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

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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), CO₂, 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 pearl 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), CO₂, 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
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
dramatic reduction in economic yield.

Moreover, soil moisture is the first most
important 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
development 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 immersed 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 discussed. 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°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°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°C, but not at 45°C. At constant exposure to 47°C, 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°C), 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°C 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. In contrast, 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) reported 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.
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

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### TABLE 1

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<tr>
<th>Stage</th>
<th>Effect</th>
<th>References</th>
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<tbody>
<tr>
<td>Seedling phase drought effect</td>
<td>1. During emergence and early seedling phase drought causes plant death/poor crop stand, resulting yield losses</td>
<td>Seetharam et al. (1984)</td>
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<td></td>
<td>2. After crop establishment (within seedling phase) drought</td>
<td>Carberry et al., (1985)</td>
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<td>secondary not development</td>
<td>Lahiri and Kerbanda (1965)</td>
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<td>Lahiri and Kumar (1966)</td>
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<td></td>
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<td>Stomph (1990)</td>
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<tr>
<td>Vegetative phase drought effect</td>
<td>4. Little/no adverse effect on grain yield</td>
<td>Mahalakshmi and Bidinger (1985)</td>
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<td></td>
<td>5. Delays flowering and increases number of ears/plant which</td>
<td>Mahalakshmi et al. (1985)</td>
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<td>compensate potential loss in main shoot</td>
<td>Bidinger et al. (1987)</td>
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<td></td>
<td>Raymond (1968)</td>
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<td>Egharveba (1977)</td>
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<td></td>
<td></td>
<td>Mahalakshmi et al. (1987)</td>
</tr>
<tr>
<td>Reproductive phase drought/terminal drought</td>
<td>6. Drought at flowering and grain filling reduces drastically grain yield and its components as it is most sensitive to drought</td>
<td>Mahalakshmi et al. (1985)</td>
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<td></td>
<td>Bidinger et al. (1987)</td>
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<td>Fussel et al. (1991)</td>
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<td>De Rouw and Winkel (1998)</td>
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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-Linzaraz 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 concentrated 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 greenhouse 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 necessarily 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 (Amon, 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 tolerant 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 restrict 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 potential 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 polyethylene glycol (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 polyethylene glycol.

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 GA3, 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 GA3. 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, phosphoglucomutase 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 vacuolar 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) studied the effects of increased salinity (NaCl + CaCl) on seedlings of pearlmlillet. They reported that the genotypes exhibiting lower mortality had a high root weight, shoot:root ratio and the greater plant height. Sufficient genetic variation 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 variability for growth and yield attributes 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 Na2CO3 and reported considerable variation in pearl millet for salt growth. They also revealed significant differences among genotypes on the basis of salinity threshold Ct, the Na2CO3 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). Therefore, 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 $\text{Na}^+$ and consequently the $\text{Na}/\text{K}$ ratio increased significantly in salt tolerance sorghum salinised treatments. Thus, genotypes tolerant to soil salinity showed a higher $\text{Na}^+/\text{K}^+$ ratio. Therefore, osmotic adjustment, ion inclusion and the proportion of $\text{Na}^+/\text{K}^+$ 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 $\text{F}_{1}$ genotypes, the allele $\text{Acp1}$ could be considered as a putative molecular linked to salt tolerance in maize. The transfer of $\text{E. coli}$ 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 Glomus 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 $\text{ABA}$, $\text{GA}_3$ and $\text{NaCl}$ on seed germination under $\text{ABA}$ (65%) and salt treatments, however, germination under $\text{GA}_3$ was 90 per cent.

**Spray of chemicals**

Application of $\text{ABA}$ 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 $\text{Na}^+$ 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 mepipquat 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 $\text{P}_2\text{O}_5$ and 45 kg $\text{N}$/ha) in pearl millet increased the water use up to 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 $\text{N}$ 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 recombinant DNA techniques may help in the improvement of pearl millet crop salinity tolerance.

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