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Pearl Millet: Genetic Improvement for Tolerance to Abiotic Stresses

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Abstract

Pearl millet (*Pennisetum glaucum*) is an important cereal grown in adverse agroclimatic conditions where other crops fail to produce economic yields. Because of the cultivation of pearl millet mainly in rainfed production systems of arid and semi-arid regions, drought is a primary constraint in its cultivation. In addition, high temperatures and salinity are emerging as new challenges in pearl millet cultivation in specific production environments. This chapter reviews the research dealing with improvement in drought tolerance of pearl millet and also updates the progress made in improving high temperature and salinity tolerance. Response of pearl millet to moisture stress at various growth stages has clearly established that yield losses are maximum when moisture stress coincides with grain filling stage, which is commonly referred to as terminal water stress. Various physiological and morphological traits have been examined as alternative selection criteria to further enhance tolerance to terminal drought. Conventional approaches to improve drought tolerance in pearl millet have a very short history and attempts have met with some success. Various novel approaches have been attempted in pearl millet for enhancing yield under drought environments. These include use of adapted germplasm, genetic diversification of adapted landraces through introgression of suitable elite genetic material, and exploitation of heterosis to amalgamate drought tolerance and high yield. Molecular breeding is fast emerging as a supplement approach to enhance drought adaptation at a faster rate with greater precision. Molecular marker-based genetic linkage maps of pearl millet are available and genomic regions determining yield under drought environments have been identified preparing a road map for marker-assisted selection. Genetic differences in tolerance to salinity and high temperature at both seedling and grain filling stages have been established and screening techniques standardized. The germplasm and breeding material with a higher degree of tolerance to high temperature and salinity have been identified in order to use them in breeding programs.

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12.1
Introduction

Pearl millet (*Pennisetum glaucum* (L). R. Br.), a C_4 plant belonging to the family Poaceae, has a very high photosynthetic efficiency and dry matter production capacity. It is grown under the most adverse agroclimatic conditions where other crops fail to produce economic yields. Pearl millet is usually cultivated in regions with characteristically low and erratic rainfall, high mean temperature, high potential evaporation, and infertile and shallow soils with poor water holding capacity. In spite of this, pearl millet has a remarkable ability to respond to favorable environments because of its short developmental stages and capacity for high growth rate, thus making it an excellent crop for short growing season and under improved crop management.

Pearl millet is cultivated on about 30 m ha in more than 30 countries of 5 continents, namely, Asia, Africa, North America, South America, and Australia (Figure 12.1). The majority of crop area is in Asia (>10 m ha) and Africa (about 18 m ha). At individual country level, India has the highest area (9.3 m ha) and production (9.5 m tons) and the major pearl millet growing Indian states are Rajasthan, Maharashtra, Gujarat, Uttar Pradesh, and Haryana. In Africa, the majority of pearl millet acreage is in western Africa where it is grown in 17 countries, though Niger, Nigeria, Burkina Faso, Mali and Senegal account for nearly 90% of

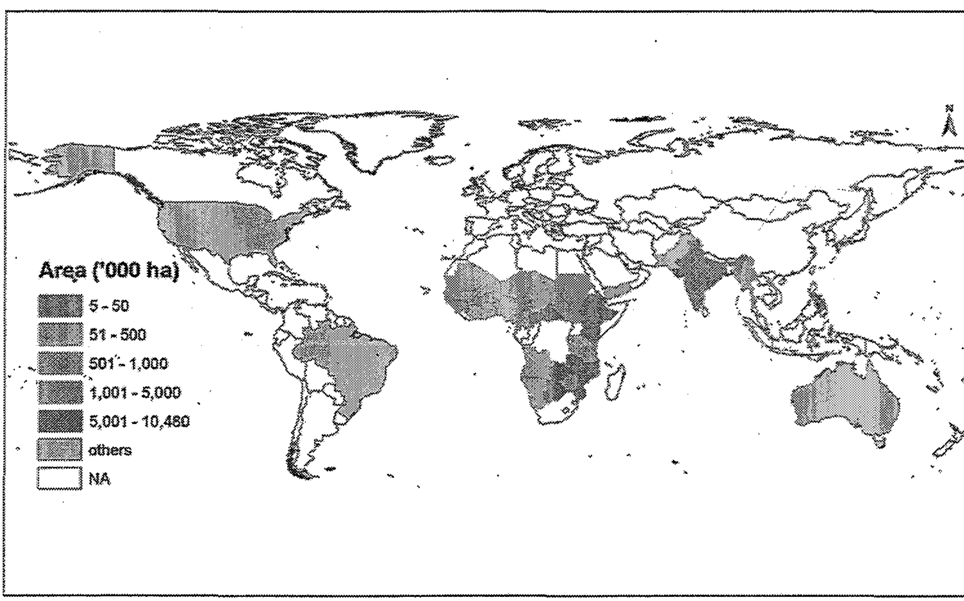

Figure 12.1 Distribution of pearl millet cultivation across world.

total cultivated area in Africa. Pearl millet cultivation is also recently expanding to some of the non-traditional areas such as Brazil (about 2 m ha), and it is being experimented as a grain and forage crop in the United States, Canada, Mexico, the West Asia and North Africa (WANA), and Central Asia.

Pearl millet is primarily grown for food for human consumption and its dry fodder forms the basis of livestock ration during the dry period of year (November–January) in India [1]. Its grains are mostly used for human consumption in the form of diverse food types such as leavened and unleavened flat breads and porridges. Several bakery products and extruded and weaning food products are also prepared. Besides, pearl millet is a highly nutritious cereal with high level of metabolizable energy and protein and more balanced amino acid profile [2]. Its grains have higher densities of iron and zinc [3], the two most important micronutrients for human. Pearl millet flour can also be substituted up to 20% for wheat flour in making leavened bread. Grains of pearl millet are also used as cattle and poultry feed. Pearl millet is also an excellent forage crop because of its lower hydrocyanic acid content than sorghum. Its green fodder is rich in protein, calcium, phosphorous, and other minerals with oxalic acid within safe limits.

Pearl millet production is confronted with relatively fewer biotic stresses compared to other crops. Among the diseases, downy mildew (*Sclerospora graminicola* (Sacc.) Schroet.) is the most important constraint in both India and Africa, especially on hybrids in India. Other diseases of relatively minor importance include smut (*Moesziomyces penicillariae*), rust (*Puccinia substriata* var. *penicillariae*), blast (*Pyricularia grisea*), and ergot (*Claviceps fusiformis*). Insect–pests and parasitic weed Striga are significant challenges in Africa but not in India.

Because of the cultivation of pearl millet largely in rainfed production systems of semiarid and arid regions of world, crop growth is constrained by several abiotic stresses. Drought is the primary abiotic constraint and is caused by low and erratic distribution of rainfall. The mean annual rainfall in pearl millet-growing areas in India ranges from 150 to 750 mm and most of it is received during June–September [4]. In western Africa, the crop is cultivated in regions with annual rainfall ranging from 300 to 900 mm [5], the majority of which is received between May and October. The bulk of the crop in the Sahelian zone is grown with an annual rainfall of 300–600 mm and a growing season of 75–100 days. The Sudanian zone receives an annual rainfall of 600–900 mm with a growing season of 100–150 days. The coefficient of variation of annual rainfall ranges from 20% to 30% leading to variable drought conditions within and between crop seasons.

Other abiotic constraints to pearl millet production include high temperatures, both during the germination and seedling stage in the rainy season, and during the flowering period during the summer season (in parts of India). Salinity is also being increasingly recognized as a significant abiotic constraint in many pearl millet growing areas in Africa and India, but more so in the prospective areas in the WANA region and Central Asia. This chapter largely deals with drought tolerance as significant research efforts have gone into the understanding of and breeding for this trait. It also presents preliminary observations on heat and salinity tolerance.

12.2 Drought: Its Nature and Effects

A great deal of work has been done on understanding the response of pearl millet to moisture stress at various growth stages with a view to understanding its adaptation to drought stress conditions. It has been conclusively established that effects of water stress depend on the developmental stage during which the crop is subjected to stress. Consequently, pearl millet research has concentrated on exploring the effects of drought at specific growth stages.

12.2.1 Seedling Phase

Severe moisture stress during emergence and the early seedling phase causes seedling death, which results in poor crop establishment. Poor and uneven crop stands are some of the major causes of yield losses in pearl millet [6–8] in the semi-arid tropics. Stress occurring after crop establishment but within the seedling phase has little effect on grain yield [9] provided it is relieved at the later stages before flowering.

Drought during the seedling phase affects seedling growth in several ways. The rate of leaf appearance in seedling is affected by the timing of available water, that is, an early drought will prolong the seedling phase [10]. It has been further showed that drought affects the close relationship between leaf formation and secondary root development. Secondary roots are formed only when there is soil moisture at the coleoptile node [11]. Genetic variation in the rate of leaf appearance and secondary root formation and their relative rates have been observed under drought [10]. There are no known reports dealing with the genetic manipulation of this trait in a breeding program.

12.2.2 Vegetative Phase

Water stress during vegetative growth may have little adverse effect on grain yield of pearl millet as it has been shown to increase the number of panicles per plant [12–14]. It has been established that only 25% of the tillers produce panicles in pearl millet under normal conditions [15]. The apparent excess production of tillers provides potential compensation for a damaged main shoot or primary tillers [16, 17]. High tillering and asynchrony of tillering contribute to adaptation to drought stress during the vegetative growth phase [18–20]. Water stress during the vegetative phase reduced the dominance of the main shoot and allowed additional tillers to complete their development [12, 21]. Accumulation of abscisic acid under water stress may be responsible for this reduction in apical dominance.

Water stress during the vegetative growth phase delays flowering of the main shoot [12, 13, 20]. This phenological plasticity increases the chances for escape, first from the most sensitive stage of growth until the stress has been relieved, and second by closing stomata at relatively high water potentials during drought in the vegetative period [22]. The crop thus conserves the limited water resources, increasing the chances to survive the extended periods of stomatal behavior changes. Stomatal opening down to water potentials as low as 2.3 MPa, during stress after flowering, has been observed [23]. Late-flowering genotypes do have a longer GS1 period, that is, the time between seedling emergence to panicle initiation [24, 25] is longer than that for early maturing genotypes. Thus, such genotypes have a higher chance to escape drought stress during the most critical growth phases.

12.2.3 Reproductive Phase

Grain yield losses are highest when stress coincides with the most sensitive stages of crop growth [26]. It has been found that pearl millet is most sensitive to water stress during flowering and grain filling stages [9, 20, 27]. Grain yield and its components are drastically reduced when drought occurs during this stage [12, 13, 28]. Yield reduction is due to both decrease in the number of panicles per plant and decrease in the grain mass. Seed setting that determines the number of grains per panicle is usually less affected if terminal stress occurs after flowering [13, 20].

The reduction in grain mass is mainly due to a shortening of the grain filling period rather than due to a reduction in grain growth rate [29]. This appears to be caused by restriction of the current assimilate supply and not by a reduction in the grain storage capacity [29]. Stomatal closure and a consequent reduction in photosynthetic activity under drought stress have been documented for pearl millet, though only at very low water potentials [23, 30–32]. Pearl millet has the capacity to compensate for such a reduction in the supply of assimilates to the grains by mobilizing stored soluble sugars [28]. This contribution of stored assimilates to the grain growth during drought stress has not been quantified. The link between grain development and the transfer of assimilates from the leaves, with the stems playing a buffering role, appears to be one of the main adaptations of pearl millet to terminal drought stress [33].

12.3 Genetic Improvement in Drought Tolerance

Pearl millet is grown as a rainfed crop in areas where rainfall is too limited for higher yielding cereals such as sorghum or maize. Hence, improving drought tolerance is a priority in pearl millet breeding programs. Breeding for increased adaptation to drought is, however, a challenging task due to various complexities associated with drought adaptation mechanism, uncertainty in timing, intensity and duration of stress, and a large genotype × environment interactions. Conventional approaches to improve drought tolerance in pearl millet have a very short history and attempts have met with some, though limited, success. Recently, molecular breeding is being viewed as an additional tool to improve drought tolerance with greater precision and efficiency.

12.3.1
Conventional Breeding

Empirical breeding for drought tolerance has mainly addressed the issue of criteria and environment of selection for improving drought adaptation. Various novel approaches have been attempted in pearl millet for enhancing yield under drought environments.

12.3.1.1 Selection Environment

Choosing an appropriate selection environment to improve productivity under drought has been a subject of the major debate in plant breeding, and several theoretical and empirical studies have been reported. Some believe that cultivars targeted for drought conditions can be identified under non-drought conditions (indirect approach), while others think that selection of drought environments should be undertaken under drought stress (direct approach).

The indirect approach involves selection for high yield potential under non-stress conditions with the assumption that genotypes selected under optimum conditions [34–36] would also perform well under drought. In this approach, drought resistance is an unidentified component of performance over different environments and more emphasis is laid on yield potential. The main advantage of this approach is that yield potential and its components have higher heritability in optimum conditions than that under stress conditions [37, 38]. Since yield potential has been reported to be a significant factor in pearl millet in determining the yield under moisture stress [13, 14, 28, 39], improvement in yield potential may have some spillover effects under water stress conditions.

The direct approach recommends that varieties for drought-prone areas must be selected, developed, and tested in the target drought environments [40–42]. Theoretical analyses also indicate that selection for stress environments should be done in stress environments [41, 43, 44]. In this approach, improvement in yield under moisture stress requires dissociation from yield potential under optimum conditions as a major selection criterion [45–47] and the emphasis is placed on drought adaptation and yield under drought conditions.

The subject of selection environments for improving pearl millet in drought environments has received little experimental attention. There are no reports available in pearl millet comparing relative gains in performance under drought conditions through selection in drought vis-à-vis non-drought environments. However, there are indirect inferences. For example, low correlations are often reported between yields of pearl millet measured in stress and optimum conditions [48–50], which indicate that yield performance under drought and non-drought conditions are separate genetic entities and direct selection for yield performance in the target

Table 12.1 Percent contribution of high yield potential, escape, and drought tolerance in determining performance of pearl millet under drought environments.

No. of genotypes	Types of lines tested	Yield potential	Escape	Drought tolerance	Reference
105	Landraces	5	22	73	[126]
30	Hybrids	15	—	—	[50]
14	Cultivars	0.4–9.3	23–81	18–68	[42]
40	Breeding material	4–23	23–37	41–47	[28]
216	Breeding lines	2–12	46–56	34–36	[13]

drought environments would be required to make greater gains in productivity. This is further substantiated by existence of significant crossover genotype × environment interactions observed across optimum and stress environments [51–56]. Using evaluation data from drought stressed and non-stressed environments, many studies showed that drought tolerance and escape were major determinants of performance in drought environments (Table 12.1). On the other hand, high yield potential accounted for 10–15% variation toward performance in drought environments. This has highlighted the importance of evaluation and selection in drought-prone locations and early maturity, and suggested for *in situ* breeding for drought environments. Alternatively, simple and efficient screening techniques might be employed for evaluating large number of genotypes under managed drought conditions.

The work on screening techniques in pearl millet, for adaptation to drought, has primarily focused on terminal drought stress, because it causes higher and irreversible yield losses. Field screening for response to terminal drought can be carried out by withholding irrigation to impose water stress during the rain-free seasons to study the effects of drought stress and to identify whole plant traits associated with adaptation to a particular stress [12–14, 20, 21, 57]. One such technique has been developed at ICRISAT, which compares genotype performance in artificially created terminal stress (flowering to maturity) treatments with performance under fully irrigated, stress-free conditions [13, 14, 28]. Drought resistance is then determined on the basis of genotype performance in the stressed treatment after accounting for differences due to escape and yield potential among genotypes. However, off-season drought screening may not necessarily give results similar to naturally occurring stress in a rainy season crop like pearl millet, as fluctuations in atmospheric conditions or changes in phenology due to different day lengths may alter the results. The technique [58] that involves growing plants in main crop season on sloping plots that are opposite to each other and connected to subchannel lines with polyethylene sheets avoids this problem by increasing the runoff and reducing the water availability. However, this technique has neither been validated nor used in applied breeding programs.

Line-source sprinkler irrigation technique [59], which delivers a continuously declining amount of water, has been extensively used for screening sorghum [60, 61], rice [62], and pearl millet [63, 64], especially when crop response to moisture stress is non-linear. The major disadvantage, however, with this technique is that even low winds may significantly alter the sprinkler patterns [59] and only a relatively small number of entries can be accurately tested to detect significant differences. It is because of these two factors that line-source sprinklers are no longer used in routine assessments of drought response in pearl millet breeding programs.

Additional limitation of artificially created screening techniques is that they are unable to expose the test material to all the combinations of stress the crop might subsequently experience given that drought stress occurs in a wide range of combinations based on variability in timing, severity, and duration of drought. This necessitates selection in the target environments that are highly prone to terminal drought. There are extensive evidences from other crops that cultivars for stress environments should be selected, developed, and tested under target environments [47, 65–68].

Due to the complexity of drought adaptation, it seems doubtful that any one method or technique will be universally used to measure drought stress [69] because the variability in timing, intensity, and duration of moisture stress is almost infinite and screening methods can expose genotypes to only a few combinations [70]. In empirical breeding programs, evaluation and selection are conducted through multilocation testing of test material in locations that are highly prone to drought stress [47, 68]. The All India Coordinated Pearl Millet Improvement Project (AICPMIP) has carved out a special zone for testing and evaluation of experimental cultivars in locations receiving <400 mm of annual rainfall in order to identify and release cultivars adapted to drought environments and the results are encouraging [71].

Thus, maximum progress can be gained with a good understanding of the predominant patterns of drought occurrence in the target environment, appropriate material that expresses sufficient genetic variability for the most appropriate traits for good adaptation, and reliable conditions for yield testing under drought conditions.

12.3.1.2 Selection Criteria

Several efforts have been made to identify traits that can be used as selection criteria in breeding drought tolerant genotypes. Most research has concentrated on the identification of physiological parameters like dehydration tolerance [72–76], dehydration avoidance [77], growth maintenance through stability of cellular membrane [78–80], osmotic adjustment [69, 81, 82], desiccation and heat tolerance [69], leaf gas exchange rate [83–85], and radiation reflectance [77] in various crops, including pearl millet [86]. However, most of these have hardly found any place in routine breeding programs, particularly in developing countries, owing to the lack of simple and easy techniques for selecting such characters on a large scale. On the other hand, morphological characters that can be measured easily appeal most to plant breeders for use as selection criteria.

Growth in greenhouse pots under different soil moisture regimes, germination of seeds and growth of pearl millet seedlings in dimannitol solutions, and stability of extracted chlorophyll under heat treatments to test drought resistance has been used in pearl millet [87]. Such studies under controlled conditions, however, do not necessarily represent the limiting moisture conditions of the field.

A rapid development of the crop in the initial stages, that is, early vigor, has been correlated with drought tolerance as measured by time taken for wilting initiation and permanent wilting in pearl millet [88]. A crop with more rapid leaf area development could intercept a greater portion of incident radiation and limit water losses by soil evaporation. However, there are apprehensions that greater transpiration from a larger leaf area will exhaust soil water resources and cause severe water deficit in later growth stages [33].

Early flowering, the most important factor determining yield under terminal water stress [14, 28], is recognized as another selection criterion, although its advantage is due to drought escape rather than due to drought tolerance. Genetic variability for earliness is widely available in pearl millet [89, 90] and simple selection has been successful under most circumstances [91]. The most widely used sources of earliness are the *Iniadi*-type landraces from western Africa [92, 93]. New early-flowering cultivars bred by using *Iniadi* landraces have been widely adopted by farmers in India and Africa. However, value of earliness as a selection criterion is significant only if drought predictably occurs toward the end of the growing season.

Panicle threshing percentage is another criterion proposed for improving tolerance to terminal drought that indicates the plants' ability to set and fill grain under water limiting conditions and it integrates the effects of assimilation and translocation under water stress. Research has indicated that it usually explains a large proportion of the variation among genotypes for grain yield under terminal drought stress [28, 77, 94]. Results of a selection study on panicle threshing percentage also indicated that grain yield can be increased under stress conditions [94]. Furthermore, it has been shown that even in a small set of inbred lines, the narrow sense heritability for threshing percentage was sufficiently high to expect significant gain from selection for this trait under drought conditions [95]. Using this selection criterion, an open-pollinated variety (OPV) (ICMV 221) has been developed from a high-yielding and early-maturing composite at ICRISAT.

Low tillering and large panicles are commonly being used as selection criteria in pearl millet breeding. Selecting for these traits results in higher grain yield per panicle [14, 96], which are important yield components in pearl millet [97–99]. These traits are frequently assessed visually, under both drought and non-drought conditions. Variability in panicles size, yield per panicle, and tillering is abundant in pearl millet [90, 96, 100–105]. However, their specific contribution to improved grain yield and stability under terminal drought condition has not been quantified.

Some studies have also used mathematical models to identify crop cultivars that are productive in stressful marginal environments by comparing the change in seed yield between stress and non-stress (optimum) environments [14, 35, 44, 73, 106–108]. Drought susceptibility index [106] that is based on the ratio of yield of individual lines under stress and non-stress conditions to the line means across stress and non-stress has also been widely used in identifying genotypes adapted to stress [14, 50, 108–111]. Drought response index to provide an indicator of drought tolerance that was independent of escape and yield potential in favorable environments has also been developed [14]. Drought susceptibility index of pearl millet genotypes is a useful criterion to identify genotypes adapted to drought stress conditions, but should be used in combination with yield under stress [50]. It has also been demonstrated that drought response index would be useful to identify genotypes adapted to stress environments, if days to flower don't differ considerably among test entries [50].

12.3.1.3 Yield Improvement

Yield improvement in pearl millet under drought is essential for ensuring high grain yield under stress environments. Though drought tolerance might be perceived differently by physiologists, breeders, agronomists, or biochemists [112], farmers measure the success of new cultivar under drought environments by a known (often >15%) yield advantage. Various genetic approaches have been successfully employed to achieve significant gains in pearl millet productivity under drought conditions. These strategies include use of adapted germplasm, genetic diversification of adapted landraces through introgression of suitable elite genetic material, and exploitation of heterosis.

12.3.1.3.1 Use of Adapted Germplasm for Stress Environments The base material required for a successful breeding program may differ for the drought and more favorable environments. Success in drought environments is often much more a consequence of adaptation to environmental stresses than it is of yield potential *per se*, which is not effectively expressed under severe stress. Plant breeders focusing on drought environments are faced with the choice of trying to improve either the adaptation of high yielding, but poorly adapted germplasm, or the yield potential of already adapted germplasm, often in the form of local landraces [113]. Improving adaptation to marginal environments is the more difficult alternative than is improving yield potential, as adaptation is much less well understood, physiologically and genetically, than is yield potential. However, improving yield potential in traditional landraces is constrained by a characteristic plant type that favors adaptation over productivity [16, 17].

The breeding material should provide a good starting point for the program, that is, high productivity under drought conditions, as well as sufficient genetic variation to allow gains from selection. Pearl millet landraces that evolved in dry areas as a result of natural and human selection over centuries exhibit good adaptation to drought and other naturally occurring stresses [55, 56, 114–117] and represent a largely untapped reservoir of useful genes for adaptation to stress environments. A few attempts have been made to exploit them in pearl millet breeding programs in a systematic way. Given that landraces are genetically heterogeneous populations [118, 119], they make very appropriate base genetic material for improving adaptation to drought and other abiotic stresses. A few cycles of mass selection in landraces can increase yield considerably [120, 121]. Landrace-based populations adapted to drought have also been shown as a useful source material for breeding inbred restorer lines [122]. However, selection needs to be carried out in target environments so that adapted germplasm can express its potential fully in area of its adaptation [41, 123].

A commercial pearl millet variety, CZP 9802, has been developed from selected drought-adapted landraces [124]. In the Indian national testing system for new cultivars, its grain yield performance was 25–58% superior to two national checks (ICTP 8203 and Pusa 266) in drought environments and it also maintained its superiority under near-optimum growth conditions by a margin of 16–47% for stover yield and 4–6% for grain yield. It demonstrated that landrace-derived cultivars can have unique features of adaptation to drought stress in addition to responsiveness to improved conditions. As a result, pearl millet variety CZP 9802 was released by the Government of India for cultivation in drought-affected pearl millet-growing areas in the states of Rajasthan, Gujarat, and Haryana; and it has been adopted very well in drought-prone areas of north-western India [125].

12.3.1.3.2 **Genetic Diversification of Drought-Adapted Germplasm** The traditional cultivars and landraces of pearl millet from drier regions possess good levels of drought adaptation [126], but fail to capitalize on yield-enhancing nutrient and moisture conditions, in the native soils, or externally applied [55, 127]. On the other hand, elite genetic material has a greater yield potential expressed under better endowed conditions, but lacks adaptation to severe drought stress conditions [16, 55, 120, 127]. Detailed physiological studies suggest that these two contrasting groups of genetic materials have differential pathways to yield formation under drought stress [16, 17]. The use of elite breeding material may ensure the yield potential, but leaves behind the difficult task of improving adaptation. Landraces may ensure adaptation to drought stress, but they would need to be improved considerably for productivity. This situation suggests good prospects of breeding for drought-prone environments by diversifying the base of adapted landraces through use of appropriate genetic material to amalgamate the adaptation of landraces with high productivity of elite genetic materials. Given that the Indian landraces are characteristically high tillering and have small-to-medium sized seeds, African elite materials possessing complimentary traits like lustrous and bold grain, compact and large panicles, and rapid grain filling are potential sources for introgression of variation [128].

Several attempts have been made in this direction through hybridization of selected landraces and elite materials (Table 12.2). There was considerable improvement in both grain and stover yield in crosses with individual crosses providing up to 50% higher grain and stover yields under drought stress [56, 114, 116, 129]. Also, crosses had enhanced adaptation range, beyond that of their parental populations as they were better able than their landrace parents to capitalize on the additional resources of good growing seasons and simultaneously have a better capacity than their elite parents to tolerate drought [56, 116, 129–131]. These results suggested that the hybridization between landraces and exotic populations breaks up gene complexes of two contrasting groups of genetic material [41, 132, 133] and is effective in combining drought tolerance and high productivity.

Table 12.2 Mean per cent improvement in performance of crosses between landraces and elite composites over landraces.

No. of landraces	No. of elite lines	Average improvement in crosses for grain yield	Average improvement in crosses for stover yield	Reference
4	5	9	17	[117]
4	3	17	11	[115]
3	4	20	26	[116]
3	6	3	7	[130]
5	5	2	13	[129]

12.3.1.3.3 **Exploitation of Heterosis** Pearl millet is a naturally cross-pollinated crop and several sources of highly stable cytoplasmic genetic male sterility (CMS) systems are now available [134–136]. These two attributes render pearl millet an excellent crop to exploit heterosis through production of commercial hybrids. There are numerous reports of high magnitude of heterosis in pearl millet [48, 49, 137], but a vast majority of them are from drought-free high-productivity environments, leading to argument that heterosis is best exploited under highly productive environments.

The exploitation of heterosis in pearl millet for yield enhancement under drought conditions has been explored through developing hybrids between elite male-sterile lines and pollinators developed from drought-adapted landraces to combine the adaptation of landraces with a higher productivity potential achieved through heterosis expressed in hybrids. Many studies, based on a wide range of male-sterile lines and landraces, have quantified the degree of improvement in hybrids over adapted landraces under water-limited conditions (Table 12.3). Average improvement in grain yield of landrace-based topcross hybrids (TCHs) over their landrace pollinators was 15% with potential benefit of up to 75% in best hybrids. Choice of male-sterile lines had considerable effect on the manifestation of heterosis for grain and stover yields [138, 139] and thus has a great bearing on manipulating grain/stover relationship of hybrids.

Table 12.3 Mean and maximum (in parentheses) heterosis (%) in pearl millet topcross hybrids over landrace pollinators.

No. of male-sterile (A) lines	No. of landrace pollinators	Average heterosis (%) for grain yield	Reference
2	19	31 (75)	[138]
3	6	15 (28)	[182]
12	6	18 (61)	[140]
15	1	3 (26)	[183]
7	7	5 (17)	[139]
1	4	32	[121]
2	15	22	[184]

Considering that in drought-prone regions, livestock (maintained largely on pearl millet dry stover) is an integral component of rural economy, any improvement in grain yield should not be at the cost of stover yield, and hence total biomass productivity needs to be increased. This objective was achieved through landrace-based hybrids. An average of 15% heterosis in growth rate in TCHs based on landrace pollinators [138] has been reported, which translated to a positive biomass heterosis. The partitioning of this extra biomass to either grain or fodder appeared to be controlled by the harvest index of the seed parent, resulting in differential heterosis for either grain or stover yields, depending upon the seed parent used [139].

Research has also shown that variation in biomass heterosis is the major determinant of both grain-yield heterosis and stover-yield heterosis [140]. However, contribution of harvest index heterosis to grain- and stover-yield heterosis has been observed to be of a compromising nature. Harvest index heterosis leads to a positive higher grain-yield heterosis but negative heterosis for stover yield, suggesting that the strategy for increasing grain yield by improving harvest index will not result in the desired outcome in the marginal drought environments where stover yield is also important. There are reports of exploitable genetic differences among the male-sterile lines and landrace-based restorers in their ability to produce heterotic crosses for biomass [140–143] and selection for biomass can be highly effective [144, 145]. These results have clearly demonstrated that it is possible to improve the grain and stover production to meet farmers' needs, while retaining critical adaptation to drought environments by exploiting heterosis between drought-adapted pollinators and carefully selected male-sterile seed parents that partition the extra dry matter to both grain and stover. Thus, exploiting heterosis in hybrids is an effective and rapid way to improve pearl millet production, while retaining critical adaptation to drought environments.

These results have been extended to pearl millet hybrid breeding for drought-prone environments of northwestern India. Since last one decade, a large number of hybrids and open-pollinated varieties have been tested under drought environments and it has been explicitly shown that hybrids provided 25% higher grain yield than OPVs [71]. This magnitude of advantage in grain productivity of hybrids shows that hybrids have greater yielding capacity than OPVs under drought environments and are likely to play a much greater role in enhancing pearl millet productivity in drought-prone regions.

12.3.2
Molecular Breeding

Because of the intrinsic difficulties in breeding for drought adaptation by conventional phenotypic selection [146, 147], this field has become a prime focus for molecular marker-assisted breeding. Efforts in this direction started in pearl millet in the early 1990s with the development of a molecular marker-based genetic linkage map that largely comprised of RFLP loci [148]. This linkage map was short (about 300 cM), but was longer than subsequent maps [149–151] based on crosses of cultivated pearl millet with accessions of its wild progenitors. The linkage map has been expanded [152] and current genetic linkage map of pearl millet is 1148 cM long [153].

Genetic mapping has targeted terminal drought tolerance. Research at ICRISAT has identified quantitative trait loci (QTL) that had significant effects on pearl millet yield in drought stress environments [105, 154, 155]. Comparison of hybrids with and without these QTL showed that QTL-based hybrids were significantly, but modestly, higher yielding in a series of terminal drought stress environments [154]. However, this gain under stress was achieved at the cost of a lower yield in the non-drought environments. A major QTL mapped on Linkage Group (LG) 2 accounted for up to 32% of the phenotypic variation in grain yield under post-flowering drought stress environments [155, 156]. In addition, a number of other QTL were detected that were associated with maintenance of grain yield-determining component traits [157].

The QTL with little interaction with environment [158] has been transferred to drought-sensitive pearl millet lines through marker-assisted backcross breeding [159]. Several introgressed lines carrying LG 2 genomic region exhibited positive general combining ability (GCA) for grain yield under terminal stress that was associated with a higher panicle harvest index [157]. Physiological dissections indicated that lines having QTLs had lower transpiration rate compared to lines not carrying this QTL. There are reports that LG 2 QTL is also associated with salinity tolerance [160].

12.4
Heat Tolerance

Several growth processes like the rate of germination, rate of coleoptile elongation, or the rate of photosynthesis require rather high optimum temperatures, for example, 35 °C in pearl millet [161], which is indicative of good adaptation of pearl millet to the hot growing conditions in the Sahel and in many parts of India. The high temperature tolerance has relevance at both seedling and reproductive stages of crop.

12.4.1
Tolerance at Seedling Stage

Germination rate and final germination percentage are reduced following short exposure to 50 °C, but not at 45 °C [161, 162]. At constant exposure to 47 °C, no germination has been observed under controlled environment conditions. Field studies in the Sahel [10] indicated that pearl millet seedlings are most vulnerable to high temperatures during the first 10 days of sowing. This was confirmed by field studies in the Indian Thar Desert [163]. During other stages of seedling growth, the effect of high temperatures is small when the available water is sufficient for transpiration that cools the leaves [10, 163]. Controlled environment studies with young seedlings have shown that pearl millet responds to supraoptimal temperature conditions with the production of a series of heat shock proteins [164]. A conditioning or hardening effect of intermediate temperatures has also been observed.

High seedbed temperature (>45 °C) is one of the most important factors causing poor plant stands of pearl millet [165]. Poor seedbed preparation, inappropriate sowing methods, poor seed quality, and low soil fertility are other factors responsible for low and variable plant populations. Plant stand losses due to these factors can be minimized by better agronomic management, but losses due to high soil surface temperature are difficult to control by cultural methods. Therefore, genetic improvement in tolerance of high seedbed temperature assumes importance.

A rapid screening procedure for seedling emergence under high temperatures, using a large steel tank and infrared heat lamps mounted on an adjustable rack suspended over the tank is in place [8]. Temperatures can be adjusted by raising and lowering the lamp rack. This procedure was used for a selection experiment in two populations for two cycles and found that it was effective in increasing emergence under high temperature conditions in the absence of water stress [166].

Peacock *et al.* [163] identified genetic differences in seedling survival under high soil surface temperatures using a field screening procedure during the hot and dry seasons in sandy soils in the Thar Desert in India. The method is rapid and inexpensive and can be used with a large number of genotypes. Its usefulness, however, is limited because tests can be conducted only during 2 months in a year, and experiment's failure due to occasional rains is possible. The present use of this method in a selection study indicates that it is effective in identifying genotypes with superior seedling heat tolerance [167, 168].

To overcome limitations of the field screening procedure, a controlled environment method using a sand bed that can be heated electrically and a laboratory method based on measuring membrane thermostability have been developed [169]. Initial results from a selection study in variable populations show that both procedures appear to be effective in increasing seedling survival under heat stress. Results from these two procedures show good correlations with field results. Their advantage appears to be higher heritabilities and more flexibility in their application [167, 168].

12.4.2 Tolerance at Reproductive Stage

In view of climate change and rising temperatures, tolerance of crops to high temperature during their reproductive stage has recently assumed high significance. A temperature rise of 0.5–1.2 °C by 2020, 0.88–3.16 °C by 2050, and 1.56–5.44 °C by 2080 has been projected for South Asia [170]. It has also been projected that by the end of twenty first century, mean annual temperatures in India will increase by 3–6 °C [171]. Climate change models have indicated drastic reductions in yield of cereal crops in tropical regions with moderate increase (1–2 °C) in temperature. This is likely to result in significant changes in cropping pattern and areas of crop production, and maize and sorghum might be replaced by pearl millet in some of the semi-arid regions of Asia and Africa.

The impact of high temperature stress during reproductive period has been studied in many crops. High temperature stress (>35 °C) for 1 h has been found to induce spikelet sterility in rice [172, 173]. Similarly, temperature higher than 36 °C is reported to reduce pollen viability in maize [174] leading to reduction in yields. Similar effects of short spells of high temperature during flowering on fertility have been reported in sorghum [175] and wheat [176]. Contrary to this, pearl millet has good degree of tolerance to high temperatures of up to 42 °C during flowering. Hence it has occupied considerable areas (>600 000 ha) in the hot and dry post-rainy season (locally referred to as summer) in the northern and western parts of India. In summer season, pearl millet hybrids of 80–85 day duration can provide 4–5 tons/ha of grain and 8–10 tons/ha of dry stover under irrigated and well-managed conditions. Owing to higher air temperatures (often above 42 °C) coinciding with flowering in this region, the summer crop suffers from spikelet sterility leading to drastic reductions in grain yield. Only a few hybrids have shown good seed set under such high temperature conditions, leaving a limited choice of cultivars that always runs the risk of such cultivars breaking down to downy mildew. Thus, there is a need to identify sources of flowering-period heat tolerance to strengthen the hybrid breeding program for summer season.

ICRISAT made initial efforts in this direction by conducting some pilot studies under both controlled environmental and field conditions in target environments of northwestern India. In the controlled environments, screening for heat tolerance is conducted under growth chambers (simulated for a normal day where maximum temperature reaches 43 °C) by exposing pearl millet to high-temperature stress at boot leaf stage [177]). Screening for heat tolerance is also conducted under field conditions in target environment of northwestern India. Since the occurrence of high temperatures is unpredictable and breeding lines generally have a wide range of maturity, material is planted at three different dates during February–March at about 10 days interval at three–four locations with high temperatures so that the temperatures of ≥42 °C coincide with flowering of all the entries at least in one of the planting dates at each location. Weather loggers are installed in the experimental field to record air temperatures on hourly basis. The nursery is irrigated at regular intervals to avoid moisture stress in the field.

Dates of emergence of boot leaf and flowering are recorded in each planting date, and panicles are bagged after pollination to protect them from bird damage. At dough stage, seed set is recorded and data on seed set of plants that got exposed during flowering to air temperatures of ≥42 °C across the three dates are used to identify those with higher seed set (>60%) and presumably with high levels of heat tolerance.

Large genetic variation in tolerance to heat at reproductive stage among pearl millet breeding lines and populations has been observed, and heat-tolerant sources have been identified. Based on multilocational screening during the 2009–2010 summer season, two maintainer lines ICMB 92777 and ICMB 05666 were found to have >60% seed set when the air temperature during flowering exceeded 42 °C.

In addition, four B-lines (ICMB 00333, ICMB 01888, ICMB 02333, and ICMB 03555) were found as heat tolerant on the basis of 2010 screening that needs further validation in multiyear and multilocation testing. Populations like ICMV 82132, MC 94, ICTP 8202 and MC- Bulk have also been identified as sources of heat tolerance for further selection. Three germplasm accessions (IP 19799, IP 19877, and IP 19743) were also identified as heat tolerant (seed set of >50%), and can also be further utilized for diversifying the genetic base of heat-tolerant materials in pearl millet. However, the mechanism of heat tolerance is yet to be investigated in these materials.

The lines identified for heat tolerance need to be validated for this trait and those found stable can be used for developing mapping populations to identify QTL for use in marker-assisted breeding. Among the three major abiotic production constraints presented in this chapter, marker-assisted breeding is likely to be more successful for flowering period heat tolerance because the upper limit of temperature is known well predictably unlike salinity and drought stress. The main challenge would be to identify reliable QTL because the temperatures during flowering time below the predicted maximum might vary (sometime below 40 °C) due to occasional rains and cloud cover, and thus pose a challenge to reliable phenotyping for this trait. Development of a controlled environment facility for high temperatures maintenance during flowering would accelerate the process of QTL identification.

12.5 Salinity Tolerance

Salinity is a major constraint to crop production, especially in the arid and semiarid regions of the world, where low precipitation, high surface evaporation, irrigation with saline water, rising water tables, and poor irrigation practices generally increase the levels of soluble salts. Increased frequency of drought events over most land areas [178, 179], coupled with higher temperature, will intensify salinization due to increasing upward capillary transport of water and water-soluble salts from the groundwater to the root zone with no or negligible leaching under water-limiting environments [180, 181]. Thus, salinization is expected to be increasing in the future climate change scenario. At present, about 77 m ha (5–7% of the cultivable lands) are affected by salinity across the globe. Management of saline soils by flushing out of salts using fresh water is costly, and is limited by availability of fresh water. Thus, crop production by using salinity-tolerant crops is one of the best options. Pearl millet having high in-built tolerance to saline soils will be in advantageous position and can be deployed in saline lands for grain and forage production.

Some preliminary research work has been done at ICRISAT on salinity tolerance in pearl millet in collaboration with the International Center for Biosaline Agriculture (ICBA), and its NARS partners in both India and WANA region. Advanced breeding materials have been screened for salinity tolerance at ICRISAT, Patancheru, India, and ICBA, Dubai, initially through pot culture method, which is followed by screening of these identified materials in salinity-affected fields. In pot

Table 12.4 Performance of salinity-tolerant pearl millet breeding material under saline fields at Gangavathi, Karnataka, India during 2004–2005 [185].

Type of breeding material	Range	
	Grain yield (kg/ha)	Dry fodder yield (kg/ha)
B-Lines: ICMB 01222, ICMB 96333, ICMB 95222	940–1265	3980–6940
Sensitive B-line (control)	797	2486
R-lines: HTP 94/54, CZI 9621, ICMP 451	1081–1311	4113–6721
Sensitive R-line (control)	974	3794
Germplasm accessions: IP 6105, IP 6098, IP 22269	1155–1411	4196–6117
Improved populations: Dauro genepool, Sudan Pop III, HHVBC Tall	1452–1996	4009–6117

culture method, breeding material is grown in pots with salinity treatment in an outdoor environment equipped with a rainout shelter along with controls. At ICRISAT, a 200 mM NaCl treatment is provided for screening tolerant genotypes, whereas screening is done at 5, 10, and 15 dS/m salinity levels at ICBA. This salinity-tolerant material identified under controlled environments then undergoes testing in salinity-affected fields at Gangavathi (Karnataka, India), Rumais (Sultanate of Oman), Dubai (UAE), and some other locations in WANA region. The trials are drip irrigated with saline water (7.5–8.25 dS/m) at Dubai and Rumais, while they are conducted under saline rainfed conditions at Gangavathi.

Screening resulted in identification of advanced breeding lines, parental lines of potential hybrids, improved population (including open-pollinated varieties), gene pools and composites, and germplasm accessions with high biomass (forage) presumably with high degree of salinity tolerance under salinity levels up to 15 dS/m (Table 12.4). In the short-to-medium terms, some of these materials can be released for cultivation after extensive validation of their yield performances in on-farm trials. Working on these lines, a pearl millet variety "HASHAKI 1" has been identified for release in Uzbekistan in 2012 as a high-forage variety for salt-affected areas. The identified salinity-tolerant pearl millet lines should be utilized in breeding programs to develop salinity-tolerant locally adapted cultivars (both OPVs and hybrids). This will enable farmers in salt-affected areas to adopt and grow a new crop such as pearl millet in lands that otherwise are fallow most of the years.

Since populations have shown large intra-population variability for forage yield in saline soils, and forage yield under saline conditions has been shown to have significant and high positive correlation ($r^2 = 0.92$) with salinity tolerance index (STI), direct selection for forage yield in saline soils can effectively enhance not only forage yield but also salinity tolerance. Direct selection for grain yield under saline conditions can also enhance salinity tolerance for this trait, although it would be less effective than selection for tolerance with respect to forage yield because the correlation between grain yield under salinity conditions and salinity tolerance index, though significant and positive, is smaller in magnitude.

Several parental lines and populations with both high grain yield ratio (ratio of yield under salinity versus control) and stover yield ratio were identified in pearl millet and there was highly significant and positive correlation between grain yield ratio and stover yield ratio ($r^2 = 0.80$), implying that selection for high stover yield ratio is likely to also lead to concomitant genetic improvement in grain yield ratio, and that simultaneous selection for both productivity and STI will be highly effective. Parental lines with large contrasts for grain yield ratio have been identified to develop mapping populations to identify QTL for salinity tolerance.

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