ADVANCES IN PEARL MILLET TO MITIGATE ADVERSE ENVIRONMENT CONDITIONS EMERGED DUE TO GLOBAL WARMING

R. K. ARYA*, M. K. SINGH[1], A. K. YADAV[2], ASHWANI KUMAR[3] AND SURESH KUMAR[4]

Department of Genetics and Plant Breeding
CCS Haryana Agricultural University,
Hisar-125 004 (Haryana), India
*(e-mail : rajesharya@hau.ernet.in)

SUMMARY

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is one of the most important crops of inhabitants of hot and dry conditions of the arid and semi-arid regions of Africa and Asia. Like other crops, pearl millet is affected by temperature, rainfall (timing and quantity), CO_2, solar radiation, soil types and the interaction of these elements. Now-a-days, global warming may cause serious problem in agricultural production, particularly in arid and semi-arid regions of the world. As the abiotic stresses affect the seed germination, plant growth and development, resulting in drastic reduction in yield. Pearl millet is a multipurpose crop grown in these areas due to its tolerance to high temperature, drought and salinity. But, further improvement for abiotic tolerance is of instant need, for economization of agriculture in these areas. Therefore, to develop/identify tolerant genotypes, knowledge of screening methods, stress tolerance mechanisms along with breeding techniques is important. Abiotic stresses decrease the rate of germination and may also inhibit the germination depending on heat tolerance of the genotype. A lot of genetic variability is available for heat, drought and salt tolerance in peal millet. Breeding for heat tolerance information of genetic variability, gene action (additive and non-additive), heritability, stability and correlation in relation to heat tolerance is available. Gene interactions on stress tolerance showed its complex nature of inherence. Both conventional as well as molecular breeding techniques were utilized for genetic improvement for tolerance against abiotic stresses in pearl millet.

Key words : Heat, drought, salinity, tolerance, pearl millet

Today, entire world is concerned about the impact of climate change on plants and animals. Noble peace prize-2007 was awarded to Inter-governmental Panel on Climate Change (IPCC) for their efforts to build up and disseminate greater knowledge about man-made climate change and resulting in natural disasters. Over the last 150-200 years, climate change has been taking place so fast that certain plant species have found it hard to adapt. The relationship between climate change and agriculture is an essential step towards enacting effective and efficient solution. The climate change will have dramatic consequences for agriculture (Subrahmanyam and Hanamashetti, 2011).

Climate change and agriculture are interrelated processes, both of which take place on a global scale.

Moreover, climate change has the potential to affect agriculture through changes in temperature, rainfall (timing and quantity), CO_2, solar radiation and the interaction of these elements. The effect of climate on agriculture is related to variabilities in local weather parameters rather than in global climate patterns. The earth's average surface temperature has increased by 1 degree F in just over the last century. Consequently, researchers consider any assessment has to be individually considering each location.

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is one of the most important crops of inhabitants of hot and dry conditions of the arid and semi-arid regions of Africa and Asia (Arya and Yadav, 2009). With its ability to adapt to diverse agro-ecological conditions, it may have unique

[1]Department of Dry Land.
[2]IHBT, Palampur (H. P.).
[3]Govt. P. G. Nehru College, Jhajjar (Haryana)
[4]Department of Agronomy.

position in the world agriculture. It is a multipurpose cereal grown for grain, stover and green fodder. It shall continue to play a prominent role in the integrated agricultural and livestock economy of the country particularly in rainfed areas due to its drought hardiness and tolerance to high temperature (Arya *et al.*, 2010). It has the virtue of having exceptionally highest productivity per day both for grain as well as fodder. In the limiting environments, pearl millet is the only successful cereal and a major source of nutrition for the poor farming community. It also responds well to improved moisture and soil fertility conditions (Qi *et al.,* 2004).

Pearl millet growing environments are characterized by low and erratic rainfall, high temperature and poor soil fertility. The soil temperatures in farmers' field in India and Africa commonly exceed 45°C and the temperatures as high as 60°C have occasionally been measured (Yadav *et al.*, 2010). Heat stress produces direct or indirect stress injury. This complicated effect of elevated temperature is due to disturbances in metabolic reactions caused by slow vaporization of cellular water content. Wahid *et al.* (2007) reported that heat stress due to increased temperature was an agricultural problem in many areas in the world. Transitory or constantly high temperatures cause an array of morpho-anatomical, physiological and biochemical changes in plants, which affect plant growth and development and may lead to a drastic reduction in economic yield.

Moreover, soil moisture is the first formost impotant factor, which depends on duration and intensity of rainfall. Now-a-days, rainfall is showing declining trend in majority of pearl millet growing areas. However, all the activities of crop plants from germination to maturity depend upon the availability of soil moisture and nutrients required for growth and development of plants. Pearl millet growing environments in these areas are characterized by low and erratic rainfall, high temperature and poor soil fertility.

Now-a-days, salinity is also a constraint in successful cultivation of crop plants in salt affected areas and its world wide spread has become a serious problem. The salt stress has profound ill effects on growth and deveploment of crop plants that even lead to a complete failure of crop.Therefore, its management is of utmost importance in getting economic benefits from salt affected soils. Among the various measures adopted, developing salt tolerant varieties has proved to be a breakthrough in this research in recent times (Maiti *et al.*, 2007).

Present review highlights the responses of potential genotypes of pearl millet for the different situations emmersed due to climate change such as drought, heat and soil salinity. The efforts were made during past in uncovering the mechanism of drought, heat and salt tolerance. Important selection criteria being used by plant breeders for screening and development of resistant/tolerant cultivars were also dicussed. Climate is making the agriculture sector vulnerable and there is an instant need of developing the genotypes, which are better adapted to climate change.

Effect of Heat Stress

In pearl millet, several growth processes require rather high optimum temperatures e. g. 35^{0}C for the rate of germination, rate of coleoptile elongation or the rate of photosynthesis (Garcia-Huidobro *et al.*, 1985). This is indicative of this species good adaptation to the hot growing conditions in Sahel and in many parts of India. Mid-day soil surface temperatures frequently exceed 45^{0}C in major pearl millet growing areas in India and Africa. High temperature of seedbed is one of the most important factors causing poor plant stands of pearl millet (Ong, 1983). Poor seedbed preparation, inappropriate sowing methods, poor seed quality and low soil fertility are other factors responsible for low and variable plant populations. Crop 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 for tolerance of high seedbed temperature is most important.

The soil temperatures in farmers' field in India and Africa commonly exceed 45°C and the temperatures as high as 60°C have occasionally been measured (Soman, 1981; Singh, 1993). It is also true that several growth processes in pearl millet do require rather a high temperature. The rate of germination, coleoptiles elongation and rate of photosynthesis all reported to be maximizing up to temperature of about 35°C. The pearl millet in this sense could be said to have shown a good adaptation to the hot growing conditions of Sahel and Thar deserts of Africa and Asia. The temperatures in excess of 35°C on the other hand cause inhibition in the normal growth process (Yadav *et al.*, 2010).

Heat Stress Adaptation

In pearl millet, the effects of supraoptimal

temperature have mainly been studied on seedlings (Yadav *et al*., 2010). Garcia-Huidobro *et al*. (1985) revealed that germination rate and final germination percentage were reduced following short exposure to 50^0C, but not at 45^0C. At constant exposure to 47^0C, they did not observe any germination under controlled environmental conditions. Stomph (1990) indicated during field studies in Sahel that during the first 10 days after sowing, pearl millet seedlings were most vulnerable to high temperatures. This was confirmed by field studies in the Indian Thar desert (Peacock *et al*., 1993). The effect of high temperature during other stages of seedling growth is small when the available water is sufficient for transpiration which cools the leaves (Stomph, 1990). Controlled environment investigations with seedlings have shown that pearl millet responds to supraoptimal temperature conditions with the production of a series of heat shock proteins (Howarth and Ougham, 1993). A conditioning or hardening effect of intermediate temperatures has also been observed.

The effects of supraoptimal temperatures on other growth and development of pearl millet have rarely been studied. In field studies in Sahel with two temperature regimes, Stomph (1990) reported no effects of heat on factors of seedling growth 10 days after sowing. Ong (1983) reported effects on seed set at rather low temperatures (28^0C), compared with the optimum temperatures for other processes. These results were obtained in controlled environment conditions and have not been verified under field conditions. Multi-location analysis of yield trial data from India indicates that high temperatures during the grain-filling period contribute significantly to genotypes x environment interactions in these trials (van Oostgerom *et al.,* 1995). However, no detailed studies comparing genotypes for their reaction to high temperature during seed set and grain filling are available (Khairwal *et al*., 1999).

Plant Physiology

Heat stress affects plant growth throughout its ontogeny, though heat-threshold level varies considerably at different developmental stages. For instance, during seed germination, high temperature may slow down or totally inhibit germination, depending on plant species and the intensity of the stress. At later stages, high temperature may adversely affect photosynthesis, respiration, water relations and membrane stability, and also modulate levels of hormones and primary and secondary metabolites. Furthermore, throughout plant ontogeny, enhanced expression of a variety of heat shock proteins, other stress-related proteins, and production of reactive oxygen species (ROS) constitute major plant responses to heat stress (Wahid *et al*., 2007).

In order to cope with heat stress, plants implement various mechanisms, including maintenance of membrane stability, scavenging of ROS, production of antioxidants, accumulation and adjustment of compatible solutes, induction of mitogen-activated protein kinase (MAPK) and calcium-dependent protein kinase (CDPK) cascades, and, most importantly, chaperone signaling and transcriptional activation. All these mechanisms, which are regulated at the molecular level, enable plants to thrive under heat stress.

Screening Methods for Thermo-tolerance

Various techniques have been used to study the response of genotypes of cereals at high temperature by different workers (Yadav *et al*., 2010). Screening methods are generally attempted at two levels : laboratory and field. Screening for heat tolerant genotypes can be done based on the characteristics like germination (per cent germination under stress); growth during heat stress (yield, biomass); membrane stability (soluble leakage conductivity test); photosynthetic sensitivity (chlorophyll fluorescence at 685 nm); recovery after heat stress (yield, biomass, etc.) and sensitivity of reproductive phase (flower/pod/fruit/seed production; pollen fertility).

Laboratory Techniques

Certain laboratory techniques for screening and identification of genotypes tolerant to high temperatures such as electrolyte conductivity technique, chlorophyll stability technique, seed germination test, hydroponic seedling test and embryo protein synthesis, etc. have been developed. Many laboratory techniques have been developed by various scientists. One bioassay often used in characterizing high temperature tolerance is electrolyte leakage of leaves subjected to heat stress (Shanahan *et al*., 1990). These are electrical conductivity methods (Nagarajan and Panda, 1980), Chlorophyll florescence method (Smillie, 1979) and embryo protein synthesis methods (Ougham *et al.,* 1988). Therefore, the membrane thermo-stability test would be a suitable procedure for selecting heat tolerant genotypes in a breeding programme.

Selection and Breeding for Heat Tolerance

As the germination, emergence and seedling growth stages are well defined, they lend themselves to both field and controlled environment testing. Testing for germination at high temperatures only requires incubators, which operate reliably. Lynch (1994) used a constant temperature of 45^0C to differentiate among full-sib and half-sib progenies in a selection experiment. He found significant genetic variation for this trait in two variable populations. However, heritabilities were too low to achieve measurable genetic gains for this trait.

Soman and Peacock (1985) developed a rapid screening technique for seedling emergence under high temperatures, using a large steel tank and infrared heat lamps mounted on an adjustable rack suspended over the tank. Temperature can be adjusted by raising and lowering the lamp rack. Lynch (1994) used this technique 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. However, the technique will need to be modified to increase efficiency and repeatability (Yadav *et al.*, 2010).

Peacock *et al.* (1993) identified considerable genetic differences for 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. This technique 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 two months in a year, and experiments failure due to occasional rains may occur. The present use of this method in a selection study indicates that it is effective in identifying genotypes with superior seedling heat tolerance (Weltzien *et al.*, 1994).

To overcome limitations of the field screening techniques, a controlled environment procedure using a sand bed which can be heated electrically, and a laboratory technique based on measuring membrane thermostability, have been developed. Initial results from a selection in variable populations show that both procedures appear to be effective in increasing seedling survival under heat stress. Results from these two techniques show good correlations with field results. Their advantage appears to be higher heritabilities and more flexibility in their application in pearl millet (Weltzien *et al.,* 1994).

Genetic control of temperature tolerance was investigated in pearl millet at seedling stage (Yadav *et al.*,

2011). Variances due to general combining ability and specific combining ability for all the characters studied, viz seedling thermo-tolerance index, seed to seedling thermo-tolerance index, germination, emergence rate, leaves/seedling, seedling height, seedling fresh weight and seedling dry weight were highly significant in all the three environments (two stress and one normal) indicating the importance of both additive and non-additive genetic variances. The non-additive (dominance) component was more prominent for all the characters. It suggested that heterosis breeding could be successful. The genotypes 'CVJ 2-5-3-1-3' and '(77/371×BSECT CP 1)' were identified as the best general combiners for both the heat tolerance indices. Seven hybrids, namely, 'H77/833-2 × 96AC-93', '1305 × 96AC-93', '(77/371 × BSECT CP-1) × Togo II', 'H77/29-2 × CVJ 2-5-3-1-3', '1305 × 99HS-18', 'G73 107 × 77/245' and H77/833-2 × H77/29-2 were identified having high value of heat tolerance indices, seedling thermo-tolerance index and seed to seedling thermo-tolerance index. The estimates of additive genetic variance and narrow sense heritability for seedling thermo-tolerance index and seed to seedling thermo-tolerance index were high (Yadav *et al.*, 2011). Patil and Jadepa (2009) repoted that alleles controlling the grain yield in stress and non-stress environment were partially different, therefore, need to select in target environment to improve the performance of the genotypes.

Molecular chaperones (Hsps) have been shown to facilitate protein folding or assembly under various developmental and adverse environmental conditions. Reddy *et al.* (2010) isolated a cDNA encoding a cytoplasmic Hsp70 (PgHsc70) from *Pennisetum glaucum* by screening heat-stress cDNA library. Transcript induction data, presence of several putative stress-responsive transcription factor-binding sites in the promoter region of PgHsc70 and the presence of a protective *in vitro* chaperone activity of this protein against damage caused by heat and salinity, when expressed in *E. coli,* suggest its probable role in conferring abiotic stress tolerance to this plant.

Effect of Drought Stress

Any kind of stress at early stages of plant growth reduced the number of tillering drastically and also provided stimulus to the plant for early flowering, resulting in reduction in plant's normal size which ultimately produced small earhead thus drastic reduction in grain yield along with fodder yield was noticed.

TABLE 1
Effect of drought on pearl millet

Stage	Effect	References
Seedling phase drought effect	1. During emergence and early seedling phase drought causes plant death/poor crop stand, resulting yield losses	Seetharam *et al.* (1984) Carberry *et al.*, (1985) Soman *et al.* (1987)
	2. After crop establishment (within seedling phase) drought little effect on survival or grain yield	Lahiri and Kerbanda (1965) Lahiri and Kumar (1966)
	3. Seedling phase drought affects rate of leaf appearance and secondary not development	Stomph (1990)
Vegetative phase drought effect	4. Little/no adverse effect on grain yield	Mahalakshmi and Bidinger (1985)
	5. Delays flowering and increases number of ears/plant which compensate potential loss in main shoot	Mahalakshmi *et al.* (1985) Bidinger *et al.* (1987) Raymond (1968) Egharevba (1977) Mahalakshmi *et al.* (1987)
Reproductive phase drought/ terminal drought	6. Dought at flowering and grain filling reduces drastically the grain yield and its components as it is most sensitive to drought	Mahalakshmi *et al.* (1985) Bidinger *et al.* (1987) Fussel *et al.* (1991) De Rouw and Winkel (1998)

However, highly favourable environmental conditions prevailing during early growth period which stimulated plant for profused tillering and more speedy plant growth delayed the flowering and more accumulation of biomass due to long life span of the plant. If favourable conditions also continue during the grain filling period, it will produce maximum yield both grain as well as fodder. But, if unfavourable conditions operate during grain filling period than there will be reduction in grain size and weight which results in reduction in grain yield (Arya *et al.*, 2010). In Pearl millet drought stress at the different stages of crop growth and development from germination to maturity may have major/little or no adverse effect on grain yield has been studied by various researchers summarised in Table 1.

Drought Adaptation

Pearl millet is one of the most drought tolerant crop plants because of its short development stages, capacity to grow speedily under favourable conditions, rapid growth after stress, and effective control of water loss and heat tolerance (Bidinger *et al.,* 1982). Addition to this, its development plasticity (to change growth rate and plant architecture in response to water availability) enables pearl millet to maximize yield in drought prone areas (Siband, 1983; Winkel and Do, 1992).

The capacity of high tillering and asynchrony of tillering in pearl millet contribute to its drought stress during the vegetative growth phase (Nanda and Chenoy 1958; Raymond, 1968; Siband, 1983; Mahalakshmi *et al.,* 1987; De Rouw and Winkel, 1998).

Further, it is an established fact that the stress at the vegetative growth phase delayed the flowering on the main shoot. This phenological plasticity increases the chances for escape from stress in two ways : (1) by delaying the flowering (most sensitive stage) under the stress has been relieved and (2) by closing stomata at relatively high water potential during drought in the vegetative period (Henson and Mahalakshmi, 1985). Thus, pearl millet conserves the limited water resources, and increases the chance of survival by extending early season drought. Once the crop initiates its flowering stage, the stomatal behaviour changes. Winkel *et al*. (2001) reported that ontology modified the effect of water stress on stomatal control, leaf duration and biomass partitioning in pearl millet. Stomatal opening down to water potentials as low as 2-3 Mpa, during stress after flowering. Late flowering plants have a longer time between emergence to panicle initiation (Maiti and Bidinger 1981, Lambert, 1983) as longer as compared to early maturing, therefore, such genotypes have more chance to escape drought spell stress during the most critical growth phases.

Under terminal drought stress, the reduction in grain mass appears to be mainly due to a shortening of grain filling period rather than to a reduction in grain growth rate. This seems to be due to restriction of the current assimilate supply and not by a reduction of the

grain storage capacity (Bieler *et al*., 1993).

Under drought stress, the closing of stomata reduces the photosynthesis in pearl millet though only at very low water potentials (Black and Squire, 1979); but Fussell *et al.* (1980) reported that pearl millet had the capacity to compensate for such a reduction in the supply of assimilates to the grains by mobilizing stored soluble sugars. This contribution of stored assimilates to the grain growth during drought stress has, however, not been quantified and the transfer of assimilates for the leaves with the stress buffering stock, appears to be one of the main adaptations of pearl millet to terminal drought stress.

The various physiological parameters i. e. processes contributing to dehydration tolerance, dehydration avoidance, growth maintenance through stability of cellular membrane, osmotic adjustment, desiccation and heat tolerance have been considered as criteria association with adaptation to drought in different crops (Khairwal *et al.,* 1999). Out of these, a few parameters have been examined in pearl millet. Bidinger and Witambe (1989) suggested solution for traits that contribute to radiation reflectance i. e. glaucousness and leaf pubescence based on evidence from other crops.

Physiology of Drought Stress Tolerance

Payne (2000) reported that in pearl millet, environmental stresses also caused poor root development, which caused reduced water supply to plant and increased resistance to water uptake. These can improve soil nutrients availability, increase effective crop cover and reduce canopy vapour pressure deficient.

According to Yadav and Bhatnagar (2001) stress susceptibility index (S) was negatively correlated with yield under stress, but should be used as a selection criterion in combination with yield under stress environment to select genotypes adapted to stress. Drought response index (DRI) was positively correlated with yield under stress, but had no association with yield under non-stress, it was also reported that DRI might be helpful to identify genotypes with high productivity under stress.

Application of 0.3% potassium iodide solution at anthesis was found to be effective in causing drought stress and thus used as a screening tool in pearl millet (Ashraf *et al*., 2003 a,b). They also reported its significant association with water deficit in growth parameters such as fresh and dry weights of shoot and grain yield.

According to Kusaka *et al.* (2005) the total root length was significantly correlated with the relative growth ratio of the shoot within 4-21 days after withholding water. However, osmotic adjustment also exhibited strong association with relative growth ratio of the shoot and leaf turgor potential. But the effect of total root length and osmotic adjustment in terms of contributing to the variance in relative growth ratio of the shoot was comparatively low under drought conditions. They concluded that osmotic adjustment and total root length were dependent on the degree of water deficit. Moreover, these traits were the most important factors maintaining turgor pressure and plant growth under stress during the seedling stage.

According to Zegada-Linzarazu and Iijima (2005) the water uptake efficiency of deep roots was significantly increased in barnyard millet, but not in pearl millet by drought in topsoil layers. The drought resistance in pearl millet was explained by higher water use efficiency.

Under drought, the leaf gas exchange of plants is reduced and this leads to lower biomass accumulation and grain yield (Kholová *et al*., 2010). Stomatal conductance is influenced by many factors internal and external to the leaf. Stomatal conductance is not only linked to internal biochemical processes but is influenced by a range of physical factors such as the hydraulic conductance of xylem (Sperry *et al.*, 2005). It is reported that stomatal conductance in pearl millet was capable of adjustment in response to LA restriction or to a change in the LA ratio (LAR) (Henson and Mahalakshmi, 1985). According to Black and Squire (1979), a restriction in photosynthetically active LA led to an increased stomatal conductance of the remaining LA, showing the capacity of stomata to adjust to changes in LA. So pearl millet stomatal conductance and LA appear to be inter-related. Thus, work on pearl millet has concentreted on understanding how the leaf canopy develops to maximize water use (Bidinger and Hash, 2003), or considers the reduction of LA under drought as an adaptation (Wallace *et al.*, 1993).

Screening Techniques

Simple and efficient screening techniques are pre-requisite for evaluating large number of genotypes for stress resistance breeding (Khairwal *et al.* 2009). In pearl millet, the work on selection techniques for adaptation to drought has basically focused on terminal drought stress, as it causes higher and irreversible yield losses (Khairwal *et al*., 2009). Various research workers

developed different screening techniques to screen the drought tolerant/resistant genotypes are discussed here.

1. Growth in green house pots under different soil moisture status, germination of seeds and growth of seedlings in di-mannital solutions and stability of extracted chlorophyll under heat treatments to test drought resistance (Fanous, 1967). However, such studies under controlled conditions do not necessary represent the limiting moisture status of the soil.

2. Early vigour (rapid development of seedling) has been positively correlated with drought tolerance as measured by time taken for wilting initiation and permanent wilting (Manga and Yadav, 1995). A genotype with more rapid leaf area development could intercept a greater portion of incident radiation and limit water losses by evaporation. However, more transpiration from a large leaf area will exhaust soil water and cause severe moisture deficit (Winkel and Do, 1992).

3. Early flowering and low tillering combined with a big main earhead help the plant to escape from terminal drought by reducing the growth duration. Earliness is simple selection method based on single plant evaluations can be expected to be successful under most circumstances (Rattunde *et al.,* 1989). Selection for low tillering and large panicles can be achieved by selecting for higher grain yield per earhead (Yadav, 1994).

4. Threshing percentage [(grain yield/earhead yield) x 100] in drought situation in a whole plant response that is being examined as a selection criterion for improved adaptation to terminal drought stress (Bidinger and Mahalakshmi, 1993). It represents the plant ability to set and fill seeds and it integrates the effects of all the physiological traits bearing on the effectiveness of assimilation and translocation under stress. It can be measured easily and accurately, its coefficient of variation is usually low and it generally explains a large proportion of the variation among genotypes for grain yield under terminal drought stress.

5. Field screening technique : field screening during the rain free hot season for response to drought at specific growth stages can be carried out by withholding irrigation to impose moisture stress.

In which genotypes performance in mid season (panicle initiation to flowering) or terminal (flowering to maturity) stress treatments compared with performance under fully irrigated, stress free conditions. Drought resistance is calculated on the basis of genotype performance in the stressed treatment after accounting for flowering differences and yield potential differences among genotypes (Khairwal *et al.*, 1999). This technique is used very effectively.

6. Modified field technique described by Sagar and Kapoor (1986) involves growing of plants in sloping plots that are opposite each other and connected to sub-channels lined with polyethylene sheets. The runoff is thus increased and water availability reduced. However, it has to be widely used. It is useful when the crop response to moisture stress is linear.

7. Line-source sprinkler irrigation technique (Hanks *et al.,* 1976), which delivers a continuously declining amount of water, enables description of non-linear responses to mid-season stress in pearl millet (Bidinger *et al.,* 1982). It has been extensively and effectively used in pearl millet (Mahalakshmi *et al.*, 1990).

The drought tolerance is a complex trait, therefore, any one technique may not be universally used to measure drought stress, due to variability in timing, intensity and duration of water stress is generally infinite and screening techniques can expose genotypes to only gene combinations.

Genetic Improvement for Drought Stress

The success of breeding programme for drought resistance mainly depends on the identification of appropriate breeding material and the use of appropriate selection sites (Ceccarelli, *et al.,* 1992; Caccarelli, 1994) According to Simonds (1991) selection for stress environments should be carried out in stress environments. Although, the improved productivity under stress conditions is directly linked to the improvement of yield stability over a wide range of environments, some researchers think that high yield under stress free environment can be combined with adaptation to drought, while others don't believe. Breeding for high yield in drought prone areas could thus follow other indirect or direct approach.

Indirect approach, selection for high yield potential under favourable conditions with assumption that genotype selected under optimum environmental conditions will also perform relatively well under sub-optimal conditions (Arnon, 1972). Yield potential has been reported to be a significant factor in pearl millet in determining the yield under moisture stress (Fussell *et al.,* 1991), thus, increase in yield potential is expected to result in some enhancement in yield under moisture stress as well when the predominant stress is terminal and the stress is not severe. However, such results are outcome of off-season data only and no validation under rainy season or natural drought (Khairwal *et al.,* 1999).

In direct approach, genotypes for drought prone areas must be selected, developed and tested in the target environment (Johnson, 1980; Simonds, 1991). According to this approach, improvement in yield under stress has no association with yield potential under favourable conditions (Ceccarelli *et al.,* 1992) and main emphasis given on stress adaptation and yield under stress environment. Moreover, the nature of genotype x environment interaction determines the relative importance of each approach, for each set of conditions. Therefore, highest gain can be achieved by understanding the predominant patterns of drought occurrence in the target environment, appropriate genetic stock which expresses sufficient genetic variability for the most appropriate traits for good adaptation and reliable conditions for yield testing under stress environment.

Pearl millet genotypes contrasting in yield under terminal drought conditions are known (Bidinger *et al.*, 1987). Quantitative trait loci (QTLs) for terminal drought have been identified (Yadav *et al.*, 2002) and confirmed in another genetic background (Yadav *et al.*, 2004). Near-isogenic lines (NILs) having a major terminal drought tolerance QTL on linkage group 2 have been generated and these lines have confirmed the role of the QTL in achieving a higher yield under terminal drought stress (Serraj *et al.*, 2005). The major effect of the QTL is to improve grain filling, but the underlying mechanisms are not known. Root growth under drought varied among NILs (Vadez and Sinclair, 2001). It was found that the fraction of transpirable soil water threshold of tolerant parental genotypes was lower compared with sensitive genotypes in the vegetative developmental stage. This meant that the transpiration dropped upon progressive soil drying in relatively dryer soil in the tolerant lines than in the sensitive lines (Kholová *et al.*, 2010).

Marker-assisted transfer of desirable drought tolerent QTL alleles to elite parent backgrounds, and results from introgression line validation in multiple terminal drought stress environments. Using H 77/833-23PRLT 2/89-33 (Yadav *et al.*, 2002), a QTL associated with drought tolerance of grain yield was obtained on LG 2 in two of the three stress environments, explaining up to 32% of the variation in drought tolerance response of grain yield. In a further study, Bidinger *et al*. (2007) also identified a major grain yield QTL on LG 2 which accounted for a significant proportion of the phenotypic variance for grain yield in both stress (27-38%) and the stress-free irrigated control (28%) environments. Highly specialized genetic stocks [QTL-near-isogenic lines (NILs), a high-resolution cross, and a germplasm population] and genomic resources (gene sequences, gene-based markers, and comparative genomics information) specifically developed for these purposes are discussed (Yadav *et al*., 2011).

Effect of Salt Stress

Salt stress affects crop productivity by inhibiting the absorption of water and minerals owing to the prevailing osmotic stress in the soil profile. Moreover, it has considerable effects to restict the growth and development of pearl millet at different stages i. e. germination, seedling growth, vegetative, reproductive stage and yield. Likewise, it was also reported that the increasing salinity levels decreased the seed germination and early seedling growth of pearl millet. Moreover, reduction in the germination (%), root length, fresh/dry weights of roots and coleoptiles and osmotic potential with increasing salt stress (Maiti *et al*., 2007).

Alam *et al.* (2002) reported that increase in the concentration of salt in brackish water (3000-9000 ppm) decreased significantly plant height and dry matter production. They also revealed that pearl millet had the poteintial of cultivation in moderately saline soils. Herrera *et al*. (2003) identified *Pennisetum purpurium* plantlets resistance to drought and salinity *in vitro* culture exposed to five NaCl or polyethyleneglycol (0, 0.5, 1.0, 1.5 and 2.0 g/l) concentrations. The callus development decreased with the increased NaCl concentration. The best results were obtained between 0.5 and 0.1 g/l NaCl or polyethyleneglycol.

Recent physiological studies on the pearl millet genotypes have elegantly established that they differ in transpiration rate and ABA concentration. A low transpiration rate (Munns and Richards, 2007) and a high

ABA concentration (Voisin *et al*., 2006) also play an important role in reduced salt uptake (Yadav *et al*., 2011).

Biochemical Changes under Salt Stress

Salt stress changes the biochemical and metabolic activities in crop plants. Increasing levels of salinity, decrease in pigment content and plant dimensions. However, increase in Ca, Na, N and P contents and reported in pearl millet. Proline content was also increased significantly at the high salinity levels in pearl millet (Maiti *et al*., 2007).

Jain and Sharma (2005) reported that less germination under ABA and NaCl, a dramatic increase in phosphotase activities was observed than that of control. However, under GA_3 no significant decrease in germination per cent was noticed, but higher phosphotase activities were observed, indicating that metabolism of phosphotase in germinating seeds of pearl millet was regulated differently by ABA, NaCl and GA_3. They suggested that changes in the phosphotase enzymes might play important role in acclimatization of pearl millet seeds, to the changing environment.

The invertase activity significantly increased in leaves and decreased in roots of *Pennisetum clandestium* at 150 and 200 mM NaCl reported by Muscolo *et al*. (2003). They also revealed an accumulation of hexoses and a lower activity of glucokinase, phosphoglucoisomerase and pyruvate kinase in plants exposed to high salt stress. The glucose-6-phosphate dehydrogenase decreased with increasing salt concentration. The phosphoenolpyruvate carboxykinase activity slightly and progressively also increased. Salt stress also increased the activity of NADP±specific isocitrate dehydrogenase in leaves and roots.

Tyagi *et al*. (2006) reported a novel isoform of ATPase c subunit from pearl millet that is differentially regulated in response to salinity and calcium. The vacuolar ATPase supported to maintain the pH of the vacuoles and play a major role in the functioning of vacuoler sodium-proton antiporter. They cloned three isoforms of vacuolar ATPase subunit c (VHA-c) from pearl millet with homologies among themselves varying from 38% to similar to 73% at the nuclear acid level. The three isoforms are regulated in a tissue-specific manner under salinity stress. Isoform I is upregulated under stress. Isoform II is expressed down regulated in roots, and upregulated in shoots. While isoform III is constitutively expressed in roots and shoots and does not respond to stress. The tissue specific expression of isoform II under salt stress was also observed after exogenous application of calcium. The presence of three isoforms of PgVHA-c and their differential regulation during plant development, and also under also under abiotic stress.

Genetic Variability and Selection Under Salt Stress

Ashraf *et al.,* (2003b) stidied the effects of increased salinity (NaCl + CaCl) on seedlings of pearlmillet. They reported that the genotypes exhibiting lower mortality had a high root weight, shoot:root ratio and the greater plant height. Sufficient genetic varation in response to salinity was observed, which suggest that selection of individual plants with increased salinity tolerance is possible within pearl millet. Moreover, hybrids gave higher yield in salt stress condition than the populations, which suggests that there is a good scope of developing salt tolerant hybrids. Bold seeded hybrids with bristles have high salinity tolerance (Maiti *et al*., 2007).

Pearl millet genotypes exhibited varibility for growth and yield atributes at different salinity levels Chopra & Chopra, (1997). Kulkarni *et al*. (2006); Maiti *et al.,* (2007) reported significant reduction in seedling root length due to increased concentration of Na_2CO_3 and repoted considerable variation in pearl millet for salt growth. They also revealed significant differences among genotypes on the basis of salinity threshold Ct, the Na_2CO_3 solution concentration at which root length begins to decrease. The contration caused a 50% decrease in root length (C50) and the concentration causing zero root growth (C0). Threrefore, among these three characters used, it is concluded that C50 appears to be a useful character by means and quantifying salinity tolerance. Only few studies have been directed to select salinity tolerant pearl millet genotypes under salinity in field and its utilization of genetic improvement for salinity tolerance (Maiti *et al*., 2007).

Ashraf and Mc Neilly (1992) reported potential variation in salinity tolerance in pearl millet with respect to shoot and root growth and plant dry weight by raising 24 entries after two weeks of growth in saline solution culture at EC 20 dS/m [sup-1]. Although salinity markedly inhibited growth of all accessions, considerable variations were noticed in 24 genotypes and some were also selected for salinity tolerance. They also suggested that selection for increased tolerance to salinity in pearl millet may be possible. Selected seedlings were grown and polycrossed.

It was also suggested that further improvement in salinity tolerance in pearl millet may be expected from further selection and breeding, using the similar method. Maiti *et al.* (2007) reported that the concentration of Na^+ and consequently the Na/K ratio increased significantly in salt tolerance sorghum salinised treatments. Thus, genotypes tolerant to soil salinity showed a higher Na^+/K^+ ratio. Therefore, osmotic adjustment, ion inclusion and the proportion of Na^+/K^+ act as mechanisms of resistance to salinity.

Generally, the good adaptability is available in pearl millet against the abiotic factors, thus less attention is given on salinity tolerance in pearl millet. In a comparative study, Hajor *et al.* (1996) revealed that pearl millet was far more tolerant than sorghum, suggesting the utilization of pearl millet in reclamation of soil with a moderate salinity.

The molecular basis of salinity tolerance has been investigated. Rao and McNeilly (1999) reported that salinity tolerance was under the control of genes with additive and non-additive effects. Abdel *et al.* (1997) studied the molecular basis of tolerance of salinity where SDS-PAGE revealed that in most of the very tolerant F_2 genotypes, the allele Acp1 could be considered as a putative molecular linked to salt tolerance in maize. The transfer of *E. coli* GutD gene into maize and regeneration of salt-tolerance transgenetic plants was studied. The synthesis and accumulation of sorbitol are detected in transgenetic maize crop plants and these have increased salt stress tolerance. Fungus Glomu mosseae was also reported to enhance the salinity tolerance (Feng *et al.*, 2000).

Recent research advances in salt tolerance of pearl millet are dedicated to the selection of resistant genotypes for salinity. However, further progress reveals that the genetic variability in relation to salinity tolerance is also an important tool for crop species to exploit saline habitats but other prevailing environmental factors may prevent the effective selection pressure for the evolution of resistant genotypes.

Stress Management

Seed priming

Ashraf *et al.* (2003 a, b) made an attempt to improve salt tolerance in pearl millet at the germination and vegetative stages by soaking the seeds in polyethylene glycol solution (PEG-8000, -0.672 MPa). They also reported that polyethylene glycol increased the final germination percentage, but not the germination rate under both saline and non-saline conditions. Jain and Sharma (2005) studied the effect of ABA, GA_3 and NaCl on seed germination under ABA (65%) and salt treatments, however, germination under GA_3 was 90 per cent.

Spray of chemicals

Application of ABA treatment on seedlings increased salt resistance and dry weight of maize seedlings increased in saline conditions due to enhanced osmotic adjustment and the exclusion of Na^+ from the shoot (Maiti *et al.*, 2007). The foliar spray of brassinosteroid (0.1 ppm), triacontanol (10 ppm), salicylic acid (100 ppm), NNA (40 ppm) and mepiquat chloride (50 ppm) on pearl millet increased grain yield, grain protein and sugar content, due to their significant effect on plant chlorophyll, soluble protein, nitrate reductase activity, indoleacetic acid oxidase activity and N uptake. Among the growth regulators, brassinosteroid was the most effective followed by triacontanol (Sivakumar *et al.*, 2001).

Fertilizer application

Sivakumar and Salaam (1999) reported that fertilizer application (30 kg P_2O_5 and 45 kg N/ha) in pearl millet increased the water use upto 7-14 per cent. Increased yield due to the application of fertilizer was accompanied by an increase in the water use efficiency (WUE). The beneficial effect of fertilizer application could be attributed to the rapid early growth of leaves that could contribute to reduction of soil evaporative losses and increased WUE. To overcome the effects of sodium salt stress, the application of higher doses of N fertilizers up to 120 kg/ha was found effective to increase the dry matter yield, plant height, protein content and uptake of nutrients in pearl millet grown under sodic soils (Singh *et al.*, 2014).

Future Thurst

However, further concentrated research efforts are needed to reveal the mechanisms of adaptation in relation to heat, drought and salt tolerance in pearl millet especially in arid and semi-arid conditions. There is a limited progress in genetic manipulation for developing abiotic stress tolerance in pearl millet. Thus, apart from

the conventional selection and breeding, the tissue culture, protoplast fusion and recombinanat DNA techniques may help in the improvement of pearl millet crop salinity tolerance.

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