rainy season does not exceed 50%.

To illustrate annual rainfall variation, data for 3 individual years were used to calculate the ratio of actual evapotranspiration to open pan evaporation (ET:E_o). Data were calculated on a weekly basis for a millet crop growing in the two locations using a standard soil water balance model (Reddy, unpubl.) and appropriate climate and soils input data (Table 1). Sowing and flowering dates are those of the local cultivar from the International Pearl Millet Adaptation Trials for those years and locations.

Rainfall and the ET:E_o were good for the first several weeks of the season at Jodhpur in all 3 years (Fig. 4). (ET-E_o ratios depend mainly on soil evaporation in the early stages; a low ratio at early stages is not indicative of crop stress.) Dry periods occurred at weeks 6 and 7 in 1977 and weeks 4 and 5 and weeks 9-11 in 1978 (ET-E_o ratios below 0.7 are indicators of probable crop stress by 30-40 days after emergence). Although total rainfall was above normal, 1979 was particularly dry. Most of the total seasonal rainfall occurred in 2 weeks in the early part of the season. Soil moisture and predicted ET:E_o values during flowering and grain

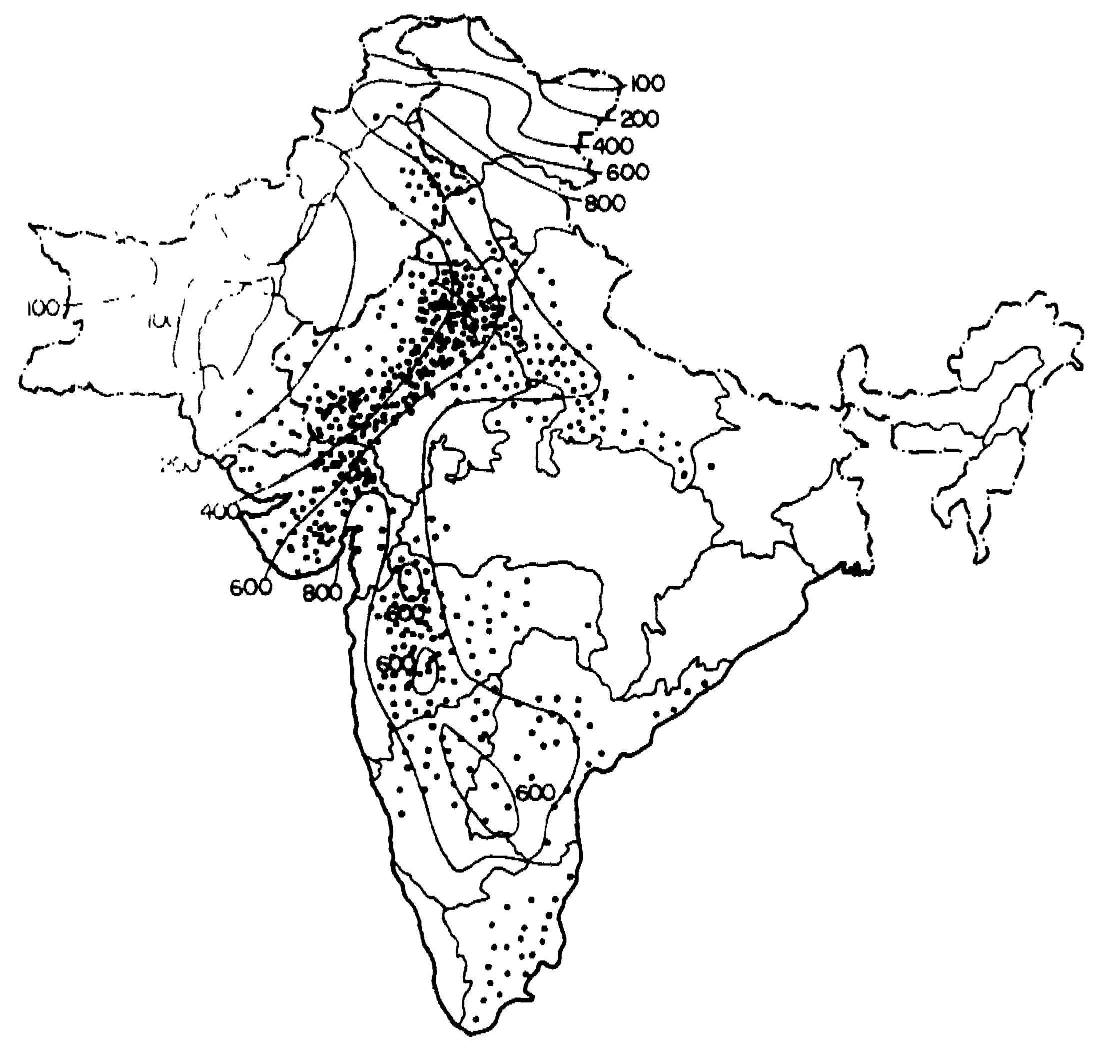


...an area planted to pearl millet in 1978 in relation to the mean annual rainfall isohyets. One dot equals 20,00

...illing were very low.

There was a dry period in the middle of the 1977 season at Bambey. There was ...tle rain in weeks 2-5, but rainfall and ET:E_o ratios were good during flowering ...d grain filling (Fig. 5). Rainfall in 1978 was well distributed throughout the ...son. In 1979, as in 1977, there were good sowing rains, followed by a dry period ...several weeks after sowing. Rainfall thereafter was regular, but amounts in some ...eks were small and several short dry periods occurred during the remainder of ...e season.

To the degree that these years are typical, it is clear that drought stress is a ...gular and frequently severe hazard to millet production.



. South Asian area planted to pearl millet in 1978 in relation to the mean annual rainfall isohyets. One dot
0,000 ha.

ADAPTATION TO MOISTURE STRESS

The concentration of pearl millet in rainfall zones of less than 600 mm/year testifies to the relative adaptation of the crop both to low average rainfall and to high annual variability in rainfall. Rachie and Majmudar (1980) suggested that this adaptation might be due more to a combination of short duration and heat tolerance than to specific (physiological) drought resistance mechanisms. There is evidence that several developmental and morphological features of pearl millet are important in its ability to produce a grain yield in a variable moisture situation. But too little is known of the possible physiological adaptation mechanisms to drought to evaluate their importance.

Developmental plasticity: adaptation to a variable moisture environment

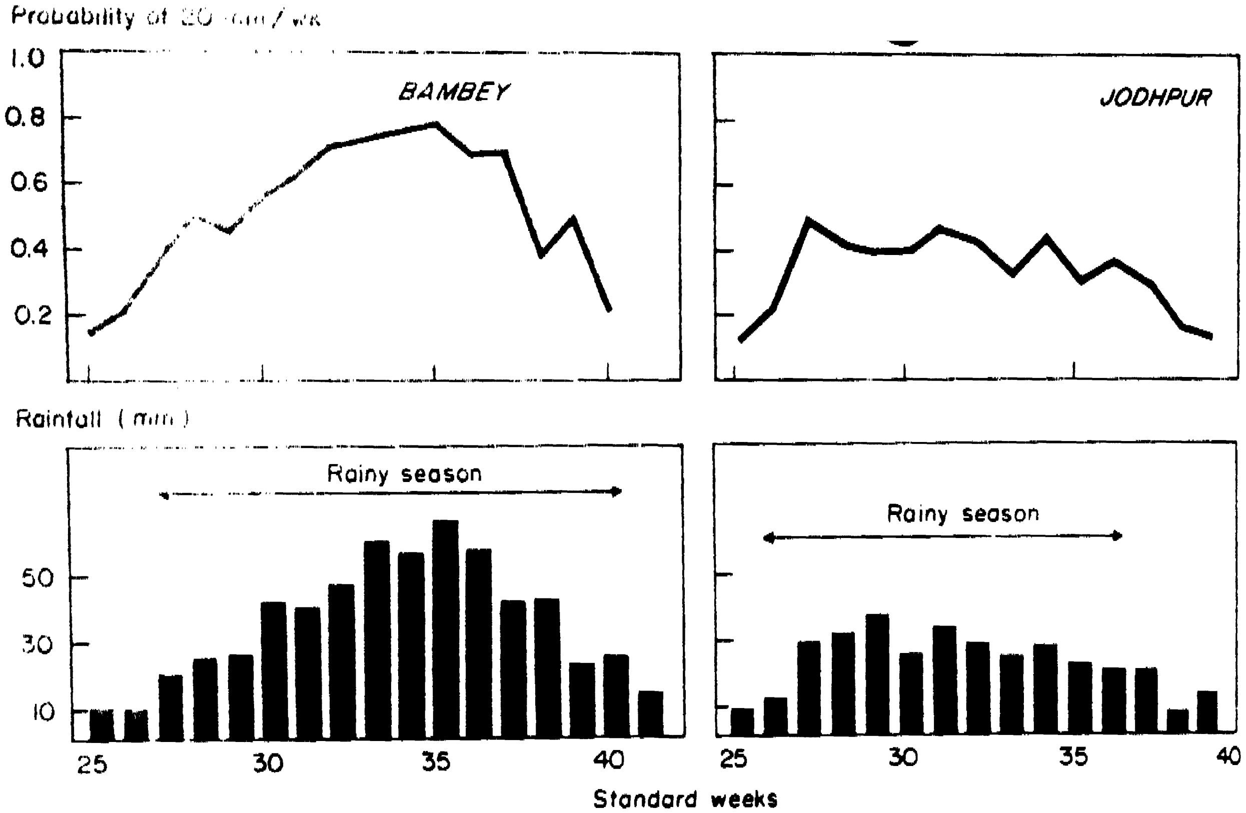
Table 1. Rainfall and soil data for Bambey, Senegal, and for Jodhpur, India.

	Bambey[a]	Jodhpur[b]
Latitude	14° 42′ N	26° 18′ N
Annual rainfall (mm)	650	383
CV of mean rainfall (%)	25	57
Rainy season[c]		
Duration (wk)	14	11
Total rainfall (mm)	582	297
Mean weekly rainfall (mm)	42	27
Mean weekly PET (mm)	31	39
Soil data		
Coarse sand (%)	20-25	19-20
Fine sand (%)	65-75	66-71
Silt (%)	0-3	3-5
Clay (%)	2-5	6-9
Field capacity (%)	6-10	7-10
Wilting point (%)	1.5-4	2-5
Depth[d] (cm)	150	60-90
Available soil water[e] (mm)	90	60

[a]ICRISAT Agroclimatology Program (unpubl.) and Dancette (1970).
[b]Virmani et al 1978, ICRISAT Agroclimatology Program (unpubl.), All India Coordinated Research Project for Dryland Agriculture (unpubl.).
[c]Defined as the period during which the ratio of rainfall to potential evapotranspiration (PET) > 0.33.
[d]Soil depth at Bambey exceeds 200 cm; 150 cm is estimate of actual wetted soil profile. Soil depth at Jodhpur is actual depth.
[e]Estimates used in calculating soil water balances in Figure 3, 4.

combination of short reproductive and grain-filling periods with a variable length of vegetative phase which generally determines the total season length. Short-duration cultivars (70-75 days to maturity) require about 20 days from emergence to floral initiation, 25 days from initiation to flowering, and 25 days for grain filling (G. Alagarswamy unpubl.). Variation in development of longer-duration cultivars is generally in the vegetative period because floral initiation is controlled by photoperiod (Kowal and Kassam 1978, Norman and Begg 1968). This has allowed an evolutionary adjustment of time of flowering to local moisture patterns (even where planting dates vary because the arrival of sowing rains varies), while keeping the duration of the important reproductive and grain filling periods short. Because drought stress during the vegetative period damages yields less than drought in later stages (Lahiri and Kharabanda 1965, Lahiri and Kumar 1966), an extension of this period results in only a marginal increase in the risk of drought injury relative to an extension of the reproductive or grain filling periods.

Many millet cultivars also interrupt development when exposed to severe stress during the late vegetative or early reproductive stages, resuming development only when moisture is again available. Flowering under these conditions may be noticeably delayed (Fig. 6), providing an escape mechanism from stress if conditions after the stress period favor continued crop growth. This has been a useful



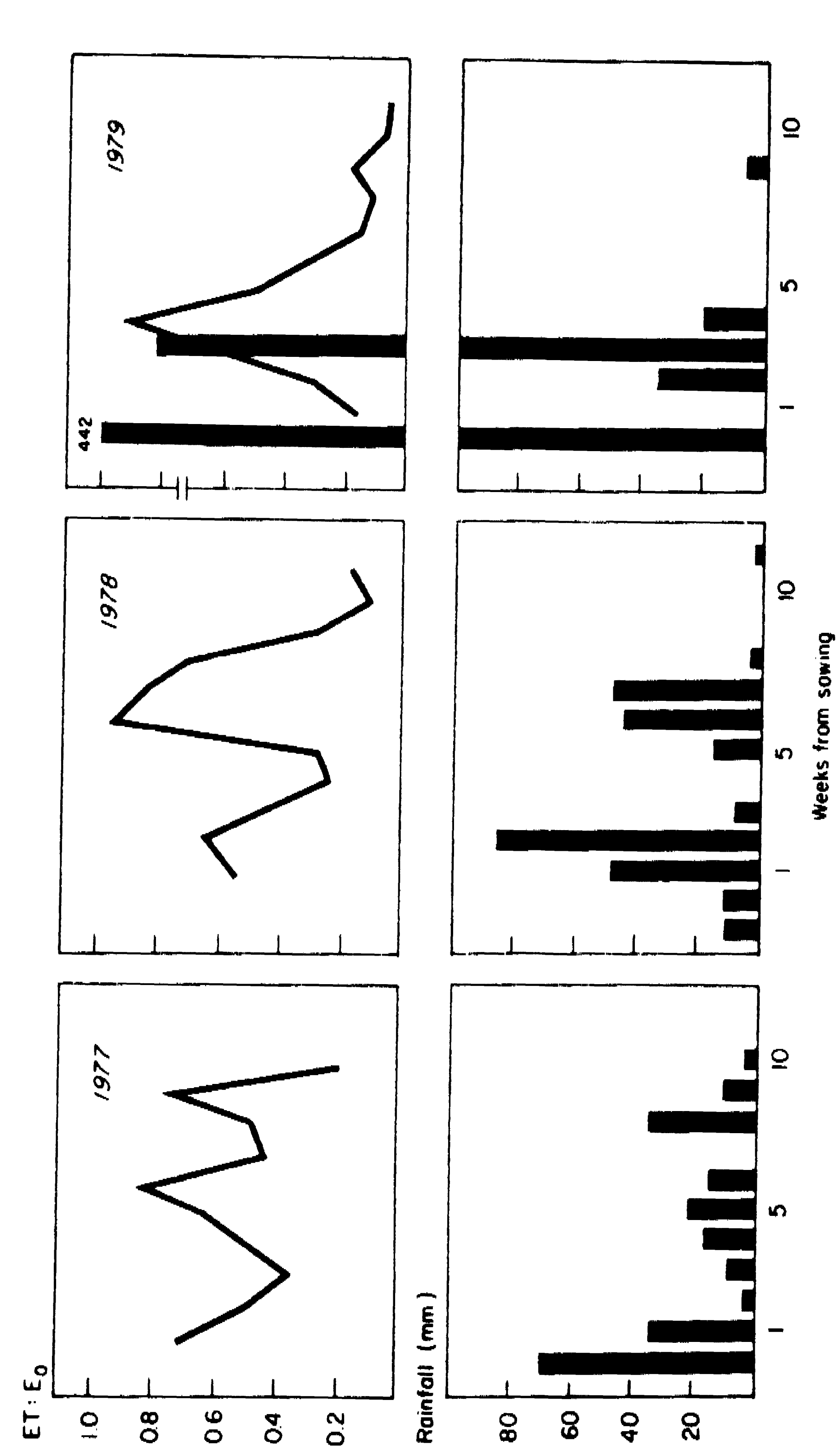
3. Mean weekly rainfall and the probability of receiving 20 mm/week for Bambey, Senegal and Jodhpur, India. Standard week 25 begins 18 June; see text for definition of the rainy season.

mechanism in drought screening trials at ICRISAT, in which a stress period is applied from approximately panicle initiation to flowering, after which sufficient irrigation is provided to complete development. Lines with this ability to suspend development often perform well in these conditions.

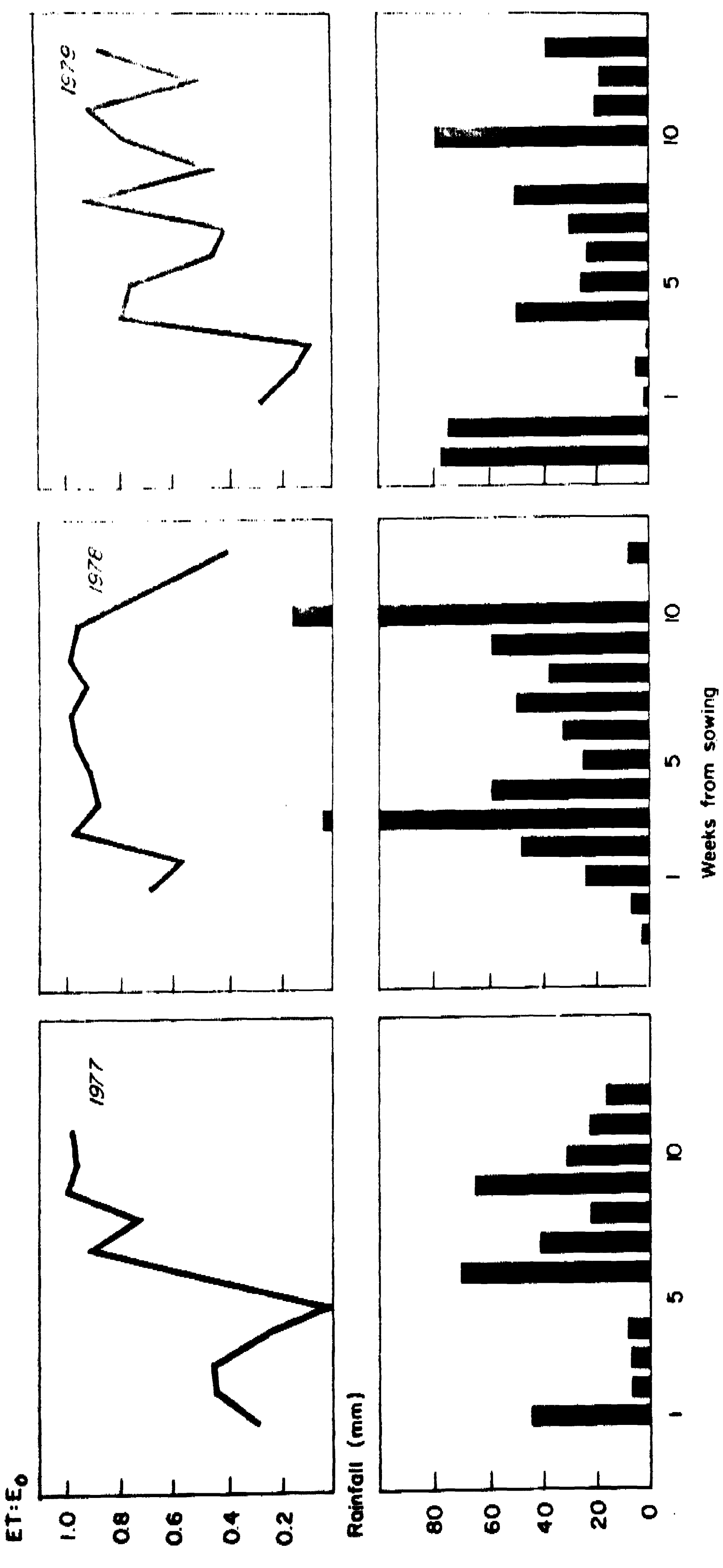
Pearl millet also has the ability to respond to moisture after a stress period during the reproductive or early grain filling periods. This ability shows in stimulation of secondary tillers that would not have developed or would not have completed development under normal conditions. Most land race cultivars (and many improved ones) have an asynchronous tillering habit (Raymond 1968) that maintains a potential for regrowth if drought affects the main stem and primary tillers. In some cases, final head numbers, crop growth, and grain yield may not differ from those of a nonstressed comparison crop, provided sufficient moisture is available after the stress period to complete development of the secondary basal tillers (Fig. 7, G. Alagarswamy, unpubl.).

Under intermittent drought conditions, certain land race materials will produce several flushes of heads from small tillers formed in the upper nodes of the primary tillers as well as from secondary basal tillers. These nodal tillers form only 2-3 leaves and a small head, but do so in a very short period of time, 10-20 days to flowering (Nanda and Chinoy 1958). The presence and productivity of the nodal tillers has strong negative relationship to grain set and grain growth in the head of the parent shoot. When these are poor (for example, when the parent shoot flowers during a period of severe stress), the nodal tillers may compensate to a significant degree.

addition to the developmental plasticity to utilize short or intermittent

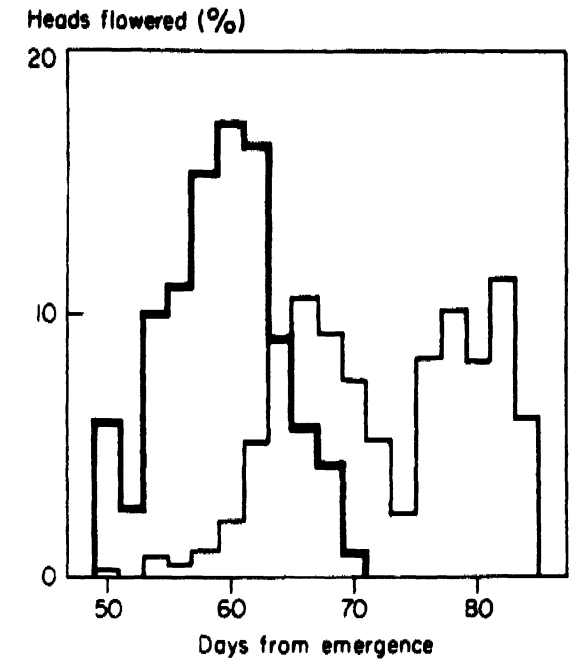


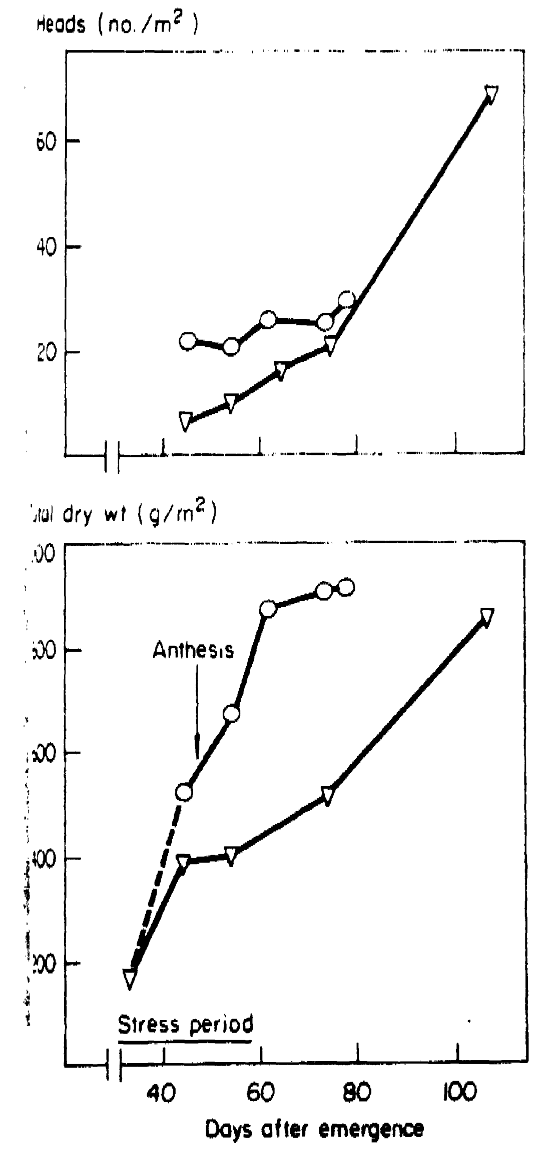
4. Weekly rainfall and predicted weekly ratios of actual evapotranspiration to pan evaporation ($ET:E_o$) during the 1977 to 1979 cropping seasons for Jodhpur, India.



5. Weekly rainfall and predicted weekly ratios of actual evapotranspiration to pan evaporation (ET:E_o) during the 1977 to 1979 cropping seasons for Bambey, Senegal.

6. Frequency distribution of days to flowering (individual heads) of cultivar BD763 in irrigated-control (bold line) and midseason stress (fine line) treatments. The stress treatment was terminated on the 45th day from emergence. n = 298 for the control and 359 for stress treatments.





7. Total dry weight and head numbers per unit area for cultivar ICH 118 under irrigation (○) and midseason-drought stress (▽) treatments. The stress period was imposed from about 30 to 62 days after emergence.

periods of favorable moisture, pearl millet also has a capacity for high rates of crop growth and for efficient conversion of intercepted radiation to dry matter (Begg 1965). This presumably permits the crop to maximize growth during favorable periods.

Physiological adaptive features: adaptation to drought and heat stress

Control of water loss and internal water status. From the limited information available, pearl millet appears to have several mechanisms for the control of internal water status. Stomatal conductance has been shown to be sensitive both to rates of canopy transpiration and to differences in vapor pressure between the leaf and the atmosphere under adequate soil moisture levels (Squire 1979, Black and Squire 1979). Over a range of saturation deficits from 1.3 to 2.6 kPa (at a constant irradiance), Black and Squire (1979) measured a twofold to threefold variation in stomatal conductance.

There is also evidence of variation in internal resistance to water transport in the crop where soil moisture levels are adequate, since bulk leaf water potentials were found to vary only slightly (3 bars) over a threefold range of estimated leaf transpiration rates (ICRISAT 1980).

Both of these mechanisms have value for adaptation to atmospheric stress conditions (high radiation, high temperature, and low humidity) rather than for edaphic stress conditions. Presumably the mechanisms permit maximization of carbon dioxide uptake consistent with the maintenance of a nonstress internal water status in such conditions.

Under conditions of inadequate soil water availability, the response to low saturation deficits was not observed (Squire 1979). Leaf water potentials were found to be linearly dependent on transpiration rates (ICRISAT 1980). Stomatal conductance was either dependent on radiation (Squire 1979) or, in a more severe stress case, on threshold leaf water potential (ICRISAT 1980). Under such conditions, millet appears to behave similarly to other cereal crops and its advantage, if any, is in its greater heat tolerance when transpirational cooling is lost with stomatal closure.

Little is known about the contribution of other possible mechanisms to drought resistance in pearl millet. Measurement of osmotic potentials under stress conditions do not suggest that osmotic adjustment is important in the crop (Henson, Mahalakshmi, Bidinger, and Alagarswamy, unpubl.). Studies on abscisic acid accumulation under stress have indicated considerable genetic variation in this response, but its relationship to drought resistance is yet to be determined (Austin et al, this vol). Work in Australia has indicated the capacity for deep rooting in forage cultivars (Begg et al 1964, Wetselaar and Norman 1960). However, depth of root penetration may be influenced by extended vegetative periods and high rates of dry matter production in forage types. Studies on shorter duration grain types have suggested relatively shallow rooting (Gregory, this vol).

High temperature adaptation. Again from limited evidence, pearl millet appears to have both a relatively high temperature optimum and a significant tolerance for heat stress beyond the optimum. Temperature optimum (leaf temperature) for photosynthesis of intact leaves was reported to be 35-40° C with rates greater than 75% of maximum at temperatures as high as 45° C (McPhearson and Slatyer 1973). For oxygen evolution of isolated chloroplast, rates at 43° C were similar to those at 25° C (Sullivan et al 1977). This range exceeds that which would be experienced by normally transpiring leaves (which would be below air temperatures) and extends well into the range of temperatures experienced by leaves with loss of transpirational cooling.

More appropriate to these conditions are direct measurements of the heat tolerance indicated by electrolyte leakage from the cells of heat-treated leaf discs (Sullivan et al 1977). The pearl millet cultivars tested had a relatively low degree of injury (< 20% after treatment at 48° C for 1 hour) compared to sorghum (30-38% injury under the same conditions). In contrast, estimates of drought tolerance using a similar technique (a period of desiccation of the leaf discs rather than heat treatment) suggested that pearl millet was less tolerant than sorghum of the direct effect of drought stress on a cellular level (Sullivan 1972).

Present knowledge suggests that pearl millet is adapted to its environment largely by means of an opportunistic strategy:

1. Short duration of basic developmental stages plus the capacity for high growth rates under favorable conditions allows the crop to maximize periods of favorable moisture.
2. Considerable plasticity in development and the possibility for rapid regrowth following the end of a stress period allow the crop to adjust to intermittent periods of favorable and unfavorable conditions.
3. Adaptation to atmospheric stress through effective control of water loss, through resistance to water movement, and through a high temperature optimum for photosynthesis results in a very efficient use of a high temperature, high radiation, low humidity environment, provided that sufficient soil water is present.
4. Survival of periods of combined edaphic and atmospheric stress by the suspension of development and by tolerance for heat stress when transpirational cooling is lost.

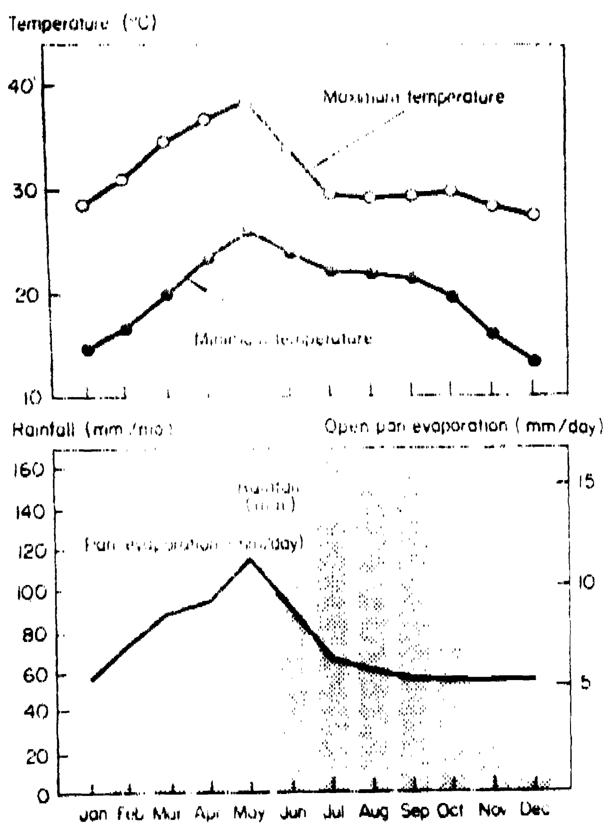
IMPROVEMENT OF DROUGHT RESISTANCE

The ICRISAT program is the basis for this discussion as it is the only one of which we are aware that has published reports of research specifically on the improvement of drought resistance in pearl millet. Drought stress occurs naturally in most millet breeding programs. Thus, segregating materials are routinely selected and advanced materials evaluated in such conditions. But performance under drought conditions, rather than drought resistance itself, is the selection criterion.

Factors affecting performance under drought stress

Measured grain yields (the simplest definition of performance) in a given stress condition are influenced by three factors: 1) the basic yield potential of the cultivar, 2) the developmental pattern of the cultivar (which may allow it to partially or totally escape the effects of that stress), and 3) the drought resistance or susceptibility of the cultivar.

We illustrate this with data from three years of replicated trials of advanced



8. Monthly mean rainfall, open pan evaporation, and maximum and minimum temperatures at Hyderabad, India. The summer season (Feb-May) is used for drought resistance work.

breeding materials from ICRISAT. The trials are conducted every year during the rainfree summer season (Feb-May) when atmospheric conditions favor severe stress. Maximum temperatures range from 33 to 40° C, open pan evaporation rates reach 8-11 mm/day, and daily radiation averages 500-600 lx (Fig. 8). Controlled irrigation is used to create two standard stress treatments, from panicle initiation to flowering (midseason stress) and from flowering to maturity (terminal stress). Varieties in these trials vary in maturity (Table 2) and the onset and termination of the stress treatments are aimed at average dates of floral initiation and flowering. Grain yields from these two treatments are compared with those from a fully irrigated control treatment, which provides an estimate of the yield potential of the material under the climatic conditions of the summer season.

The influence of both yield potential and phenology (days to flowering) on stress treatment yields is clear under these conditions (Fig. 9). When these two effects are combined into a single regression equation, we can explain 40-60% of the observed yield variation under stress conditions (Table 3). This knowledge is useful, but it does not provide a basis for attempting to specifically improve cultivar performance under drought stress. Improvement in yield potential may result in some improvement in performance under stress (Fig. 9), but breeding for drought escape (phenology) is of use only where stress occurs in regular, predictable patterns. In a variable rainfall environment, a cultivar that escapes stress one year may be seriously affected the next year if the timing of the stress differs.

On the other hand, about half of the variability in yield under stress conditions is apparently due to specific cultivar × stress interaction. If it were possible to identify the factors contributing to this interaction and to specifically incorporate these into otherwise good cultivars (or to select against those responsible for poor performance), progress might be more rapid. But the utilization of specific

Table 2. Mean yields, da[illegible] flowering, and drought indices from Advanced Screen 1979. Hyderabad, India.[a]

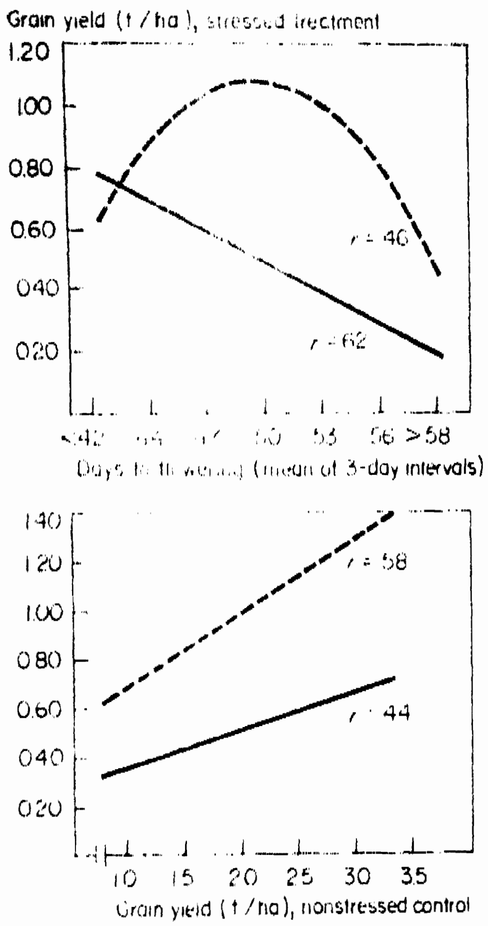
Pedigree	Control		Midseason stress		Flowering stress	
	Yield (t/ha)	Days to flowering	Yield (t/ha)	Drought index	Yield (t/ha)	Drought index
LC-Cx75	4.0	49	3.1	− 0.6	1.6	0.4
7224	4.0	55	3.8	1.0	1.2	− 0.7
SSC-Cx75	3.8	49	3.4	0.8	1.7	1.5
700490/GNS-1	3.5	54	3.0	− 0.3	0.9	− 1.5
RF-Ax76	3.6	47	2.8	− 0.3	1.7	1.3
ICMS 7703	3.6	49	3.0	− 0.0	1.3	− 0.7
Mali NNK	3.5	50	2.3	− 1.7	1.2	− 0.6
A-836/GNS-1	3.5	52	2.5	− 1.4	1.2	− 0.4
ICI-7504	3.2	50	3.1	0.8	1.0	− 1.5
IP-1964	3.1	50	2.8	0.2	1.5	1.9
700250-25	3.0	52	3.4	1.7	1.2	0.8
J-1197	3.0	51	2.5	− 0.4	1.3	0.8
7203	2.9	51	2.7	0.1	1.1	0.3
Serere 4A	2.9	48	2.2	0.2	1.2	− 0.3
BK-560-230	2.9	43	2.1	0.0	1.2	− 0.8
700516	2.9	57	2.7	1.2	0.7	− 0.0
B-816//J-1623/WC-2	2.8	56	2.1	− 0.6	0.8	− 0.3
Serere-39	2.7	58	1.8	− 1.1	0.7	0.1
1/2 HK Nain	2.6	50	2.1	− 0.7	1.0	− 0.5
700441	2.6	50	2.1	− 0.5	1.1	0.2
J-1623/J-1644-1	2.6	49	2.0	− 1.1	0.8	− 1.6
Cassady	2.4	47	2.0	0.2	1.2	0.2
J-1150	2.3	54	2.6	0.9	1.1	− 1.6
BJ-104	2.3	42	1.7	− 0.1	1.2	0.3
CD-67-13	2.3	55	2.1	− 0.2	0.6	− 0.7
SE%	14.9	3.4	12.5		27.5	
CD at 5%	0.64	2.5	0.45		0.45	

[a]Net plot size: 4.5 m². Replications: 4.

hysiological or morphological characteristics as selection criteria is possible nly 1) where evidence is clear that incorporation of these characteristics into reeding materials will improve their yield performance under stress and 2) here there are simple efficient techniques for selecting for these characters on he scale necessary for a breeding program. For most physiological and many orphological characteristics, one or both conditions (usually the first) are cking (Bidinger 1980).

This is clearly the case with pearl millet. Little research is available on drought sistance mechanisms and there is no solid evidence that breeding for those echanisms will produce cultivars with higher or more stable yields under stress. the absence of such evidence the expenditure of the manpower and resources cessary to breed for such mechanisms is not justifiable.

Therefore we are concentrating on 1) the identification of lines with probable sistance to stress and 2) determining if initial selection for performance under ecific, repeatable stress conditions, followed by direct evaluation of resistance,



9. Grain yields in midseason (----) and terminal (——) stress treatments in relation to days to flowering and grain yield in the nonstressed control treatment.

Table 3. Summary of the variation in stress yields explained by yield potential and by drought escape. 1977-79 Advanced Screens.

Year	Entries (no.)	Days to flowering	Percentage variation explained (r^2): Midseason stress[a] f(yc, bl, bl²)	Percentage variation explained (r^2): Terminal stress[a] f(yc, bl)
1977	40	38-61	49	44
1978	64	39-60	42	55
1979	25	42-58	67	61

[a]f = function of, yc = yield potential measured in nonstressed conditions, bl = days to flowering.

will be useful as a means of identifying lines with drought resistance characteristics.

Identification of resistance to drought stress

In the ICRISAT program, drought resistance or susceptibility is identified with variation in grain yield under stress which is not explained by yield potential and drought escape. This is done by applying regression equations of the type shown in Table 4 to data sets from groups of lines or cultivars tested together in the previously described controlled stress treatments. This procedure establishes the

Table 4. Regression equations used to develop stress indices for lines in the Advanced Screen.[a]

Midseason stress	$\hat{y}_s = a + b_1(Y_c) + b_2(bl) - b_3(bl^2)$
Terminal stress	$\hat{y}_s = a + b_1(Y_c) - b_2(bl)$
Drought index	$\dfrac{Y_s - \hat{y}_s}{\text{Std. error of } \hat{y}_s}$

[a]$\hat{y}_s$ = regression estimates of stress yield, Y_s = measured stress yield, Y_c = nonstress control yield, and bl = days to flowering.

general effects of yield potential and drought escape for the entire cultivar set. These regressions are then applied to individual cultivars and the residuals for each individual cultivar (the difference between the measured yield under stress and the yield predicted) are calculated. These residuals, divided by the standard error of the regression estimates, are termed the *stress indices* for the test varieties. Table 4 shows the procedure for calculating stress index.

The sign of the index indicates resistance (positive sign — measured yield exceeding predicted yield) or susceptibility (negative sign — measured yield less than predicted yield). The magnitude of the index indicates the degree of the response. Because the residual includes experimental error as well as specific cultivar × stress interaction, we focus attention only on those cultivars with indices of less than −1.3 or more than +1.3. These represent the upper and lower 10% of the normal distribution of the indices. Thus there is a reasonable probability ($p \geq .80$) that the effects are real and not random.

For advanced breeding lines screened for drought resistance, program scientists use the drought index as one of several pieces of information (including various disease scores and yield test results) to make decisions on the advancement of individual lines. Table 2 shows one such data set, the 1979 Advanced Screen. Several entries illustrate the type of responses commonly observed: LC-Cx75 (an ICRISAT experimental line) yielded well in both stress treatments, but mainly on the strength of its yield potential (yield in the control treatment) because its stress index for both treatments was near 0. The selection 7000250-25 (from Nigerian material) and IP1964 yielded relatively well in the midseason and terminal stress treatments, respectively, but more on the strength of a resistant response because the yield potential of both was only average. BJ104 (a standard Indian hybrid) yielded poorly in the midseason stress, due largely to a low yield potential in the summer season, but did relatively well in the terminal stress, mainly because early flowering allowed escape from stress. Finally, the line derived from the cross J-1623/J-1644-1 performed poorly in both stress situations because of an apparent susceptibility to both stress treatments.

Breeding for drought resistance

The definition of stress resistance or susceptibility used to evaluate advanced materials is not useful as a selection criterion in the early segregating generations of a breeding program. Seed, space, and labor requirements do not allow replicated tests with control plots to identify lines with high positive stress indices in F_1/S_1 generations. Also, doubts about the effectiveness of selection for yield in early generations apply equally to any yield-based estimate of drought resistance or susceptibility. Therefore, we are investigating the alternative approach of selection for performance under well-defined stress conditions as a means of identifying lines with resistance to stress or with a combination of resistance and yield potential.

To test this approach, we are using the midseason controlled-stress treatment described above (panicle initiation to flowering) as a selection environment. This has two advantages: 1) Selection conditions are repeatable to a reasonable degree in an off-season nursery and therefore initial selection and subsequent evaluations are for response to the same conditions. This should avoid some problems of selection in a variable, natural-stress environment; and 2) Because this is a known stress environment, selection for escape rather than resistance can be minimized by avoiding disproportionate selection in those maturity groups that favor escape. In addition, the environmental conditions of the summer season maximize the selection pressure for segregating lines least affected by stress or best able to recover rapidly from it. In a sense, this procedure is analogous to a managed disease-screening nursery in which a severe disease pressure can be placed on test materials to maximize the expression of resistance and in which selected lines can be retested to verify their responses.

The disadvantages of this approach are that lines are exposed only to a single stress treatment and are selected in an off-season environment. The latter objection is partially covered by evaluating (but not advancing) selected F_3/S_1 lines in the normal season before their reselection in the following dry season.

This system involves visual selection in the first generation (F_2/S_0). Beginning with the F_3/S_1 generations, however, grain yield is also measured and used for selection along with visual scores of the lines both at the end of the stress period and after recovery. Particular emphasis is on the ability to recover rapidly from the stress exposure principally through tiller regrowth, as this appears to be the character for which major variability exists.

We emphasize that this approach is still experimental. Direct selection in controlled stress conditions has not been shown to be the most effective procedure for identifying lines with either good performance or resistance under naturally occurring stress conditions. Nor is it clear that selection for performance in early generations is the most efficient way to identify lines with stress resistance. To answer these questions, parallel selection in the same crosses and populations under selection in stress conditions is being carried out in both the normal crop season (to represent the current breeding practice) and in a nonstressed summer season planting (to separate possible effects of selection for adaptation to summer-season environmental conditions from selection for adaptation to drought stress). Final evaluation will be a comparison of the performance of the products of each of the three selection environments, over all three environments, and in several naturally occurring stress environments. Performance analysis in each stress environment will be in terms of yield potential, escape, and resistance to determine if stress exposure during selection has influenced the relative contribution of each factor to final performance. The F_3/S_1 selection generation has just been harvested. Final comparisons of finished products will be available in several years.

PROSPECTS FOR IMPROVEMENT IN DROUGHT RESISTANCE

The most promising short-term approach for improving the drought resistance of pearl millet is probably the exploitation of differences in developmental patterns and in rates of recovery after a stress period. These include such responses as 1) delay in development during severe stress, 2) degree of asynchrony in tiller development which allows some tillers to escape a stress period that damages others, and 3) rapid release and growth of secondary tillers after stress damage to the main tillers. Pearl millet has considerable genetic variation for these characteristics and they can be easily selected for in a managed stress nursery, where stress occurrence can be timed to maximize the value of the responses. Additional experiments on these mechanisms should be done, particularly on the specificity of these responses to the timing and duration of stress. We are now selecting indirectly for these responses, because lines selected on the basis of yield performance under stress are often lines with one or more of these responses.

Selection for specific physiological response mechanisms of drought resistance is a future, rather than a current, possibility. Research to identify these mechanisms and to determine if using them as selection criteria will improve cultivar performance under stress has not yet been done.

The possibility of exploiting avoidance mechanisms in pearl millet seems limited. Because of the nature of rainfall, soils, and potential evapotranspiration in many arid and semiarid environments, the amount of water available in soils (relative to potential rates of water use) will be small. Therefore, plant mechanisms to exploit these will be of limited usefulness. Tolerance mechanisms may be more useful in pearl millet in these circumstances (the earlier discussion of heat tolerance in the crop supports this). But tolerance mechanisms are generally better known in theory than in practice in crop plants.

Millet has an additional, somewhat different, factor that may prove an advantage in the improvement of its drought resistance: there are fewer competing priorities in millet improvement than in other major tropical cereals. Disease and insect problems in millet, while present, are generally less extensive and perhaps less serious than in maize, rice, and sorghum. Yield potential is also less of an actual limitation to yield at the *farmer level* than in the case of other cereals and, hence, high yield potential may be a lower priority in pearl millet. Part of this is because of the generally low input levels under which the crop is grown (a factor that may change with time), but also because factors such as drought often do not permit millet to fully express its yield potential. We hope these factors will allow millet breeders to concentrate relatively more of their inputs on drought resistance.

In summary, if relatively simple and reliable methods can be developed for improvement in drought resistance, the opportunity for at least modest improvements should be good. But there will clearly be years and environments without enough rainfall for a crop — and no amount of research will change that. Hope-fully, improvement of yields in the average years (which do include stress periods) will allow farmers to better withstand the poor years.

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