

Seedling Survival of Abiotic Stress: Sorghum and Pearl Millet

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Abstract

This paper reviews the responses of sorghum and pearl millet seedlings to abiotic stress and considers the implications for crop production, particularly with respect to the arid and semi-arid tropics. The growing season in much of this area is characterized by high temperatures, high evaporative demand, unreliable and irregular rainfall, and soils of poor structure, low fertility, and low water-holding capacity. Poor seedbed preparation and inadequate sowing methods can increase the likelihood of abiotic stresses developing. Such conditions result in reduced seedling growth rates, injury, and ultimately mortality during the germination and seedling emergence stages. The wide range of causes of stand failure means there is no single solution. For a given target environment it is necessary to define the reasons for a stand establishment problem and to understand the requirements of the farmer. Genetic variation for seedling stress tolerance, however, has been shown to exist in both sorghum and pearl millet. Screening techniques have been developed and used in population improvement programs and in identification of molecular markers linked to the thermotolerance trait. Potential thus exists for the genetic improvement of these crops for survival of abiotic stresses to complement solutions brought about by changes in agronomic practice.

Failure of seedling establishment is a major factor limiting crop production. This paper discusses the main environmental causes of crop establishment failure in pearl millet [*Pennisetum glaucum* (L.) R.Br.] and sorghum [*Sorghum bicolor* (L.) Moench] in the semi-arid and arid tropics. Rain-fed agriculture predominates in these areas of South Asia and the Sahelian-Sudanian zone of Africa; sorghum characteristically is grown where mean annual rainfall is 600-1000 mm and pearl millet in areas where the mean is from 200-600 mm per year (Si-

vakumar et al., 1984; Spencer and Sivakumar, 1987). The mean rainfall is not only low (and evaporative demand high), but also very erratic in its distribution through the growing season and variable between years. Pearl millet is one of the most drought- and heat-tolerant grasses to be domesticated. Its progenitors were desert grasses found on the southern fringes of the Sahara; pearl millet landraces have grown in the Sahel since 3000 BC and probably in India for some 2500 years (Brunken et al., 1977; de Wet et al., 1992). It is still primarily grown by subsistence farmers under harsh environmental conditions where no other cereal can be grown; it may be described as a crop of necessity rather than choice (Bidinger and Parthasarathy Rao, 1990).

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If pearl millet and sorghum are already so well-adapted, why is improvement needed? It is not so much a question of improving the adaptive range, but of improving yield and yield stability under conditions of abiotic stress. Improvements in yield and yield potential are well documented (e.g., Harinarayana, 1987), but these are expressed under favorable conditions quite unlike those encountered in many farmers' fields in marginal environments. Adaptation to specific environmental stresses is a larger determinant of crop yield than is yield potential in these environments (Evans, 1993). Both improved hybrids and open pollinated varieties do not necessarily possess the stress tolerance of landraces with low grain yield potential and may have no yield advantage over traditional landraces in these harsh environments (Weltzien and Witcombe, 1989; Bidinger et al., 1994; Yadav, 1994).

Although modern cultivars account for more than 50% of the area sown to pearl millet in India as a whole, adoption has been limited in locations with lower and less reliable rainfall. In these areas pearl millet is the staple cereal crop and mean yields remained unchanged from 1956 to 1988 at 144 kg ha⁻¹, with grain yields of 50 kg/ha not uncommon (Gupta et al., 1992). An increasing unpredictability of yield also was found over this time period. In sub-Saharan Africa, adoption of improved pearl millet cultivars is limited for many reasons (Bidinger and Parthasarathy Rao, 1990; Ouendeba et al., 1995). Plant breeders may be unfamiliar with the specific production conditions and thus may have set inappropriate goals (Haugerud and Collinson, 1990). Farmers in Rajasthan indicated that they have not

adopted improved cultivars of pearl millet primarily because of poor grain yield in low rainfall years (Kelley et al., 1996). Poor stand establishment and straw yield were other important characteristics (Weltzien et al., 1996). Genetic advances achieved under favorable conditions and using elite breeding material do not necessarily benefit farmers in marginal areas (Weltzien and Fischbeck, 1990). Research with pearl millet has shown it is possible, however, to produce landrace-based topcross hybrids that combine the stress adaptation of indigenous landraces with the improved yield potential from elite male sterile lines (Bidinger et al., 1994; Yadav and Manga, 1995). Considerable genetic diversity exists for survival of abiotic stresses, no doubt due to selection in response to local environmental conditions. Blum and Sullivan (1986) found that landraces of sorghum and millet that had evolved in dry regions tended to be more drought-resistant than races that evolved in humid regions. Today as human populations increase, traditional management practices and landraces may not be sufficient.

Abiotic Causes of Crop Establishment Failure

Despite the level of environmental adaptation that both pearl millet and sorghum display, failure of seedling establishment due to abiotic stress is a major problem. The environmental sensitivity of a plant varies throughout its development (Levitt, 1980), but the seedling phase is particularly vulnerable. The growing season in much of the arid and semi-arid tropics is characterized by high temperatures, high radiation, high evaporative demand, unreliable and irregular

rainfall, and soils of poor structure, low fertility, and low water-holding capacity. Farmers sow on the first significant rainfall of the monsoon. The timing of the onset of the monsoon is variable both in time and place (Van Oosterom et al., 1996). A hot, dry seedbed environment during crop establishment is very likely, with soil surface temperatures often greater than 55°C (Figure 1; Gupta, 1986; Hoogmoed and Klaij, 1990; Peacock et al., 1993).

For a farmer in such environments, the timing of seed sowing is critical. If the farmer chooses to sow after an early, pre-

monsoon rain, seedbed conditions will be extremely hot and there is high risk of low moisture availability without subsequent substantial rainfall. Delay in sowing after rain can result in insufficient moisture in the seed zone of the soil for germination to take place. In the sandy soils of many pearl millet growing environments, moisture depletion to less than 2% often occurs three to four days after rainfall (Peacock et al., 1990). If sowing is delayed until a later rain, chances of drought stress at the end of the season are greater. Van Oosterom et al. (1996) calculated the probability of an 80-day rainy season based on sowing date, and found if planting were

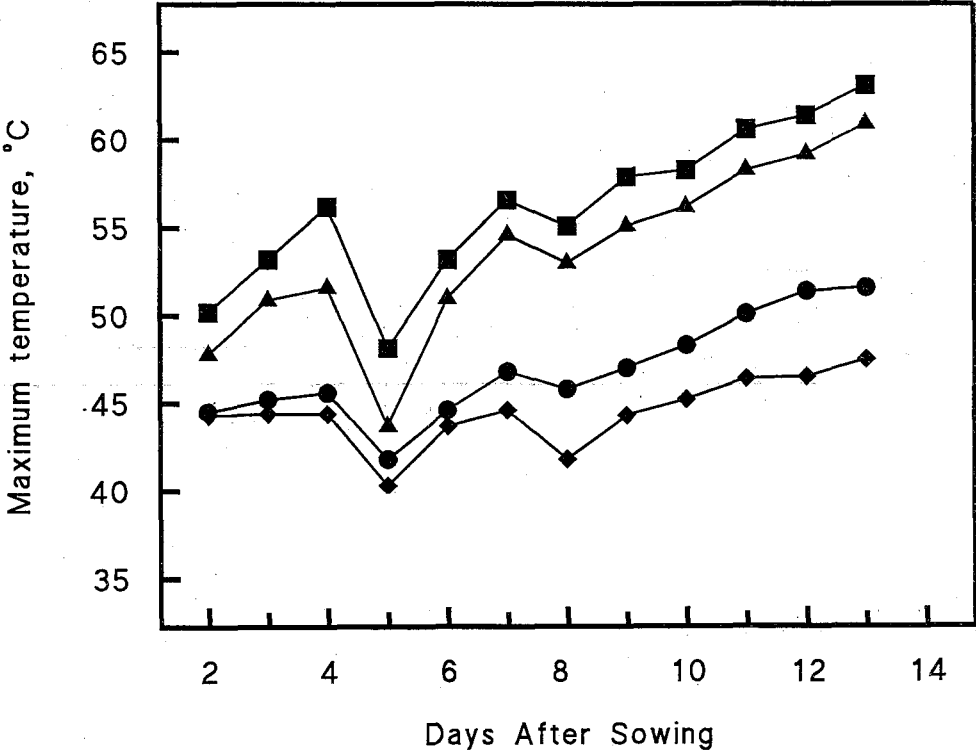


Figure 1. Maximum daily temperature recorded for each day of the first two weeks after sowing in June 1991, at Fatehpur-Shekhawati Research Station, Rajasthan Agricultural University, India. Measurements were taken of air temperature (●) and soil temperatures at depths of 0.5 cm (■); 1.5 cm (▲); and 5 cm (◆). Each temperature point is the mean of three readings.

delayed from early June to late June, the probability dropped from over 80% to less than 50% in most sites in Rajasthan. By mid July, the probability was 20% or less in all sites. Thus if resowing has to take place due to poor crop establishment, the risks of crop failure increase because the length of the growing season is reduced. In addition, soil nitrate availability is decreased due to leaching (Greenland, 1958). Late planting results in lower grain yields (Krause et al., 1990; Maiti and Soto, 1990), although Reddy and Visser (1993) found differences between genotypes in the yield reduction of both straw and grain as influenced by sowing date. Re-sowing also places additional demands on labor and seed.

Poor stand establishment results not only in sub-optimal plant populations in farmers' fields but also in an uneven distribution of plants (Soman et al., 1987a). Although the tillering capacity of pearl millet might enable it to compensate better than sorghum for variation in plant population, controlled experiments simulating the range of plant populations and spacing found in farmers' fields indicated that yields were greatly reduced by uneven plant spacing; the same total plant population yielded 47% less in an uneven spacing compared to the control. No amount of favorable weather during the growing season can compensate for the poor plant stands so common in the semi-arid tropics. Farmers often use high seeding rates, which could compensate for seedling survival of only 50%, but often stands of 10% or lower are found in farmers' fields (Soman et al., 1987b).

Seedling death can occur at one of three defined stages in crop establishment: ger-

mination, emergence, and post emergence. Table 1 summarizes the major causes. We will consider the sensitivities of these crops to abiotic stresses at each of these stages and describe the screening techniques available. The prevalent climatic variables must be characterized in detail to help explain what actually affects seedling growth and survival. Mean maximum air temperatures in July range from 30 to 35°C for sorghum growing areas, and from 35 to 40°C in millet growing areas (Sivakumar et al., 1984). Summary environmental data can appear to minimize the problem; mean daily air temperature or even mean maximal daily air temperatures do not indicate diurnal variations in temperature, nor the absolute extremes reached. Moreover, the temperatures actually encountered by the germinating and emerging seedling must be

Table 1. Causes of crop establishment failure at different developmental stages.

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- A. Germination**
 - ◆ Seed quality
 - ◇ maturation conditions
 - ◇ maturity
 - ◇ threshing damage
 - ◇ storage conditions
 - ◇ seed treatment
 - ◇ dormancy
 - ◇ viability
 - ◆ Moisture availability
 - ◆ Temperature
 - B. Emergence**
 - ◆ Sewing depth
 - ◆ Temperature
 - ◆ Moisture Availability
 - ◆ Soil surface crusting/compaction
 - C. Seedling Survival**
 - ◆ Temperature
 - ◆ Moisture availability/Flooding
 - ◆ Soil nutrient status
 - ◆ Wind/ sand blast
 - ◆ Radiation
 - ◆ Humidity

considered. Figure 2 presents the diurnal temperature cycle in Rajasthan five days after sowing. Although a maximum air temperature of approximately 46°C was measured, soil temperatures at 0.5 cm depth varied from nearly 60°C at mid-day to a pre-dawn minimum of less than 20°C. At 5 cm depth (where seed is sown), the temperature ranged from 28 to 44°C during a 24-hour period. Greater depths (10 cm depth) were more buffered, but even so, a maximum of 40°C was detected. In many reports, detailed temperature measurements are not presented, making it difficult to interpret the reasons for seedling death.

The conditions for seedling establishment are hardly ideal in the semi-arid tropics. After the initial planting rain, and in the absence of subsequent rain, the soil surface rapidly dries out and gets hotter and hotter (Figure 1). The drying surface layers mean roots have to rapidly grow to access soil moisture. The shoot often has to penetrate a soil surface crust, and once emerged, the shoot is exposed to extremes of temperature, low humidity, high radiation, and wind. The sowing methods used by farmers, particularly when mechanized, are not ideal; the sowing implement used does not firm the soil around the seed, and drier soil from the surface re-

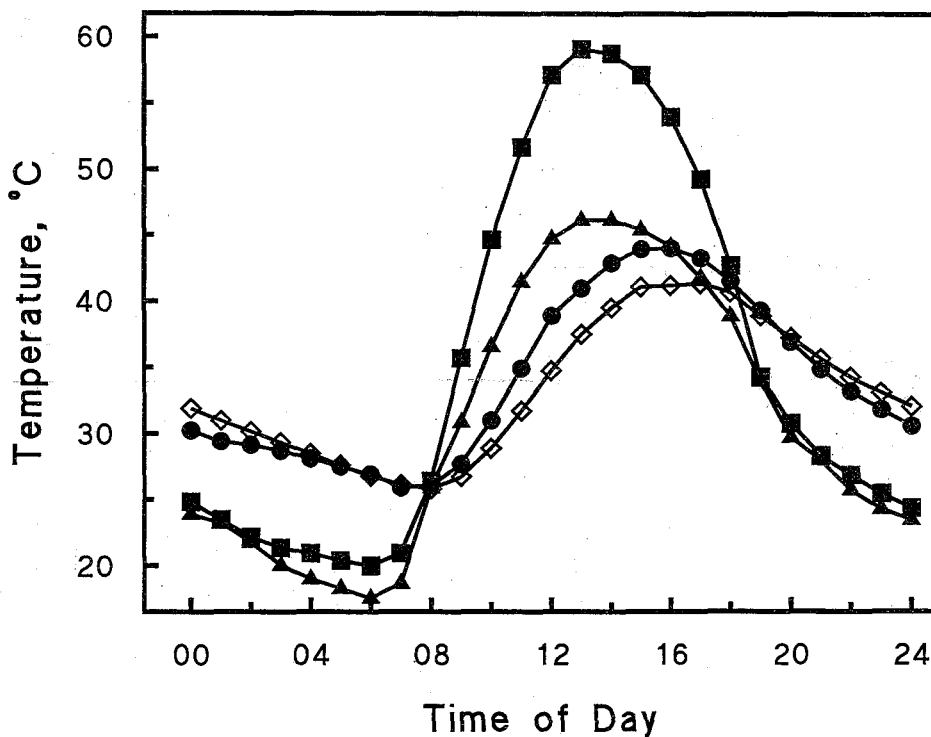


Figure 2. Diurnal temperature data recorded 5 days after sowing in June 1989 at Fatehpur, Rajasthan. Each measurement is the mean value of three thermocouples placed at either 10 cm (◇), 5 cm (●), or 0.5 cm (■) depth of soil; or 150 cm above the soil surface (▲).

duces the average seed zone moisture content. The loose structure of sandy soil compounds this. Compacted soil around the seed would improve moisture migration from the soil to the seed. Even if farmers in the semi-arid tropics used improved soil preparation and planting technologies, genetic improvements that increase adaptation to the physical constraints to stand establishment would improve resultant stands.

Once the abiotic factors limiting stand establishment in farmers' fields have been defined, the genetic variation available for a given trait must be determined to ascertain the possibilities for improvement. Screening techniques are required to characterize this variation, to identify appropriate breeding material, and ultimately to select for improved adaptation. The technique used for routine screening must be applicable for large numbers; economical, rapid, and straightforward to assess; and able to detect heritable genetic differences. Screening also needs to fit into a fixed calendar determined by other aspects of a breeding program. Screening techniques in general can be based in either the field or the laboratory.

Screening in the target environment has the advantage of using relevant stress levels. However, there are many difficulties with respect to field screening, particularly in relation to abiotic stress. The natural climate is not always reliable and is certainly variable both day to day and year to year; screening often is limited to small portions of the year; and the target environment is not always conveniently situated. Laboratory screening is not affected by these problems and can be conducted under controlled conditions with-

out being subject to the variability of the natural environment. Laboratory-based screening often targets one aspect of response to stress, not the integrated effects of the environment on many physiological and developmental processes. Dissecting a complex process such as seedling survival of stress into component parts that are under simpler genetic control should permit rapid and precise improvement. An understanding of the physiology of seedling response to stress is required to enable the development of such screening techniques. It is important, however, that a laboratory-based technique have a significant relationship to field performance. Although the effects of heat and drought are often examined separately, in the field these stresses frequently occur concurrently, along with low fertility, and the interactions between these stresses must be considered as well. For example, reduced water supplies may result in heat injury due to reduced transpirational cooling.

Germination

Without adequate germination, no seedling establishment is possible. Seeds can fail to germinate due to problems with viability as well as abiotic stress. Soman et al. (1987b) found that the germination of seeds that emerged poorly in farmers' fields was excellent under standard laboratory conditions. However, many factors, both management and environmental, affect the germinability of seeds, as indicated in Table 1. Harvest of immature pearl millet seed can limit subsequent germination and seedling vigor, although Appa Rao et al. (1993) found full germinability by 21 days after pollination. By 28 days, maximum dry matter accumula-

tion had occurred and subsequent seedling vigor was maximal. This confirmed the results of Fussell and Pearson (1980) who found that harvest at or after the middle of grain filling did not reduce seed viability. They suggested that this robustness of the grain-filling process and early viability of seeds confer ecological advantage to a crop grown in semi-arid climates where grain development may be terminated by drought or high temperatures. However, longevity of germinability was found to be maximal if seeds were allowed to mature for at least 35 days after pollination (Kameswara Rao et al., 1991). Immature sorghum seeds also reach a high germination capacity by two weeks before physiological maturity (Maiti et al., 1985; Mora-Aguilar et al., 1992). Sorghum seeds developing on plants subjected to drought stress showed a high level of germination earlier in the maturation period as compared to control seeds (Benech-Arnold et al., 1991).

Pre-harvest sprouting also leads to loss of seed viability (Maiti et al., 1985). Germinability has also long been known to be affected by environmental conditions experienced by the mother plant during grain filling (Clark et al., 1967). The influence of environment during the development and maturation of seeds is evidenced by the difference in seedling responses of seed produced in different seasons and/or sites (Peacock et al., 1993). This must be considered when assessing seedling characteristics of different genotypes of both sorghum and pearl millet. In addition, Lawlor et al. (1990) showed that the production environment influenced the minimum temperatures for germination and root elongation of sorghum seedlings. There are few reported

studies on the influence of high temperatures during grain filling on subsequent seed germination. Both Fussell and Pearson (1980) and Mohamed et al. (1985) examined the effect of temperatures between 19 and 33°C on pearl millet. Seeds that had developed at 19°C had poor viability, but there was no difference in the viability of seed produced in the other environments tested.

Germinability is affected by seed storage conditions and seed treatment. In India, sun heating of sorghum grain to reduce insect infestation is common (More et al., 1992). Short-term exposure to high temperatures (12 minutes at 70°C) did not affect germinability and was sufficient to effectively reduce insect infestation as well as fungal contamination. Higher temperatures, however, significantly reduced germination. Longer term temperature treatments were not considered. Singh et al. (1988) examined 35 lines of pearl millet for the retention of viability in response to accelerated aging (80% RH, 40°C, 14 days). Variation between genotypes was found with a range of viability loss between 18 and 84 percent.

Moisture levels in farmers' fields generally are sufficient to ensure adequate germination (Soman et al., 1987b; Peacock et al., 1993). Smith et al. (1989), using polyethylene glycol to simulate drought stress, found pearl millet seed germination more resistant to low water potentials than that of sorghum, although differences between genotypes are apparent (Gurmu and Naylor, 1991). In moist soil, temperature is the main environmental factor governing the germination of seeds. However, in both pearl millet and sorghum, the final germination per-

centage is maximal over a wide range of temperatures (from approximately 12 to 40°C) with small variation between genotypes (Carberry and Campbell, 1989; Dunbabin et al., 1994; Garcia-Huidobro et al., 1982a; Harris et al., 1987; Khalifa and Ong, 1990; Mohamed et al., 1988; Brar and Stewart, 1994; Radford and Henzell, 1990; Mortlock and Vanderlip, 1989). The rate of germination, defined as the reciprocal of the time taken for half the population to germinate, usually increases linearly with temperature, at least within a defined range. From controlled temperature experiments, it is possible to calculate base, maximal, and optimal temperatures for germination, the so-called cardinal temperatures (Garcia-Huidobro et al., 1982a). These authors found an optimum temperature of 34°C for germination at constant temperature, with base and maximum temperatures of 12°C and 47°C, respectively.

Greater genotypic variation is found in the effect of temperature on the rate of germination (Dunbabin et al., 1994; Mohamed et al., 1988; Khalifa and Ong, 1990). Within a seed population, Garcia-Huidobro et al. (1982a) detected large variations in germination rates and found seeds that germinated earlier were less sensitive to high temperatures. The rate of germination largely determines how long a seedling will take to emerge in a particular soil environment and, therefore, the duration of its exposure to high temperature. In general, pearl millet germinates more quickly within its optimal range than does sorghum (Mortlock and Vanderlip, 1989). The high optimum temperature for germination and seedling growth indicates the general adaptation of pearl millet and sorghum. Above the optimal

temperature, however, both the final percentage of germination and germination rate fall rapidly. This great sensitivity to supra optimal temperatures suggests that small differences in soil temperature at the time of germination may have profound effects on germination and hence establishment of the crop.

The above reports all measure germination at constant temperatures, whereas in the field a diurnal cycle of temperatures is found, even if seed zone temperatures are not as extreme as those at the soil surface (Figures 1 and 2). Garcia-Huidobro et al. (1982b) found that germination rates at alternating temperatures were greater at higher amplitudes of temperature variation, although temperatures above 42°C inhibited germination. In this case, the two temperature regimes were for 12 hours at constant temperatures rather than a normal diurnal cycle. In the field, seeds usually experience high temperatures for a few hours each day rather than 12 hours. The sensitivity of seeds to high temperature is likely to delay or prevent successful germination in the field. Shorter term treatments at high temperature were examined by Garcia-Huidobro et al. (1985). Seeds were most sensitive to short-term treatments at 45°C or 50°C when they were absorbing water. The adverse effects of high temperature were much less severe when seeds were allowed to imbibe water for eight hours at control temps before exposure to high temperature. This implies that germination would be more successful when seeds are sown in the early evening, after which soil temperatures remain relatively low for at least 18 hours. Laboratory germination studies in general overestimate field germination and emergence (Raj and

Khairwal, 1994). Factors that affect successful emergence in the field are discussed in the next section.

Emergence and Seedling Survival

Even if seed germination is successful, diminishing soil water availability after germination greatly affects seedling growth and survival. Line source irrigation systems, which provide a range of moisture regimes, have been used to understand the development and effects of moisture stress. Sorghum cultivars exhibit genotypic differences in their ability to both emerge at low soil moisture conditions (Soman, 1990) and subsequently grow (O'Neill and Diaby, 1987). Locally adapted Malian millet varieties not only did not show genotypic differences but also were capable of up to three times greater seedling growth than the best sorghum entry under water stress (O'Neill and Diaby, 1987).

Polyethylene glycol can be used to simulate drought under controlled temperature conditions. For example, similarities in early seedling growth in two contrasting sorghum cultivars were found under field and simulated drought conditions (Gurmu and Naylor, 1991). Cell elongation is reduced at low water potentials and thus roots may not be able to grow sufficiently fast to permit escape from the rapidly drying surface layers of soil and penetration of deeper moisture containing layers. Significant genotypic variation in seedling root growth exists in pearl millet (M'Ragwa et al., 1995). Longer term survival on drying soil depends on the initiation and growth of nodal roots. In both pearl millet and sorghum, a single primary root develops on

germination of the seed, and later, when the seedling has developed two to three leaves, the first adventitious or nodal roots develop at the shoot base. Reduced soil surface moisture levels can inhibit nodal root formation (Blum and Ritchie, 1984; Gregory, 1983; Harris, 1996) although this depends on drying rate (Soman and Seetharama, 1992).

One strategy for maintaining adequate moisture in the seed and root zone for a longer time period is deeper sowing of the seed, but in this case, growth depends longer on seed reserves before emergence occurs. In both sorghum and pearl millet, deeper sowings result in longer mesocotyl length, reducing the effect of sowing depth on shoot meristem depth (Soman and Seetherama, 1992; Harris, 1996; Howarth, Peacock, and Jayachandran, unpublished). Sowing depth also consequently does not affect nodal root number or growth. Genotypic differences in mesocotyl growth rates have been shown in both sorghum and pearl millet (Mohamed et al., 1989; Radford and Henzell, 1990; Soman et al., 1989), indicating that this characteristic is worth considering if deeper plantings are to be used.

Seedling vigor measurements also have been used to assess the importance of vigor differences in seedling survival of drought stress. Early vigor had a positive association with both days to wilting initiation and days to permanent wilting under conditions of moisture stress in pearl millet (Manga and Yadav, 1995). The moisture stress in this experiment did not commence until 20 days after sowing, by which time an extensive root system would have been established. Seed size, as well, accounted for significant differ-

ence in vigor and response to drought stress; larger seeds within a seed lot produced more vigorous seedlings. Harris (1996) also found that vigor expressed as the rate of emergence in sorghum was linked to successful stand establishment; seed that emerged faster produced more complete stands. Fast seedling growth and consequent early seedling establishment is one strategy to escape a stressful environment, particularly as the conditions for seedling establishment become increasingly less optimal with time after sowing. However, rapid development of a greater leaf area might result in a faster depletion of soil water resources. Measurements of leaf growth in the field indicate that the thermotolerant pearl millet landrace IP3201 has a relatively slow rate of leaf growth compared to the thermosensitive cultivar ICMV155 under moderate stress. When the stress level was increased, however, IP3201 continued to grow, whereas ICMV155 showed a greatly reduced growth rate (Howarth, Jayachandran, and Peacock, unpublished). In extreme environments, a conservative growth strategy may ensure survival.

Temperature is the main factor determining the rate of plant growth, but developmental processes (e.g., germination, radicle elongation, leaf growth) differ in their cardinal temperatures (Ong and Montieth, 1985). Again, most studies have been conducted at constant temperatures. The temperatures for maximal mesocotyl and coleoptile rates for both sorghum and pearl millet are below maximal temperatures for germination (Carberry and Campbell, 1989; Ong and Montieth, 1985; Radford and Henzell, 1990). This indicates that the ability to germinate at high temperature, usually defined as

successful by radicle protrusion through the seed coat, may not mean that subsequent seedling growth can occur at that temperature. Radford and Henzell (1990) also found significant differences between genotypes in seedling growth rate and response to temperature. As for germination, seedlings stop growing at temperatures less than 10°C higher than the optimum temperature for growth (Ong and Montieth, 1985). Soil temperatures also affect root growth. Long term treatment at 40°C resulted in severe inhibition of primary root growth in sorghum (Pardales et al., 1991). However, after six days at 40°C, followed by treatment at 25°C, seedlings were able to recover by the initiation of nodal roots. Temperature cycling of 40°C day and 25°C night did not have a deleterious effect on root growth.

Specific effects of temperature need to be determined by controlling temperature independently of moisture status. This can be done in the field by changing the radiation absorption of the soil by covering the surface with kaolin or charcoal (Wilson et al., 1982; O'Neill and Diaby, 1987). Maximal diurnal soil temperatures can be altered by up to 20°C, both at the soil surface and at the depth of sowing. These experiments indicate that high soil surface temperatures delay or prevent seedling emergence of sorghum and pearl millet, and that in both species genetic variation exists in the ability to emerge under these conditions.

The charcoal pit screening method has considerable potential (O'Neill and Diaby, 1987). It is easy to run and requires no sophisticated equipment, but is limited to use in the hot season and cannot differentiate lines with relatively small differ-

ences in field emergence. Soman and Peacock (1985) developed a laboratory screening system for seedling emergence under high temperature with no water stress. Seeds are sown in sand-filled clay pots placed in a water bath, and the soil surface is heated with a bank of infrared lamps placed above the pots. Lynch (1994) conducted recurrent selection for emergence in this pot test and also for germination at a constant 45°C. Improved emergence under high temperature conditions was obtained using the former; the germination selection procedure was ineffective. Kasalu et al. (1993) found field emergence correlated more closely with the ability to germinate at control temperatures than with germination ability at high temperature.

A laboratory screening technique based on embryo protein synthesis for the assessment of high temperature susceptibility during germination and seedling growth of sorghum also has been developed (Ougham and Stoddart, 1985). A strong correlation was found between the ability of imbibing embryos to synthesize protein at temperatures above 40°C and germination at high temperatures. Ougham et al. (1988) subsequently compared the embryo protein synthesis method with emergence at high temperature in pots using the technique of Soman and Peacock (1985) and found a high degree of correlation, except for two lines that showed anomalous behavior, suggesting a greater complexity of the overall emergence process compared to germination.

Extensive research has been conducted to examine individual proteins induced by high temperature and their potential for

use in screening techniques. Protein synthesis is a very thermosensitive process, and in two-day old sorghum and pearl millet seedlings, temperatures above 45°C result in a very rapid shut-down in *de novo* protein synthesis (Howarth, 1989; Howarth, 1990a; Howarth and Ougham, 1993). However, either an acclimation period of two hours at 45°C or a gradual temperature increase from 35-50°C results in induced tolerance of both growth and protein synthesis at previously lethal temperatures (Howarth, 1990c, 1991; Howarth and Skøt, 1994). Synthesis of the heat shock proteins (HSP) occurs concomitantly with this acclimation process. The precise function of HSPs in thermotolerance is not understood (Vierling, 1991; Howarth and Ougham, 1993; Waters et al., 1996); however, the strong correlation between their synthesis and thermotolerance suggests they could be used in screening systems (Vierling and Nguyen, 1992). The kinetics of their synthesis and breakdown is complex (Howarth and Skøt, 1994) and must be considered before they can be used in large scale screening. Induced thermotolerance does not persist from one day to the next, although a subsequent heatshock, during which HSPs are again synthesized, returns the tissue to a thermotolerant state. The ability to survive repeated heat shock is of prime importance in parts of the world with high mid-day temperatures, and genotypic differences in this ability have been shown (Howarth, 1991).

Sustained seedling growth following emergence depends not only on the physiological processes for germination and emergence, but also on the capacity of the seedling to elongate, produce leaves, and

become autotrophic. Post-emergence seedling death due to abiotic stress under field conditions is primarily caused by the prevalent high soil surface temperatures, at least in the first ten days following sowing, and only after that does water deficit start to take effect (Stomph, 1990; Peacock et al., 1993). Peacock et al. (1990) developed a laboratory technique to control the temperature of a localized region of seedlings in order to simulate the elevated soil surface temperatures that can occur in the field. The rate of leaf growth in *Graminae* is largely determined by the temperature of the shoot apex (Watts, 1971; Peacock, 1975). At 29 hours of treatment of only the shoot meristem at 52°C (the rest of the plant being maintained at 30°C), leaf growth ceased, although plant water relations were unaffected. An accumulation of soluble carbohydrates in the shoots of plants treated at high shoot meristem temperatures and a decline in root carbohydrate concentration suggest that root starvation was occurring due to heat-induced phloem blockage (Peacock et al., 1990). Heat shock proteins may be important in protecting meristematic tissue during the daily increase in temperature and are found to be associated with this region when seedlings are heat girdled (Howarth, 1990b).

In pearl millet growing areas in the Sahel and Rajasthan, farmers' fields often contain many trees. The localized areas under these trees have a higher soil nutrient status as well as a less extreme microclimate, and frequently a better stand establishment of pearl millet. Vandenberg and Williams (1992) examined the effect of *Faidherbia albida* trees on soil surface temperature and pearl millet seedling

growth in Niger, and found that the canopy of the tree reduced the maximum soil temperature at 2 cm depth by up to 10°C, although air temperatures were less affected. In a seedling growth experiment using a shade gradient and adequate soil moisture, it was found that seedling growth rates over six weeks were correlated with the mean daytime soil surface temperature, with no seedlings surviving temperatures higher than 46.6°C. This further suggests that soil surface temperatures are critical for seedling growth and survival.

A field screening procedure for emergence and seedling survival at high soil surface temperatures has been developed and used to identify genetic differences for seedling survival (Peacock et al., 1993). This procedure is used in Rajasthan in the hot and dry pre-monsoon season and has proved effective at identifying genotypes of superior heat tolerance (Weltzien et al., 1994; Howarth et al., 1995b). Selected results are shown in Table 2, which illustrates a range of response of both emergence and seedling survival. The sorghum genotype used was the most thermosensitive entry. Local landrace populations (IP3201 and IP3175) and the hybrid HHB67 were the most thermotolerant. A population cross between IP3201 and ICMV155 has subsequently been made and the 155 fullsibs produced have been screened in the field. Bi-directional selection for seedling thermotolerance was conducted based on the considerable differential between the high and low 20% of entries found (Table 2). This technique, however, can be used only for two months of the year at most in an unpredictable environment where early monsoon rains will prevent its success. The

Table 2. Field data obtained from selected pearl millet genotypes screened at Fatehpur-Shekhavati Agricultural Research Station, Rajasthan Agricultural University.

Entry	Emergence	Thermotolerance index
HHB 67	0.77	0.86
IP 3201	0.75	0.85
IP 3175	0.75	0.79
ICMH 451	0.74	0.75
Sadoré Local	0.73	0.73
W Raj. Pop.	0.65	0.70
ICMH 423	0.77	0.61
ICTP 8203	0.65	0.57
ICMV 155	0.44	0.47
BSEC C4	0.79	0.37
Sorghum (SPV386)	0.59	0.30
Cycle I selection (high)*	0.65	0.69
Cycle I selection (low)*	0.54	0.38

Thermotolerance index calculated as the ratio of seedlings surviving to the total number of seedlings that emerged.

All results the mean of experiments conducted in 1989 and 1990 (from Peacock et al., 1993) except for * which represent the mean values for the selected fraction (high or low 20%) from 155 fullsibs produced from a population cross of IP 3201 and ICMV 155 and screened in 1992 (from Weltzien et al., 1994).

results obtained from field screening depend on the actual environmental conditions experienced that year.

To overcome these limitations, a number of laboratory-based methods for evaluating post emergence seedling death have been devised (Howarth et al., 1995a). These include the use of a sand bed, which can be heated electronically to simulate diurnal soil temperatures in Rajasthan, and the use of an electrolyte leakage test as a measure of membrane thermostability. Initial results screening the 155 fullsibs produced from the IP3201 and ICMV155 cross indicate that both procedures show good correlations with field results, but with higher heritabilities and increased flexibility regarding when and where the screening techniques are

conducted (Weltzien et al., 1994; Howarth et al., 1995b).

Although temperature and drought have been considered separately, tolerance to one stress often is combined with tolerance to another (O'Neill and Diaby, 1987; Maiti et al., 1994). These stresses also often occur concurrently. As indicated in Table 1, there are a number of other environmental reasons for stand failure. For example, wind storms carrying sand can cause considerable stand reduction (Klaij and Hoogmoed, 1993). Soil fertility effects on seedlings have been less extensively studied, but low fertility can reduce survival of other stresses by affecting seedling vigor. The soils where pearl millet and sorghum grow are often of very low fertility. Payne et al. (1991), examining the influence of phosphorus and water on growth of pearl millet, found that the efficiency of dry matter production decreased under both control and drought stress conditions when the soil phosphorus supply was inadequate. The possibility of improving early growth by the use of phosphorus-containing seed coatings was examined by Rebafka et al. (1993). Pearl millet is very small-seeded with low phosphorus reserves; thus, an external supplement could improve growth. However, although seed coating did improve early growth, there were considerable deleterious effects on seedling emergence, possibly due to the absence of glumes in pearl millet. Salinity is another abiotic stress encountered during seedling establishment that can affect growth and survival. Azhar and McNeilly (1988) found considerable genetic variation in sorghum for growth under salinity stress and conducted a genetic analysis identifying considerable dominance effects.

Soil surface crusting results from the beating action of rainfall and subsequent drying of the soil at high temperature, causing difficulties for emerging seedlings, which need to break through this barrier. Soman et al. (1984) developed a screening technique for emergence under crusting conditions and found that pearl millet was much more affected than sorghum, as the seedling is smaller and less vigorous. Sorghum lines vary in their ability to emerge under soil crusting conditions. Soman et al. (1992) examined the relationship between sorghum coleoptile morphology and emergence potential and found that mesocotyl growth rate correlated best with emergence. This is effectively an avoidance strategy, as faster growing genotypes were able to emerge before maximal crust formation had occurred. Significant differences between pearl millet genotypes exist for coleoptile and mesocotyl growth rate (Soman et al., 1989). Emergence through crusts was further studied by Mason et al. (1994) using piston displacement as an *in vitro* screening technique. In this study, coleoptile length showed no correlation, but coleoptile diameter showed a high correlation with the ability of sorghum to emerge through the simulated soil crust; avoidance of a soil crust by fast growth was not possible in this test. Seedlings emerge through crusts, either due to high pressure exerted by an individual seedling or to cumulative force exerted by a group of seedlings (Taylor, 1962). Joshi (1987) found that the mixed sowing of pearl millet and greengram resulted in improved emergence because of the joint thrust from legume and pearl millet together. The use of precision planters ensures even spacing of seed, requiring individual seedlings to emerge through a crust.

Farmers rarely use precision planting equipment and often sow mixtures of cereals and legumes, thus minimizing the problem.

Improvement of Stand Establishment

This review has shown that considerable genetic variation exists for tolerance to the environmental constraints on germination, emergence, and seedling survival in sorghum and pearl millet. The desirability of a plant trait in an environment depends not only on the risk of stress but on the attitude of farmers toward risk and on the specific requirements of the local farming system (Van Oosterom et al., 1996; Weltzien et al., 1996). Each environment poses a different set of problems, and in marginal environments where the climate is highly variable, it often is difficult to precisely define the causes of crop failure, but they must be at least approximated if successful crop improvement is to occur.

As Boyer (1982) points out, there is often a dramatic difference between maximal and average yields for any given crop species. The actual yield achieved depends on the environmental conditions the crop encounters. Stress can be defined as a condition that limits a plant in realizing its potential for growth, development, and reproduction; extremes of stress result in plant death. Plants rarely grow in optimal environments, so they can be considered to be under some degree of stress at all times. For pearl millet and sorghum growing in marginal environments this is certainly the case. Variation exists in the ability to survive and grow under stress conditions. The task is to exploit this variation and combine improved tolerance to

stress with increased yield potential so that not only is the discrepancy between yield under optimal conditions and actual yield reduced but also yield stability increased.

New technologies, improved screening techniques, and knowledge of appropriate germplasm can now exploit natural variation to a greater effect. It is only possible, however, to improve the degree of tolerance; there always will be a level beyond which it is not possible to improve. For seedlings, where stress often results in death, improvement in stress tolerance targets the ability to survive these stress conditions. To improve adaptation to other stresses (for example, terminal drought), it often is necessary to target an enhancement in relative performance, often measured as yield, rather than survival. The tasks involved in improving relative performance have received much attention from breeders and physiologists (Richards, 1989; Evans, 1993; Ludlow and Muchow, 1990). Seedling survival and the ability to yield well are not expected to be as closely interrelated as are stress tolerances reflecting relative performance. Thus combining seedling stress tolerance and yielding ability would not be expected to need as much multi-location testing as is the case for relative yield improvement. Only yielding ability in the target environment should need to be evaluated for materials with improved seedling stress tolerance.

Understanding of the processes that lead to a failure of stand establishment has advanced sufficiently to permit development of specific screening methods. The screening techniques described above have direct application in the genetic im-

provement of these traits. However, fewer studies are reported in which both the genetic variation identified and screening systems developed have been exploited in crop improvement. To do this it is necessary to select for improved adaptation and then to evaluate the response to selection for improved establishment ability in the field. Screening methods tend to be developed using control genotypes with extreme differences in performance, often with many genetic differences for other traits. The results obtained often are specific to the actual cultivars and growing conditions used. It is harder to distinguish genotypes showing an intermediate response to a given stress. The capacity for improvement of stress tolerance, however, can be found within a species and is amenable to conventional breeding techniques.

Adaptation to a given constraint is complex. Plant physiology can identify not only critical components of adaptation but also genes or regions of chromosomes linked to a given trait. This is done using molecular markers, such as restriction fragment length polymorphisms (RFLPs), combined with physiological screening, which permits the mapping, identification, manipulation, and combination of specific genes involved in tolerance. The challenge is to identify specific physiological or biochemical processes and to develop rapid, high-throughput screening techniques based on them. Molecular marker maps exist for both sorghum (Hulbert et al., 1990; Chittenden et al., 1994; Pereira et al., 1994; Xu et al., 1994) and pearl millet (Liu et al., 1994) and have been used to identify quantitative trait loci (QTLs) associated with downy mildew resistance (Jones et al.,

1995; Hash et al., 1995). A similar approach is being used to detect QTLs associated with seedling thermotolerance (Howarth et al., 1994). Once identified, marker-assisted selection can be used to precisely improve the required character by following closely the movement of desired and undesirable gene segments in the breeding process.

The potential of these modern, precision breeding methods is considerable. Mapping potential physiological and biochemical components of adaptation also provides information on their involvement in adaptation and is a new way of elucidating the mechanism of plant response to the environment. Genetic mapping not only shows in a much clearer fashion how traits are genetically correlated, but how they are linked on the chromosomes. Active collaboration between geneticists, molecular biologists, physiologists, breeders, germplasm collectors, and other relevant disciplines is required to ensure success. Genetic improvement of stand establishment is thus possible by plant breeding, and potential progress is substantial.

Plant breeding, however, is not the only way forward, and management solutions also must be considered, particularly as the current tillage and sowing methods used in farmers' fields are not very sophisticated. Agronomic factors such as seed-bed preparation, sowing methods, timeliness of sowing, and sowing depth can exacerbate environmentally-induced stress and result in poor crop stands. Compaction of the soil after sowing to ensure good soil-seed contact and minimize evaporation, for example, could assist in stand establishment. Traditional sowing

methods, however, can be appropriate for the conditions encountered in some cases. For example, stand establishment, survival, and yield were better under the hill planting used in the Sahel than drilling seed (Klaij and Hoogmoed, 1993). Hill planting provides a certain amount of protection from the extremes of temperature and from sand-bearing winds. It is not easily mechanized, however, and the large number of seedlings growing together can result in rapid development of water deficit. Pre-sowing tillage increases initial stands and subsequent seedling survival (Joshi, 1987; Klaij and Hoogmoed, 1993). Surface application of farmyard manure can reduce the likelihood of crusting, maintain moisture in the surface layer of soil (Joshi, 1987), and minimize the prevalence of temperature extremes at the soil surface. This practice resulted in a faster rate of emergence, increased total emergence, and reduced seedling mortality of pearl millet (Joshi, 1987) but had no significant effect on stand establishment in sorghum (Harris, 1996).

If planting technologies are refined to more precision-based methods and mixed cropping no longer practiced, then crusting could perhaps be a bigger problem in crop establishment. Pre-sowing seed priming, either by soaking in water or in osmotic solutions, has been investigated to examine its potential to improve emergence (Bradford, 1986; Joshi, 1987; Maiti and Moreno, 1995; Harris, 1996). Primed seeds germinate more rapidly and uniformly and the rate of emergence is increased (Harris, 1996), although final stand establishment is not necessarily improved (Joshi, 1987). Priming conditions, the temperature and timing of any intervening period before sowing, and soil

conditions at sowing will all influence the results obtained and need to be optimized. Recent data from on-farm trials with upland rice, maize, and chickpea in semi-arid India show that farmers value on-farm seed priming for the benefits they gain from fast, vigorous crop establishment.

Conclusion

Increasing stand establishment through a combination of well-adapted, improved cultivars and management practices remains a challenge. Seedling traits affecting establishment warrant high priority for research. Genetic improvement is most needed in those areas where dependence on the pearl millet and sorghum crop is so great, particularly if increases in population pressure result in the expansion of crop production into more and more marginal areas. Climatic change could exacerbate this need. Locally adapted germplasm often is capable of surviving the environmental conditions and should be widely used in breeding for improved stand establishment. An understanding of both the prevailing conditions and the farmers' requirements is critical. For a farmer to adopt a change in these high risk environments, demonstration of improvements actually on farmers' fields is necessary. Varieties that perform well in national yield trials at research stations are not necessarily appropriate for these severe environments. Targeting of crop improvement research specifically for these environments is thus required.

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