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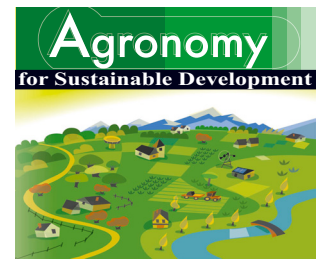
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Review article

Plant drought stress: effects, mechanisms and management

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Abstract – Scarcity of water is a severe environmental constraint to plant productivity. Drought-induced loss in crop yield probably exceeds losses from all other causes, since both the severity and duration of the stress are critical. Here, we have reviewed the effects of drought stress on the growth, phenology, water and nutrient relations, photosynthesis, assimilate partitioning, and respiration in plants. This article also describes the mechanism of drought resistance in plants on a morphological, physiological and molecular basis. Various management strategies have been proposed to cope with drought stress. Drought stress reduces leaf size, stem extension and root proliferation, disturbs plant water relations and reduces water-use efficiency. Plants display a variety of physiological and biochemical responses at cellular and whole-organism levels towards prevailing drought stress, thus making it a complex phenomenon. CO₂ assimilation by leaves is reduced mainly by stomatal closure, membrane damage and disturbed activity of various enzymes, especially those of CO₂ fixation and adenosine triphosphate synthesis. Enhanced metabolite flux through the photorespiratory pathway increases the oxidative load on the tissues as both processes generate reactive oxygen species. Injury caused by reactive oxygen species to biological macromolecules under drought stress is among the major deterrents to growth. Plants display a range of mechanisms to withstand drought stress. The major mechanisms include curtailed water loss by increased diffusive resistance, enhanced water uptake with prolific and deep root systems and its efficient use, and smaller and succulent leaves to reduce the transpirational loss. Among the nutrients, potassium ions help in osmotic adjustment; silicon increases root endodermal silicification and improves the cell water balance. Low-molecular-weight osmolytes, including glycinebetaine, proline and other amino acids, organic acids, and polyols, are crucial to sustain cellular functions under drought. Plant growth substances such as salicylic acid, auxins, gibberellins, cytokinin and abscisic acid modulate the plant responses towards drought. Polyamines, citrulline and several enzymes act as antioxidants and reduce the adverse effects of water deficit. At molecular levels several drought-responsive genes and transcription factors have been identified, such as the dehydration-responsive element-binding gene, aquaporin, late embryogenesis abundant proteins and dehydrins. Plant drought tolerance can be managed by adopting strategies such as mass screening and breeding, marker-assisted selection and exogenous application of hormones and osmoprotectants to seed or growing plants, as well as engineering for drought resistance.

drought response / stomatal oscillation / osmoprotectants / hormones / stress proteins / drought management / CO₂

1. INTRODUCTION

Faced with scarcity of water resources, drought is the single most critical threat to world food security. It was the catalyst of the great famines of the past. Because the world's water supply is limiting, future food demand for rapidly increasing population pressures is likely to further aggravate the effects of drought (Somerville and Briscoe, 2001). The severity of drought is unpredictable as it depends on many factors such as occurrence and distribution of rainfall, evaporative demands and moisture storing capacity of soils (Wery et al., 1994).

Investigations carried out in the past provide considerable insights into the mechanism of drought tolerance in

plants at molecular level (Hasegawa et al., 2000). Three main mechanisms reduce crop yield by soil water deficit: (i) reduced canopy absorption of photosynthetically active radiation, (ii) decreased radiation-use efficiency and (iii) reduced harvest index (Earl and Davis, 2003). The reproducibility of drought stress treatments is very cumbersome, which significantly impedes research on plant drought tolerance. A slow pace in revealing drought tolerance mechanisms has hampered both traditional breeding efforts and use of modern genetics approaches in the improvement of drought tolerance of crop plants (Xiong et al., 2006). Although plant responses to drought are relatively well known, plant performance under a more complex environment where multiple stresses co-occur is fragmentary. That is why the plants have to respond

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simultaneously to multiple stresses, e.g. drought, excessive light and heat, which may coincide in the field. These kinds of investigations are usually not predictable from single factor studies (Zhou et al., 2007).

It is imperative to improve the drought tolerance of crops under the changing circumstances. Currently, there are no economically viable technological means to facilitate crop production under drought. However, development of crop plants tolerant to drought stress might be a promising approach, which helps in meeting the food demands. Development of crops for enhanced drought resistance, among other things, requires the knowledge of physiological mechanisms and genetic control of the contributing traits at different plant developmental stages. Valuable work has been done on drought tolerance in plants. Ingram and Bartels (1996) more than a decade ago elegantly reviewed those appreciable efforts. More recent reviews deal with specific aspects of plant drought tolerance (Penna, 2003; Reddy et al., 2004; Agarwal et al., 2006). This review encompasses an overview of the current work reported on some effects and mechanisms of drought tolerance in higher plants and important management strategies to overcome the drought effects, mainly on field crops.

2. EFFECTS OF DROUGHT ON PLANTS

The effects of drought range from morphological to molecular levels and are evident at all phenological stages of plant growth at whatever stage the water deficit takes place. An account of various drought stress effects and their extent is elaborated below.

2.1. Crop growth and yield

The first and foremost effect of drought is impaired germination and poor stand establishment (Harris et al., 2002). Drought stress has been reported to severely reduce germination and seedling stand (Kaya et al., 2006). In a study on pea, drought stress impaired the germination and early seedling growth of five cultivars tested (Okcu et al., 2005). Moreover, in alfalfa (*Medicago sativa*), germination potential, hypocotyl length, and shoot and root fresh and dry weights were reduced by polyethylene glycol-induced water deficit, while the root length was increased (Zeid and Shedeed, 2006). However, in rice, drought stress during the vegetative stage greatly reduced the plant growth and development (Fig. 1; Tripathy et al., 2000; Manikavelu et al., 2006).

Growth is accomplished through cell division, cell enlargement and differentiation, and involves genetic, physiological, ecological and morphological events and their complex interactions. The quality and quantity of plant growth depend on these events, which are affected by water deficit (Fig. 2). Cell growth is one of the most drought-sensitive physiological processes due to the reduction in turgor pressure (Taiz and Zeiger, 2006). Under severe water deficiency, cell elongation of higher plants can be inhibited by interruption of water flow from the xylem to the surrounding elongating cells (Nonami, 1998).



Figure 1. Effect of drought stress on the vegetative growth of rice cv. IR64. Both the plants were grown under well-watered conditions up to 20 days following emergence. One pot was submitted to progressive soil drying (drought stress). The afternoon before the drought, all pots were fully watered (to saturation). After draining overnight, the pots were enclosed around the stem to prevent direct soil evaporation. A small tube was inserted for re-watering pots. The decrease in soil moisture was controlled by partial re-watering of the stressed pots to avoid a quicker imposition of stress and to homogenize the development of drought stress. A well-watered control pot was maintained at the initial target weight by adding the daily water loss back to the pot. This figure shows the plants 20 days after imposition of drought stress.

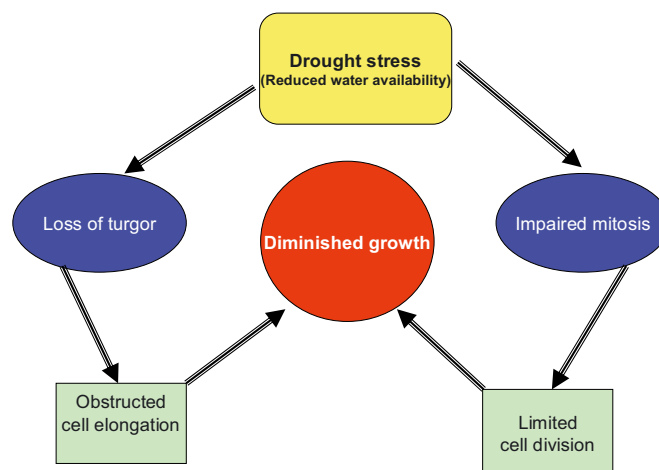


Figure 2. Description of possible mechanisms of growth reduction under drought stress. Under drought stress conditions, cell elongation in higher plants is inhibited by reduced turgor pressure. Reduced water uptake results in a decrease in tissue water contents. As a result, turgor is lost. Likewise, drought stress also trims down the photo-assimilation and metabolites required for cell division. As a consequence, impaired mitosis, cell elongation and expansion result in reduced growth.

Table I. Economic yield reduction by drought stress in some representative field crops.

Crop	Growth stage	Yield reduction	References
Barley	Seed filling	49–57%	Samarah (2005)
Maize	Grain filling	79–81%	Monneveux et al. (2005)
Maize	Reproductive	63–87%	Kamara et al. (2003)
Maize	Reproductive	70–47%	Chapman and Edmeades (1999)
Maize	Vegetative	25–60%	Atteya et al. (2003)
Maize	Reproductive	32–92%	Atteya et al. (2003)
Rice	Reproductive (mild stress)	53–92%	Lafitte et al. (2007)
Rice	Reproductive (severe stress)	48–94%	Lafitte et al. (2007)
Rice	Grain filling (mild stress)	30–55%	Basnayake et al. (2006)
Rice	Grain filling (severe stress)	60%	Basnayake et al. (2006)
Rice	Reproductive	24–84%	Venuprasad et al. (2007)
Chickpea	Reproductive	45–69%	Nayyar et al. (2006)
Pigeonpea	Reproductive	40–55%	Nam et al. (2001)
Common beans	Reproductive	58–87%	Martínez et al. (2007)
Soybean	Reproductive	46–71%	Samarah et al. (2006)
Cowpea	Reproductive	60–11%	Ogbonnaya et al. (2003)
Sunflower	Reproductive	60%	Mazahery-Laghab et al. (2003)
Canola	Reproductive	30%	Sinaki et al. (2007)
Potato	Flowering	13%	Kawakami et al. (2006)

Impaired mitosis, cell elongation and expansion result in reduced plant height, leaf area and crop growth under drought (Nonami, 1998; Kaya et al., 2006; Hussain et al., 2008).

Many yield-determining physiological processes in plants respond to water stress. Yield integrates many of these physiological processes in a complex way. Thus, it is difficult to interpret how plants accumulate, combine and display the ever-changing and indefinite physiological processes over the entire life cycle of crops. For water stress, severity, duration and timing of stress, as well as responses of plants after stress removal, and interaction between stress and other factors are extremely important (Plaut, 2003). For instance, water stress applied at pre-anthesis reduced time to anthesis, while at post-anthesis it shortened the grain-filling period in triticale genotypes (Estrada-Campuzano et al., 2008). In barley (*Hordeum vulgare*), drought stress reduced grain yield by reducing the number of tillers, spikes and grains per plant and individual grain weight. Post-anthesis drought stress was detrimental to grain yield regardless of the stress severity (Samarah, 2005).

Drought-induced yield reduction has been reported in many crop species, which depends upon the severity and duration of the stress period (Tab. I). In maize, water stress reduced yield by delaying silking, thus increasing the anthesis-to-silking interval. This trait was highly correlated with grain yield, specifically ear and kernel number per plant (Cattivelli et al., 2008). Following heading, drought had little effect on the rate of kernel filling in wheat, but its duration (time from fertilization to maturity) was shortened and dry weight reduced at maturity (Wardlaw and Willenbrink, 2000). Drought stress in soybean reduced total seed yield and the branch seed yield (Frederick et al., 2001). In pearl millet (*Pennisetum glaucum*), co-mapping of the harvest index and panicle harvest index with grain yield revealed that greater drought tolerance was achieved by greater partitioning of dry matter from stover to grains (Yadav et al., 2004).

Drought at flowering commonly results in barrenness. A major cause of this, though not the only one, was a reduction in assimilate flux to the developing ear below some threshold level necessary to sustain optimal grain growth (Yadav et al., 2004). Moisture deficit reduced cotton (*Gossypium hirsutum*) lint yield, although the timing, duration, severity and speed of development undoubtedly had pivotal roles in determining how the plant responded to moisture deficit. Lint yield was generally reduced due to reduced boll production because of fewer flowers and greater boll abortions when the stress intensity was greater during reproductive growth (Pettigrew, 2004).

Grain filling in cereals is a process of starch biosynthesis from simple carbohydrates. It is believed that four enzymes play key roles in this process: sucrose synthase, adenosine diphosphate-glucose-pyrophosphorylase, starch synthase and starch branching enzyme (Taiz and Zeiger, 2006). Decline in the rate of grain growth resulted from reduced sucrose synthase activity, while cessation of growth resulted from inactivation of adenosine diphosphate-glucose-pyrophosphorylase in the water-stressed wheat (Ahmadi and Baker, 2001). Water deficit during pollination increased the frequency of kernel abortion in maize (*Zea mays*). Under water stress, diminished grain set and kernel growth in wheat and a decreased rate of endosperm cell division was associated with elevated levels of abscisic acid in maize (Morgan, 1990; Ober et al., 1991). In pigeonpea, drought stress coinciding with the flowering stage reduced seed yield by 40–55% (Nam et al., 2001). In rice, on the other hand, water stress imposed during the grain-filling period enhanced remobilization of pre-stored carbon reserves to grains and accelerated grain filling (Yang et al., 2001). In summary, prevailing drought reduces plant growth and development, leading to hampered flower production and grain filling, and thus smaller and fewer grains. A reduction in grain filling occurs due to a reduction in the assimilate partitioning and activities of sucrose and starch synthesis enzymes.

2.2. Water relations

Relative water content, leaf water potential, stomatal resistance, rate of transpiration, leaf temperature and canopy temperature are important characteristics that influence plant water relations. Relative water content of wheat leaves was higher initially during leaf development and decreased as the dry matter accumulated and leaf matured (Siddique et al., 2001). Obviously, water-stressed wheat and rice plants had lower relative water content than non-stressed ones. Exposure of these plants to drought stress substantially decreased the leaf water potential, relative water content and transpiration rate, with a concomitant increase in leaf temperature (Siddique et al., 2001). A conservative influence of decreased stomatal conductance in non-irrigated plants was negated by a leaf-to-air vapor pressure difference caused by the associated higher leaf temperature. Transpiration rates were similar in both treatments and the lower total water use of the non-irrigated stand resulted entirely from a smaller leaf area index (Craufurad et al., 2000).

Nerd and Nobel (1991) reported that during drought stress, total water contents of *Opuntia ficus-indica* cladode were decreased by 57%. The water-storage parenchyma of the cladodes lost a greater fraction of water than the chlorenchyma, and thus showed a lower turgor potential. In another study on *Hibiscus rosa-sinensis*, relative water content, turgor potential, transpiration, stomatal conductance and water-use efficiency were decreased under drought stress (Egilla et al., 2005).

The ratio between dry matter produced and water consumed is termed as water-use efficiency at the whole-plant level (Monclus et al., 2005). Abbate et al. (2004) concluded that under limited supply, water-use efficiency of wheat was greater than in well-watered conditions. They correlated this higher water-use efficiency with stomatal closure to reduce the transpiration. In another study on clover (*Trifolium alexandrinum*), water-use efficiency was increased due to lowered water loss under drought stress, primarily by decreased transpiration rate and leaf area, and relatively lesser reduction in yield (Lazaridou and Koutroubas, 2004). Also, in *Pinus ponderosa* and *Artemisia tridentata*, drought stress did not reduce the water-use efficiency; rather, it was increased, mainly due to a rapid decrease in stomatal conductance with increasing water deficit (DeLucia et al., 1989). Lazaridou et al. (2003) further reported that leucern (*Medicago sativa*) grown under drought had greater water-use efficiency than that under irrigated conditions, for the same leaf water potential. However, in potato, early season drought stress significantly minimized the water-use efficiency, leading to greatly decreased growth and biomass accumulation (Costa et al., 1997).

In fact, although components of plant water relations are affected by reduced availability of water, stomatal opening and closing is more strongly affected. Moreover, change in leaf temperature may be an important factor in controlling leaf water status under drought stress. Drought-tolerant species maintain water-use efficiency by reducing the water loss. However, in the events where plant growth was hindered to a greater extent, water-use efficiency was also reduced significantly.

2.3. Nutrient relations

Decreasing water availability under drought generally results in limited total nutrient uptake and their diminished tissue concentrations in crop plants. An important effect of water deficit is on the acquisition of nutrients by the root and their transport to shoots. Lowered absorption of the inorganic nutrients can result from interference in nutrient uptake and the unloading mechanism, and reduced transpirational flow (Garg, 2003; McWilliams, 2003). However, plant species and genotypes of a species may vary in their response to mineral uptake under water stress. In general, moisture stress induces an increase in N, a definitive decline in P and no definitive effects on K (Garg, 2003).

Transpiration is inhibited by drought, as shown for beech (Peuke et al., 2002), but this may not necessarily affect nutrient uptake in a similar manner. Influence of drought on plant nutrition may also be related to limited availability of energy for assimilation of $\text{NO}_3^-/\text{NH}_4^+$, PO_4^{3-} and SO_4^{2-} : they must be converted in energy-dependent processes before these ions can be used for growth and development of plants (Grossman and Takahashi, 2001).

As nutrient and water requirements are closely related, fertilizer application is likely to increase the efficiency of crops in utilizing available water. This indicates a significant interaction between soil moisture deficits and nutrient acquisition. Studies show a positive response of crops to improved soil fertility under arid and semi-arid conditions. Currently, it is evident that crop yields can be substantially improved by enhancing the plant nutrient efficiency under limited moisture supply (Garg, 2003). It was shown that N and K uptake was hampered under drought stress in cotton (McWilliams, 2003). Likewise, P and PO_4^{3-} contents in the plant tissues diminished under drought, possibly because of lowered PO_4^{3-} mobility as a result of low moisture availability (Peuke and Rennenberg, 2004). In drought-treated sunflower, the degree of stomatal opening of K^+ -applied plants initially indicated quicker decline. However, at equally low soil water potential, diffusive resistance in the leaves of K^+ -applied plants remained lower than those receiving no K^+ (Lindhauer et al., 2007). In summary, drought stress reduces the availability, uptake, translocation and metabolism of nutrients. A reduced transpiration rate due to water deficit reduces the nutrient absorption and efficiency of their utilization.

2.4. Photosynthesis

A major effect of drought is reduction in photosynthesis, which arises by a decrease in leaf expansion, impaired photosynthetic machinery, premature leaf senescence and associated reduction in food production (Wahid and Rasul, 2005). When stomatal and non-stomatal limitations to photosynthesis are compared, the former can be quite small. This implies that other processes besides CO_2 uptake are being damaged. The role of drought-induced stomatal closure, which limits CO_2 uptake by leaves, is very important. In such events, restricted

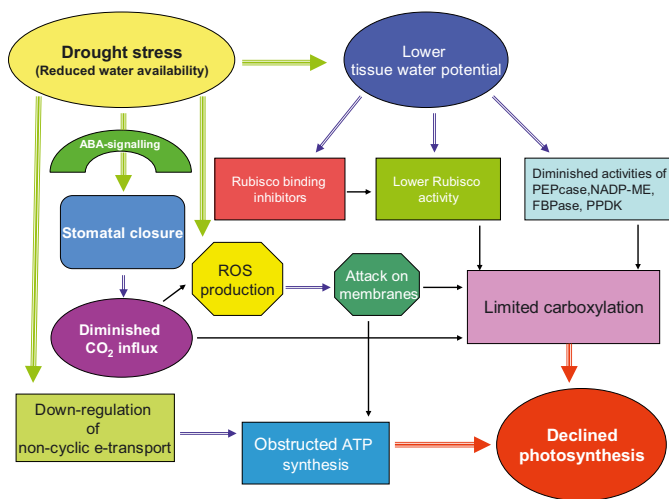


Figure 3. Photosynthesis under drought stress. Possible mechanisms in which photosynthesis is reduced under stress. Drought stress disturbs the balance between the production of reactive oxygen species and the antioxidant defense, causing accumulation of reactive oxygen species, which induces oxidative stress. Upon reduction in the amount of available water, plants close their stomata (plausibly via ABA signaling), which decreases the CO₂ influx. Reduction in CO₂ not only reduces the carboxylation directly but also directs more electrons to form reactive oxygen species. Severe drought conditions limit photosynthesis due to a decrease in the activities of ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco), phosphoenolpyruvate carboxylase (PEPCase), NADP-malic enzyme (NADP-ME), fructose-1, 6-bisphosphatase (FBPase) and pyruvate orthophosphate dikinase (PPDK). Reduced tissue water contents also increase the activity of Rubisco binding inhibitors. Moreover, non-cyclic electron transport is down-regulated to match the reduced requirements of NADPH production and thus reduces the ATP synthesis. ROS: reactive oxygen species.

CO₂ availability could possibly lead to increased susceptibility to photo-damage (Cornic and Massacci, 1996).

Drought stress produced changes in photosynthetic pigments and components (Anjum et al., 2003), damaged photosynthetic apparatus (Fu J. and Huang, 2001) and diminished activities of Calvin cycle enzymes, which are important causes of reduced crop yield (Monakhova and Chernyadèv, 2002). Another important effect that inhibits the growth and photosynthetic abilities of plants is the loss of balance between the production of reactive oxygen species and the antioxidant defense (Fu J. and Huang, 2001; Reddy et al., 2004), causing accumulation of reactive oxygen species which induces oxidative stress in proteins, membrane lipids and other cellular components (Fig. 3). Some important components of photosynthesis affected by drought are discussed below.

2.4.1. Stomatal oscillations

The first response of virtually all plants to acute water deficit is the closure of their stomata to prevent the transpirational water loss (Mansfield and Atkinson, 1990). This

may result in response to either a decrease in leaf turgor and/or water potential (Ludlow and Muchow, 1990) or to a low-humidity atmosphere (Maroco et al., 1997). The debate as to whether drought mainly limits photosynthesis through stomatal closure or metabolic impairment has continued for a long time (Sharkey, 1990; Tezara et al., 1999). During the last decade, stomatal closure was generally accepted to be the main determinant for decreased photosynthesis under mild to moderate drought (Cornic and Massacci, 1996; Yokota et al., 2002).

When the amount of available soil water is moderately or severely limiting, the first option for plants is to close stomata (Cornic and Massacci, 1996). This decreases the inflow of CO₂ into the leaves and spares more electrons for the formation of active oxygen species (Fig. 3). As the rate of transpiration decreases, the amount of heat that can be dissipated increases (Yokota et al., 2002). Various experiments have shown that stomatal responses are often more closely linked to soil moisture content than to leaf water status. This suggested that stomata respond to chemical signals, e.g. abscisic acid, produced by dehydrating roots (Fig. 3), whilst leaf water status is kept constant (Morgan, 1990; Taylor, 1991; Turner et al., 2001). Environmental conditions that enhance the rate of transpiration also increase the pH of leaf sap, which can promote abscisic acid accumulation and concomitantly diminish stomatal conductance. Increased cytokinin concentration in the xylem sap promotes stomatal opening directly and affects the sensitivity of stomata towards abscisic acid (Wilkinson and Davies, 2002).

Comparing results from different studies is complex due to interspecific differences in the response of stomatal conductance and photosynthesis to leaf water potential and/or relative water content; the parameters most often used to assess the degree of drought (Cornic and Massacci, 1996). It is clear that stomata close progressively as drought progresses, followed by a parallel decline in net photosynthesis. However, stomatal conductance is not controlled by soil water availability alone, but by a complex interaction of intrinsic and extrinsic factors.

2.4.2. Photosynthetic enzymes

Very severe drought conditions limit photosynthesis due to a decline in Rubisco activity (Bota et al., 2004). The activity of the photosynthetic electron transport chain is finely tuned to the availability of CO₂ in the chloroplast and change in photosystem II under drought conditions (Loreto et al., 1995). Dehydration results in cell shrinkage, and consequently a decline in cellular volume. This makes cellular contents more viscous. Therefore, an increase in the probability of protein-protein interaction leads to their aggregation and denaturation (Hoekstra et al., 2001). Increased concentration of solutes, leading to increased viscosity of the cytoplasm, may become toxic and may be deleterious to the functioning of enzymes, including those of the photosynthetic machinery (Hoekstra et al., 2001).

The level of Rubisco in leaves is controlled by the rate of synthesis and degradation. Even under drought stress the Rubisco holoenzyme is relatively stable with a half-life of

several days (Hoekstra et al., 2001). However, drought stress showed a rapid diminution in the abundance of Rubisco small subunit transcripts, which indicated its decreased synthesis (Vu et al., 1999). Rubisco activity is modulated in vivo either by reaction with CO₂ and Mg²⁺ to carbamylate a lysine residue in the catalytic site, or by binding inhibitors within the catalytic site (Fig. 3). Such a binding either blocks activity or the carbamylation of the lysine residue, which is essential for activity. At night, 2-carboxyarabinitol-1-phosphate is formed in many species, which binds tightly to Rubisco, inhibiting catalytic activity. It is reported that tight-binding inhibitors can decrease Rubisco activity in the light. In tobacco (*Nicotiana tabacum*), decrease in Rubisco activity under drought stress was not a primary result of changes in activation by CO₂ and Mg²⁺, and was rather due to the presence of tight-binding inhibitors (Parry et al., 2002). A rapid decline in photosynthesis under drought was accompanied by decreased maximum velocity of ribulose-1, 5-bisphosphate carboxylation by Rubisco, speed of ribulose-1, 5-bisphosphate regeneration, Rubisco and stromal fructose bis-phosphatase activities, and the quantum efficiency of photosystem II in higher plants (Reddy et al., 2004; Zhou et al., 2007). Moreover, under severe drought, carboxylation efficiency by Rubisco was greatly declined, and it acted more as oxygenase than carboxylase (Fig. 3).

During water stress, activities of the phosphoenolpyruvate carboxylase, nicotinamide adenine dinucleotide phosphate-malic enzyme, Rubisco, fructose-1, 6-bisphosphatase and pyruvate orthophosphate dikinase decreased linearly with lowered leaf water potential (Fig. 3). Pyruvate orthophosphate dikinase activities were decreased 9.1 times during water stress; a much greater reduction than other enzymes, which were from 2 to 4 times, suggesting that pyruvate orthophosphate dikinase is very likely to be the limiting enzyme to photosynthesis under water stress (Du et al., 1996).

2.4.3. Adenosine triphosphate synthesis

There is a long-standing controversy as to whether drought mainly limits photosynthesis through stomatal closure (Cornic and Massacci, 1996) or by metabolic impairment (Tezara et al., 1999). Evidence that impaired adenosine triphosphate synthesis is the main factor limiting photosynthesis even under mild drought has further stimulated the debate (Lawlor and Cornic, 2002). It is reported that impaired photophosphorylation and adenosine triphosphate synthesis are the main factors limiting photosynthesis even under mild drought (Tezara et al., 1999).

Under drought stress, production of limited nicotinamide adenine dinucleotide phosphate maintains the continuation of electron transport, although the status of the reductant may be high even when the fluxes are small, leading to a more increased demand than supply. Under drought stress, non-cyclic electron transport is down-regulated to match the requirements of decreased nicotinamide adenine dinucleotide phosphate production and cyclic electron transport is activated. This generates a proton gradient that induces the protective process of high-energy-state quenching (Golding and Johnson,

2003). Support for this model came from the isolation of a mutant deficient in high-energy-state quenching that lacked cyclic electron transport (Munekage et al., 2002). Support for cyclic electron transport under drought also came from non-steady-state measurements (Cornic et al., 2000).

Dissipation mechanisms of excess photon energy under water stress were studied in *ndhB*-inactivated tobacco (cv. Xanthi) mutants, impaired in reduced nicotinamide adenine dinucleotide phosphate dehydrogenase-dependent cyclic electron flow around photosystem I. The relative water content and net CO₂ assimilation was reduced to 30% and almost zero after an 11-day water stress regime in the mutant and wild-type plants, respectively. A decline in photosystem II activity (~75%), and an increase in malondialdehyde (~45%), an estimate of lipid peroxidation, were found in both the plant groups when subjected to water stress. Thus, a deficiency in reduced nicotinamide adenine dinucleotide phosphate dehydrogenase-dependent cyclic electron flow around photosystem I did not lead to oxidative damage because the mutant compensated for this deficiency by activating alternative dissipating routes of excess photon energy such as up-regulation of ferredoxin-dependent cyclic electron flow around photosystem I and enhanced accumulation of α -tocopherol (α -toc) quinine (Munné-Bosch et al., 2005).

In fact, the activities of the enzymes of carbon assimilation and those involved in adenosine triphosphate synthesis are retarded and sometimes inhibited depending upon the extent of available moisture. Of these, Rubisco, which shows dual functions, acts as oxygenase under water-limiting conditions; and therefore limited CO₂ fixation is noticed.

2.5. Assimilate partitioning

Assimilate translocation to reproductive sinks is vital for seed development. Seed set and filling can be limited by availability or utilization, i.e., assimilate source or sink limitation, respectively (Asch et al., 2005). Drought stress frequently enhances allocation of dry matter to the roots, which can enhance water uptake (Leport et al., 2006). De Souza and Da Silv (1987), while analyzing the partitioning and distribution of photo-assimilates in annual and perennial cotton under drought stress, reported that the root-to-shoot dry matter ratio was high in perennial cotton, thereby showing a preferential accumulation of starch and dry matter in roots as an adaptation to drought. Thus, perennial cotton apparently owed its drought resistance to the partitioning of assimilates that favored starch accumulation and growth of the root system. The export rate of sucrose from source to sink organs depends upon the current photosynthetic rate and the concentration of sucrose in the leaves (Komor, 2000). Drought stress decreases the photosynthetic rate, and disrupts the carbohydrate metabolism and level of sucrose in leaves that spills over to a decreased export rate. This is presumably due to drought stress-induced increased activity of acid invertase (Kim et al., 2000). Limited photosynthesis and sucrose accumulation in the leaves may hamper the rate of sucrose export to the sink organs and ultimately affect the reproductive development.

Apart from source limitation, the capacity of the reproductive sinks to utilize the incoming assimilates is also affected under drought stress and may also play a role in regulating reproductive abortion (Zinselmeier et al., 1999). Drought-induced carbohydrate deprivation, enhanced endogenous abscisic acid concentration, and an impaired ability to utilize the incoming sucrose by the reproductive sinks are potential factors contributing to seed abortion in grain crops (Setter et al., 2001). A reduced acid invertase activity can arrest the development of reproductive tissues due to improper phloem unloading (Goetz et al., 2001). In addition, drought stress may inhibit important functions of vacuolar invertase-mediated sucrose hydrolysis and osmotic potential modulation. In drought-stressed maize, a low invertase activity in the young ovaries lowers the ratio of hexoses to sucrose. This may inhibit cell division in the developing embryo/endosperm, resulting in weak sink intensity, and may ultimately lead to fruit abortion (Andersen et al., 2002).

In summary, drought stress not only limits the size of the source and sink tissues but the phloem loading, assimilate translocation and dry matter partitioning are also impaired. However, the extent of effects varies with the plant species, stage, duration and severity of drought.

2.6. Respiration

Drought tolerance is a cost-intensive phenomenon, as a considerable quantity of energy is spent to cope with it. The fraction of carbohydrate that is lost through respiration determines the overall metabolic efficiency of the plant (Davidson et al., 2000). The root is a major consumer of carbon fixed in photosynthesis and uses it for growth and maintenance, as well as dry matter production (Lambers et al., 1996). Plant growth and developmental processes as well as environmental conditions affect the size of this fraction (i.e. utilized in respiration). However, the rate of photosynthesis often limits plant growth when soil water availability is reduced (Huang and Fu, 2000). A negative carbon balance can occur as a result of diminished photosynthetic capacity during drought, unless simultaneous and proportionate reductions in growth and carbon consumption take place.

In wheat, depending on the growth stage, cultivar and nutritional status, more than 50% of the daily accumulated photosynthates were transported to the root, and around 60% of this fraction was respired (Lambers et al., 1996). Drought-sensitive spring wheat (Longchun, 8139-2) used a relatively greater amount of glucose to absorb water, especially in severe drought stress (Liu et al., 2004). Severe drought reduced the shoot and root biomass, photosynthesis and root respiration rate. Limited root respiration and root biomass under severe soil drying can improve growth and physiological activity of drought-tolerant wheat, which is advantageous over a drought-sensitive cultivar in arid regions (Liu and Li, 2005).

There are two mitochondrial electron transport pathways from ubiquinone to oxygen in plants. The alternative pathway branches from the cytochrome pathway and donates electrons to oxygen directly by alternative oxidase (Moore and Siedow,

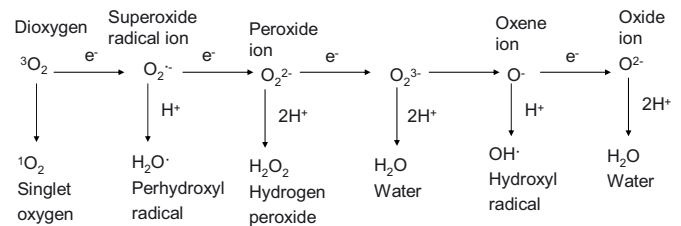


Figure 4. Generation of reactive oxygen species by energy transfer or sequential univalent reduction of ground state triplet oxygen (Apel and Hirt, 2004; reproduced with permission).

1991). The alternative pathway is not coupled with adenosine triphosphate synthesis, but can be induced in response to stress or inhibition of the main electron transfer pathway (Wagner and Moore, 1997). When plants are exposed to drought stress, they produce reactive oxygen species, which damage membrane components (Blokchina et al., 2003). In this regard, alternative oxidase activity could be useful in maintaining normal levels of metabolites and reduce reactive oxygen species production during stress. Oxygen uptake by sugar beet was characterized by a high rate, distinct cytochrome oxidase-dependent terminal oxidation and up to 80% inhibition of respiration in the presence of 0.5 mM potassium cyanide. At an early drought stage (10 days), a decrease in the activity of the cytochrome-mediated oxidation pathway was largely counterbalanced by the activation of mitochondrial alternative oxidase, whereas long-term dehydration of plants was accompanied by activation of additional oxidative systems insensitive to both potassium cyanide and salicylhydroxamate (Shugaeva et al., 2007). In summary, water deficit in the rhizosphere leads to an increased rate of root respiration, leading to an imbalance in the utilization of carbon resources, reduced production of adenosine triphosphate and enhanced generation of reactive oxygen species.

2.7. Oxidative damage

Exposure of plants to certain environmental stresses quite often leads to the generation of reactive oxygen species, including superoxide anion radicals ($\text{O}_2^{\cdot-}$), hydroxyl radicals (OH \cdot), hydrogen peroxide (H_2O_2), alkoxy radicals (RO \cdot) and singlet oxygen (O_2^1) (Munné-Bosch and Penuelas, 2003). Reactive oxygen species may react with proteins, lipids and deoxyribonucleic acid, causing oxidative damage and impairing the normal functions of cells (Foyer and Fletcher, 2001). Many cell compartments produce reactive oxygen species; of these, chloroplasts are a potentially important source because excited pigments in thylakoid membranes may interact with O_2 to form strong oxidants such as $\text{O}_2^{\cdot-}$ or O_2^1 (Niyogi, 1999; Reddy et al., 2004). Further downstream reactions produce other reactive oxygen species such as H_2O_2 and OH^{\cdot} (Fig. 4). The interaction of O_2 with reduced components of the electron transport chain in mitochondria can lead to reactive oxygen species formation (Möller, 2001), and peroxisomes produce H_2O_2 when

glycolate is oxidized into glyoxylic acid during photorespiration (Fazeli et al., 2007).

Mechanisms for the generation of reactive oxygen species in biological systems are represented by both non-enzymatic and enzymatic reactions. The partition between these two pathways under oxygen deprivation stress can be regulated by the oxygen concentration in the system. In non-enzymatic reactions, electron O_2 reduction can occur at higher oxygen concentrations (Apel and Hirt, 2004). At very low O_2 concentrations, plant terminal oxidases and the formation of reactive oxygen species via the mitochondrial electron transport chain still remain functional. Among enzymatic sources of reactive oxygen species, xanthine oxidase, an enzyme responsible for the initial activation of O_2 , should be mentioned. The electron donor xanthine oxidase can use xanthine, hypoxanthine or acetaldehyde, while the latter has been shown to accumulate under oxygen deprivation (Pfister-Sieber and Braendle, 1994; Apel and Hirt, 2004). This can represent a possible source for hypoxia-stimulated reactive oxygen species production (Fig. 4). The next enzymatic step is the dismutation of the superoxide anion by superoxide dismutase to yield H_2O_2 (Lamb and Dixon, 1997). Peroxidases and catalases also play an important role in the fine regulation of reactive oxygen species in the cell through activation and deactivation of H_2O_2 (Sairam et al., 2005). Several apoplasmic enzymes may also generate reactive oxygen species under normal and stressful conditions. Other oxidases, responsible for the two-electron transfer to dioxygen (amino acid oxidases and glucose oxidase) can contribute to H_2O_2 accumulation (Apel and Hirt, 2004).

Reactive oxygen species are formed as by-products in the electron transport chains of chloroplasts (Apel and Hirt, 2004), mitochondria and the plasma membrane (Sairam et al., 2005). The plant mitochondrial electron transport chain, with its redox-active electron carriers, is considered as the most probable candidate for intracellular reactive oxygen species formation. Mitochondria can produce reactive oxygen species due to the electron leakage at the ubiquinone site – the ubiquinone:cytochrome *b* region (Gille and Nohl, 2001) – and at the matrix side of complex I (NADH dehydrogenase) (Möller, 2001).

Superoxide radical and its reduction product H_2O_2 are potentially toxic compounds, and can also combine by the Haber-Weiss reaction to form the highly toxic OH^- (Sairam et al., 1998). Many reports show the deleterious effects of reactive oxygen species, whose production is stimulated under water stress (Blokhina et al., 2003). Reactive oxygen species cause lipid peroxidation, and consequently membrane injuries, protein degradation and enzyme inactivation (Sairam et al., 2005). Oxidative stress may also cause protein oxidation, with a loss of enzyme activity and the formation of protease-resistant cross-linked aggregates (Berlett and Stadtman, 1997). Oxidatively-damaged proteins accumulate in pea leaves subjected to moderate water stress (Moran et al., 1994).

Overall, the production of reactive oxygen species is linear with the severity of drought stress, which leads to enhanced peroxidation of membrane lipids and degradation of nucleic acids, and both structural and functional proteins.

Various organelles including chloroplasts, mitochondria and peroxisomes are the seats as well as first target of reactive oxygen species produced under drought stress.

3. DROUGHT RESISTANCE MECHANISMS

Plants respond and adapt to and survive under drought stress by the induction of various morphological, biochemical and physiological responses. Drought tolerance is defined as the ability to grow, flower and display economic yield under suboptimal water supply. Drought stress affects the water relations of plants at cellular, tissue and organ levels, causing specific as well as unspecific reactions, damage and adaptation reactions (Beck et al., 2007). To cope with the drought, tolerant plants initiate defense mechanisms against water deficit (Chaves and Oliveira, 2004), which need to be investigated in further detail (Zhou et al., 2007). In the following sections, mechanisms of drought tolerance at different levels are presented.

3.1. Morphological mechanisms

Plant drought tolerance involves changes at whole-plant, tissue, physiological and molecular levels. Manifestation of a single or a combination of inherent changes determines the ability of the plant to sustain itself under limited moisture supply. An account of various morphological mechanisms operative under drought conditions is given below.

3.1.1. Escape

Escape from drought is attained through a shortened life cycle or growing season, allowing plants to reproduce before the environment becomes dry. Flowering time is an important trait related to drought adaptation, where a short life cycle can lead to drought escape (Araus et al., 2002). Crop duration is inter-actively determined by genotype and the environment and determines the ability of the crop to escape from climatic stresses including drought (Dingkuhn and Asch, Dingkuhn). Matching growth duration of plants to soil moisture availability is critical to realize high seed yield (Siddique et al., 2003). Drought escape occurs when phenological development is successfully matched with periods of soil moisture availability, where the growing season is shorter and terminal drought stress predominates (Araus et al., 2002). In field-grown clones of robusta coffee, leaf shedding in response to drought stress occurred sequentially from older to younger leaves, suggesting that the more drought-sensitive the clone, the greater the extent of leaf shedding (DaMatta, 2004).

Time of flowering is a major trait of a crop adaptation to the environment, particularly when the growing season is restricted by terminal drought and high temperatures. Developing short-duration varieties has been an effective strategy for minimizing yield loss from terminal drought, as early maturity helps the crop to avoid the period of stress (Kumar and Abbo,

2001). However, yield is generally correlated with the length of crop duration under favorable growing conditions, and any decline in crop duration below the optimum would tax yield (Turner et al., 2001).

3.1.2. Avoidance

Drought avoidance consists of mechanisms that reduce water loss from plants, due to stomatal control of transpiration, and also maintain water uptake through an extensive and prolific root system (Turner et al., 2001; Kavar et al., 2007). The root characters such as biomass, length, density and depth are the main drought avoidance traits that contribute to final yield under terminal drought environments (Subbarao et al., 1995; Turner et al., 2001). A deep and thick root system is helpful for extracting water from considerable depths (Kavar et al., 2007).

Glaucousness or waxy bloom on leaves helps with maintenance of high tissue water potential, and is therefore considered as a desirable trait for drought tolerance (Richards et al., 1986; Ludlow and Muchow, 1990). Varying degrees of glaucousness in wheat led to increased water-use efficiency, but did not affect total water use or harvest index. Determination of leaf temperature indicated that, compared with non-glaucous leaves, glaucous leaves were 0.7 °C cooler and had a lower rate of leaf senescence (Richards et al., 1986). These authors suggested that a 0.5 °C reduction in leaf temperature for six hours per day was sufficient to extend the grain-filling period by more than three days. However, yield advantages are likely to be small as many varieties already show some degree of glaucousness.

3.1.3. Phenotypic flexibility

Plant growth is greatly affected by water deficit. At a morphological level, the shoot and root are the most affected and both are the key components of plant adaptation to drought. Plants generally limit the number and area of leaves in response to drought stress just to cut down the water budget at the cost of yield loss (Schuppler et al., 1998). Since roots are the only source to acquire water from soil, the root growth, its density, proliferation and size are key responses of plants to drought stress (Kavar et al., 2007).

It has long been established that plants bearing small leaves are typical of xeric environments. Such plants withstand drought very well, albeit their growth rate and biomass are relatively low (Ball et al., 1994). Leaf pubescence is a xeromorphic trait that helps protect the leaves from excessive heat load. Hairy leaves have reduced leaf temperatures and transpiration (Sandquist and Ehleringer, 2003) whilst inter- and intra-specific variation exists for the presence of this trait. Under high temperature and radiation stress, hairiness increases the light reflectance and minimizes water loss by increasing the boundary layer resistance to water vapor movement away from the leaf surface. Although drought stress also induces the

production of trichomes on both sides of wheat leaves, they had no significant influence on boundary layer resistance.

The water content in drought-treated mature stems declined by 4% and water potential by -0.25 MPa. It is shown that active phloem supply of assimilates and associated water reserves from mature stems was the mechanism that allowed developing stems of *Hylocereus undatus* to maintain growth under drought conditions (Nerd and Neumann, 2004). Moreover, girdling the phloem of growing stems rapidly inhibited stem elongation, but secretion of sucrose-containing nectar was maintained during drought. The water potential gradient was in the wrong direction for xylem transport from mature to young growing stems and axial hydraulic conductivity was low to negligible (Nerd and Neumann, 2004).

Roots are the key plant organ for adaptation to drought. If tolerance is defined as the ability to maintain leaf area and growth under prolonged vegetative stage stress, the main basis of variation appears to be constitutive root system architecture that allows the maintenance of more favorable plant water status (Nguyen et al., 1997). The possession of a deep and thick root system allowed access to water deep in the soil, which was considered important in determining drought resistance in upland rice (Kavar et al., 2007). Evidence suggests that it is quality, i.e. the distribution and structure, and not quantity of roots that determines the most efficient strategy for extracting water during the crop-growing season (Fig. 5). The drought tolerance of tea, onion and cotton was increased by improved root growth and root functioning. Selection for a deep and extensive root system has been advocated to increase productivity of food legumes under moisture-deficit conditions as it can optimize the capacity to acquire water (Subbarao et al., 1995).

Studies carried out on the effects of alleles of the wheat shoot dwarfing genes on root-shoot dry matter partitioning and drought resistance revealed that cultivars possessing the reduced height gene 1 and reduced height gene 2 gibberellin-insensitive dwarfing genes were more susceptible to drought stress than reduced height gene 1 and reduced height gene 2 tall cultivars (Miralles et al., 1997). The semi-dwarfing genes reduced height gene 1 and reduced height gene 2 resulted in greater root biomass at anthesis due to increased thickening of existing roots using surplus assimilates arising from the restricted stem growth. Thus, the benefit of greater assimilates available for root growth was not expressed as more extensive or deeper root growth. Differences have also been observed in the adaptive response of root distribution to soil drying (Liu et al., 2004).

To summarize, plants may escape drought stress by cutting short their growth duration, and avoid the stress with the maintenance of high tissue water potential either by reducing water loss from plants or improved water uptake, or both. Some plants may reduce their surface area either by leaf shedding or production of smaller leaves.

3.2. Physiological mechanisms

Osmotic adjustment, osmoprotection, antioxidation and a scavenging defense system have been the most important

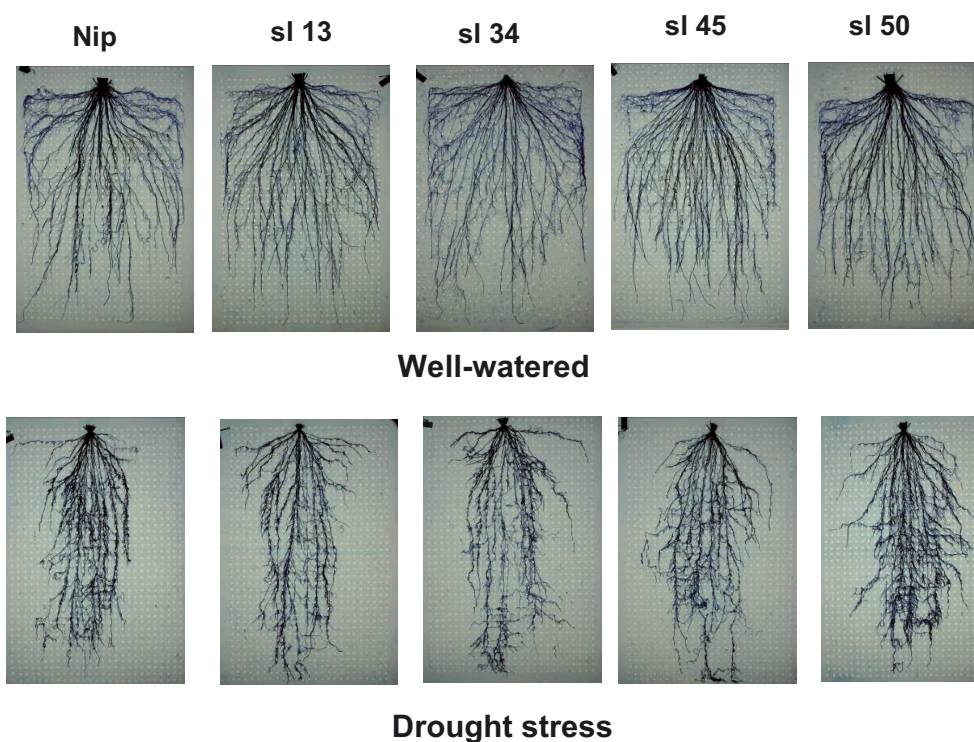


Figure 5. Root growth and proliferation under well-watered and drought stress conditions in various rice genotypes. Different rice genotypes (Nip, sl 13, sl 34, sl 45, sl 50) were grown under continuous flooded conditions (well-watered) and 15% soil moisture contents (drought stress). The study was conducted in root boxes. The figure shows root proliferation 38 days after seeding. (courtesy Ms. Mana Kano).

bases responsible for drought tolerance. The physiological basis of genetic variation in drought response is not clear; in part, because more intricate mechanisms have been suggested. Some of these mechanisms are described below.

3.2.1. Cell and tissue water conservation

Under drought stress, sensitive pea genotypes were more affected by a decline in relative water content than tolerant ones (Upreti et al., 2000). In faba bean, determination of leaf water potential was useful for describing the drought effect, but was not suitable for discriminating tolerant from sensitive genotypes. This suggested that water potential was not the defining feature of the tolerance (Riccardi et al., 2001). Nevertheless, other studies opined that determination of leaf water status in the morning and water content in leaves in the afternoon were potentially useful for screening drought tolerance in chickpea (Pannu et al., 1993).

Osmotic adjustment allows the cell to decrease osmotic potential and, as a consequence, increases the gradient for water influx and maintenance of turgor. Improved tissue water status may be achieved through osmotic adjustment and/or changes in cell wall elasticity. This is essential for maintaining physiological activity for extended periods of drought (Kramer and Boyer, 1995). Wild melon plant survived drought by maintaining its water content without wilting of leaves even under severe drought. Drought stress in combination with strong

light led to an accumulation of high concentrations of citrulline, glutamate and arginine in leaves of wild watermelon. The accumulation of citrulline and arginine may be related to the induction of dopamine receptor interacting protein gene 1, a homologue of the acetylornithine deacetylase gene in *Escherichia coli*, where it functions to incorporate the carbon skeleton of glutamate into the urea cycle (Yokota et al., 2002).

It has been identified that among various mechanisms, osmotic adjustment, abscisic acid and induction of dehydrins may confer tolerance against drought injuries by maintaining high tissue water potential (Turner et al., 2001). With the accumulation of solutes, the osmotic potential of the cell is lowered, which attracts water into the cell and helps with turgor maintenance. The maintenance of turgor despite a decrease in leaf water volume is consistent with other studies of species with elastic cell walls. Osmotic adjustment helps to maintain the cell water balance with the active accumulation of solutes in the cytoplasm, thereby minimizing the harmful effects of drought (Morgan, 1990). Osmotic adjustment is an important trait in delaying dehydrative damage in water-limited environments by continued maintenance of cell turgor and physiological processes (Taiz and Zeiger, 2006). The osmotic adjustment also facilitates a better translocation of pre-anthesis carbohydrate partitioning during grain filling (Subbarao et al., 2000), while high turgor maintenance leads to higher photosynthetic rate and growth (Ludlow and Muchow, 1990; Subbarao et al., 2000).

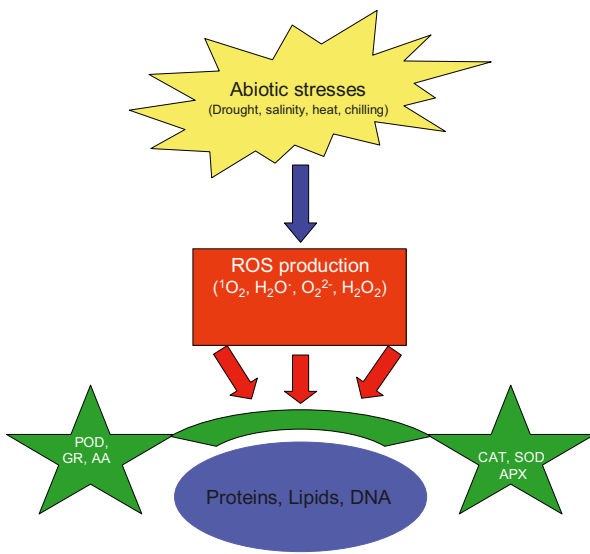


Figure 6. Role of antioxidant enzymes in the ROS scavenging mechanism. Exposure to abiotic stresses (including drought, chilling, salinity, etc.) leads to the generation of ROS, including singlet oxygen ($^1\text{O}_2$), perhydroxyl radical ($\text{H}_2\text{O}\cdot$), hydroxyl radicals ($\text{O}_2^{\cdot-}$), hydrogen peroxide (H_2O_2) and alkoxy radical (RO). The ROS may react with proteins, lipids and DNA, causing oxidative damage and impairing the normal functions of cells. The antioxidant defense system in the plant cell includes both enzymatic and non-enzymatic constituents. Amongst the enzymatic components are superoxide dismutase, catalase, peroxidase, ascorbate peroxidase and glutathione reductase. Upon exposure to abiotic stresses, tolerant cells activate their enzymatic antioxidant system, which then starts quenching the ROS and protecting the cell. ROS: reactive oxygen species.

3.2.2. Antioxidant defense

The antioxidant defense system in the plant cell constitutes both enzymatic and non-enzymatic components. Enzymatic components include superoxide dismutase, catalase, peroxidase, ascorbate peroxidase and glutathione reductase. Non-enzymatic components contain cysteine, reduced glutathione and ascorbic acid (Gong et al., 2005). In environmental stress tolerance, such as drought, high activities of antioxidant enzymes and high contents of non-enzymatic constituents are important.

The reactive oxygen species in plants are removed by a variety of antioxidant enzymes and/or lipid-soluble and water-soluble scavenging molecules (Hasegawa et al., 2000); the antioxidant enzymes being the most efficient mechanisms against oxidative stress (Farooq et al., 2008). Apart from catalase, various peroxidases and peroxiredoxins, four enzymes are involved in the ascorbate-glutathione cycle, a pathway that allows the scavenging of superoxide radicals and H_2O_2 (Fig. 6). These include ascorbate peroxidase, dehydroascorbate reductase, monodehydroascorbate reductase and glutathione reductase (Fazeli et al., 2007). Most of the ascorbate-glutathione cycle enzymes are located in the cytosol, stroma of chloroplasts, mitochondria and peroxisomes (Jiménez et al., 1998). Ascorbate peroxidase is a key antioxidant enzyme in

plants (Orvar and Ellis, 1997) whilst glutathione reductase has a central role in maintaining the reduced glutathione pool during stress (Pastori et al., 2000). Two glutathione reductase complementary deoxyribonucleic acids have been isolated; one type encoding the cytosolic isoforms (Stevens et al., 2000) and the other encoding glutathione reductase proteins dual-targeted to both chloroplasts and mitochondria in different plants (Chew et al., 2003).

Among enzymatic mechanisms, superoxide dismutase plays an important role, and catalyzes the dismutation of two molecules of superoxide into O_2 and H_2O_2 ; the first step in reactive oxygen species scavenging systems. Lima et al. (2002), from a study utilizing two rapidly drought-stressed clones of *Coffea canephora*, proposed that drought tolerance might, or at least in part, be associated with enhanced activity of antioxidant enzymes. In contrast, Pinheiro et al. (2004) did not find a link between protection against oxidative stress and drought tolerance when four clones of *C. canephora* were subjected to long-term drought.

Carotenoids and other compounds, such as abietane diterpenes, have received little attention despite their capacity to scavenge singlet oxygen and lipid peroxy-radicals, as well as to inhibit lipid peroxidation and superoxide generation under dehydrative forces (Deltoro et al., 1998). The transcript of some of the antioxidant genes such as glutathione reductase or ascorbate peroxidase was higher during recovery from a water deficit period and appeared to play a role in the protection of cellular machinery against damage by reactive oxygen species (Ratnayaka et al., 2003). A superoxide radical has a half-life of less than 1 sec and is rapidly dismutated by superoxide dismutase into H_2O_2 , a product that is relatively stable and can be detoxified by catalase and peroxidase (Apel and Hirt, 2004). These metalloenzymes constitute an important primary line of defense of cells against superoxide free radicals generated under stress conditions. Therefore, increased superoxide dismutase activity is known to confer oxidative stress tolerance (Pan et al., 2006).

Oxidative damage in the plant tissue is alleviated by a concerted action of both enzymatic and non-enzymatic antioxidant systems. These include β -carotenes, ascorbic acid, α -tocopherol, reduced glutathione and enzymes including superoxide dismutase, peroxidase, ascorbate peroxidase, catalase, polyphenol oxidase and glutathione reductase (Hasegawa et al., 2000; Prochazkova et al., 2001). Carotenes form a key part of the plant antioxidant defense system (Havaux, 1998; Wahid, 2007), but they are very susceptible to oxidative destruction. The β -carotene present in the chloroplasts of all green plants is exclusively bound to the core complexes of photosystem I and photosystem II. Protection against damaging effects of reactive oxygen species at this site is essential for chloroplast functioning. Here, β -carotene, in addition to functioning as an accessory pigment, acts as an effective antioxidant and plays a unique role in protecting photochemical processes and sustaining them (Havaux, 1998). A major protective role of β -carotene in photosynthetic tissue may be through direct quenching of triplet chlorophyll, which prevents the generation of singlet oxygen and protects from oxidative damage.

3.2.3. Cell membrane stability

Biological membranes are the first target of many abiotic stresses. It is generally accepted that the maintenance of integrity and stability of membranes under water stress is a major component of drought tolerance in plants (Bajji et al., 2002). Cell membrane stability, reciprocal to cell membrane injury, is a physiological index widely used for the evaluation of drought tolerance (Premachandra et al., 1991). Moreover, it is a genetically related phenomenon since quantitative trait loci for this have been mapped in drought-stressed rice at different growth stages (Tripathy et al., 2000). Dhanda et al. (2004) showed that membrane stability of the leaf segment was the most important trait to screen the germplasm for drought tolerance.

Cell membrane stability declined rapidly in Kentucky bluegrass exposed to drought and heat stress simultaneously (Wang and Huang, 2004). In a study on maize, K nutrition improved the drought tolerance, mainly due to improved cell membrane stability (Gnanasiri et al., 1991). Tolerance to drought evaluated as increase in cell membrane stability under water deficit conditions was differentiated between cultivars and correlated well with a reduction in relative growth rate under stress (Premachandra et al., 1991). In holm oak (*Quercus ilex*) seedlings, hardening increased drought tolerance primarily by reducing osmotic potential and stomatal regulation, improved new root growth capacity and enhanced cell membrane stability. Among treated seedlings, the greatest response occurred in seedlings subjected to moderate hardening. Variation in cell membrane stability, stomatal regulation and root growth capacity was negatively related to osmotic adjustment (Villar-Salvador et al., 2004).

The causes of membrane disruption are unknown; notwithstanding, a decrease in cellular volume causes crowding and increases the viscosity of cytoplasmic components. This increases the chances of molecular interactions that can cause protein denaturation and membrane fusion. For model membrane and protein systems, a broad range of compounds have been identified that can prevent such adverse molecular interactions. Some of these are proline, glutamate, glycinebetaine, carnitine, mannitol, sorbitol, fructans, polyols, trehalose, sucrose and oligosaccharides (Folkert et al., 2001). Another possibility of ion leakage from the cell may be due to thermal-induced inhibition of membrane-bound enzymes responsible for maintaining chemical gradients in the cell (Reynolds et al., 2001). *Arabidopsis* leaf membranes appeared to be very resistant to water deficit, as shown by their capacity to maintain polar lipid contents and the stability of their composition under severe drought (Gigon et al., 2004).

3.2.4. Plant growth regulators

Plant growth regulators, when applied externally, and phytohormones, when produced internally, are substances that influence physiological processes of plants at very low concentrations (Morgan, 1990). Both these terms have been used

interchangeably, particularly when referring to auxins, gibberellins, cytokinins, ethylene and abscisic acid (Taiz and Zeiger, 2006). Under drought, endogenous contents of auxins, gibberellins and cytokinin usually decrease, while those of abscisic acid and ethylene increase (Nilsen and Orcutte, 1996). Nevertheless, phytohormones play vital roles in drought tolerance of plants.

Auxins induce new root formation by breaking root apical dominance induced by cytokinins. As a prolific root system is vital for drought tolerance, auxins have an indirect but key role in this regard. Drought stress limits the production of endogenous auxins, usually when contents of abscisic acid and ethylene increase (Nilsen and Orcutte, 1996). Nevertheless, exogenous application of indole-3-yl-acetic acid enhanced net photosynthesis and stomatal conductance in cotton (Kumar et al., 2001). Indole-3-butyric acid is a naturally occurring auxin. Drought stress and abscisic acid application enhance indole-3-butyric acid synthesis in maize. Recently, it was revealed that Indole-3-butyric acid synthetase from *Arabidopsis* is also drought-inducible (Ludwig-Müller, 2007). Experiments with indole-3-yl-acetic acid and ethylene glycol tetra-acetic acid suggested that calcium and auxin participate in signaling mechanisms of drought-induced proline accumulation (Sadiqov et al., 2002).

Drought rhizogenesis is an adaptive strategy that occurs during progressive drought stress and is reported from Brassicaceae and related families by the formation of short, tuberized, hairless roots. These roots are capable of withstanding a prolonged drought period and give rise to a new functional root system upon rehydration. The drought rhizogenesis was highly increased in the gibberellic acid biosynthetic mutant *ga5*, suggesting that some gibberellic acids might also participate in this process (Vartanian et al., 1994).

Abscisic acid is a growth inhibitor and produced under a wide variety of environmental stresses, including drought. All plants respond to drought and many other stresses by accumulating abscisic acid. Abscisic acid is ubiquitous in all flowering plants and is generally recognized as a stress hormone that regulates gene expression and acts as a signal for the initiation of processes involved in adaptation to drought and other environmental stresses (Fig. 7). It has been proposed that abscisic acid and cytokinin have opposite roles in drought stress. Increase in abscisic acid and decline in cytokinins levels favor stomatal closure and limit water loss through transpiration under water stress (Morgan, 1990). When plants wilt, abscisic acid levels typically rise as a result of increased synthesis (Taylor, 1991). Increased abscisic acid concentration leads to many changes in development, physiology and growth. Abscisic acid alters the relative growth rates of various plant parts such as increase in the root-to-shoot dry weight ratio, inhibition of leaf area development and production of prolific and deeper roots (Sharp et al., 1994). It triggers the occurrence of a complex series of events leading to stomatal closure, which is an important water-conservation response (Turner et al., 2001). In a study on genetic variation for abscisic acid accumulation in rice, a consistent negative relationship between the ability of detached and partially dehydrated leaves to accumulate abscisic acid and leaf weight was established (Ball et al., 1994). By its

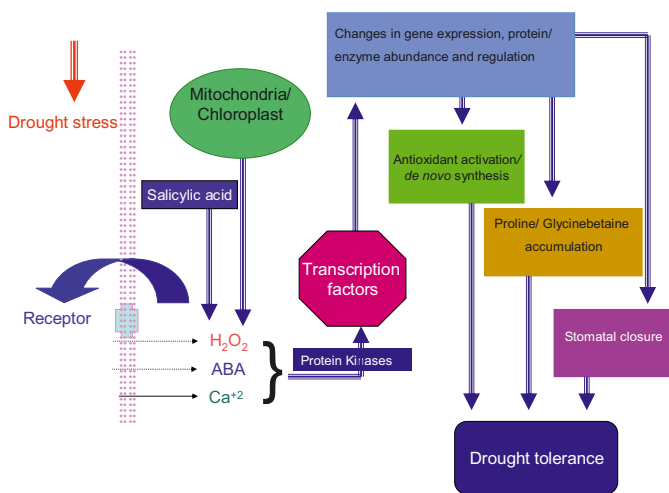


Figure 7. Proposed cellular events and signaling cascades in a plant cell responding to drought stress. Drought stress is perceived by an unknown mechanism, which then activates the signaling cascades, plausibly by abscisic acid (ABA), hydrogen peroxide (H_2O_2) and calcium (Ca^{+2}). These cascades then activate the synthesis of specific protein kinases which activate more downstream responses such as changes in gene expression. The response to these signaling cascades also results in changes in plant metabolism including activation and synthesis of antioxidants, synthesis and accumulation of osmoprotectants and solutes, and stomatal closure under acute drought stress.

effect in closing stomata, abscisic acid can control the rate of transpiration and, to some extent, may be involved in the mechanism conferring drought tolerance in plants.

Abscisic acid induces expression of various water stress-related genes. In a recent study, Zhang et al. (2005) reported a regulatory role of telomeric repeat binding factor gene 1 in abscisic acid sensitivity and drought response during seedling development. Bray (1997) suggested the existence of abscisic acid-dependent and abscisic acid-independent transduction cascades and pathways to act as a signal of drought stress and the expression of specific water stress-induced genes. Abscisic acid produces such changes that confer an ability to maintain cellular turgor to withstand dehydrative forces (Fig. 7).

Ethylene has long been considered a growth inhibitory hormone, although it is involved in environmentally driven growth inhibition and stimulation (Taiz and Zeiger, 2006). The response of cereals to drought includes loss of leaf function and premature onset of senescence in older leaves. Ethylene may serve to regulate leaf performance throughout its lifespan as well as to determine the onset of natural senescence and mediate drought-induced senescence (Young et al., 2004). Recent studies suggest that growth promotion is a common feature in ethylene responses. To escape this adversity, plants can optimize growth and tolerate abiotic stresses such as drought, and this response also involves ethylene synthesis (Pierik et al., 2007).

Among the other endogenously produced growth regulating factors, the role of salicylic acid in the induction of tolerance against several abiotic stresses has been emphasized recently. In the case of drought tolerance, the role of endogenously

produced salicylic acid is still enigmatic. Salicylic acid potentiates the generation of reactive oxygen species in photosynthetic tissues of *Arabidopsis thaliana* during osmotic stress (Borsani et al., 2001).

Polyamines are known to have profound influence on plant growth and development. Being cationic, polyamines can associate with anionic components of the membrane, such as phospholipids, thereby protecting the lipid bilayer from deteriorating effects of stress (Bouchereau et al., 1999). There has been a growing interest in the study of polyamine participation in the defense reaction of plants against environmental stresses and extensive research efforts have been made in the last two decades (Bouchereau et al., 1999; Kasukabe et al., 2004). Many genes for enzymes involved in polyamine metabolism have been cloned from several species, and their expression under several stress conditions has been analyzed. For example, the apple spermidine synthase gene when overexpressed encodes high levels of spermidine synthase, which substantially improves abiotic stress tolerance including drought (Wen et al., 2007).

Among various polyamines, a rise in the putrescence level is generally due to an enhanced arginine decarboxylase activity (Bouchereau et al., 1999). Compared with sensitive plants, stress-tolerant plants generally have a greater capacity to synthesize polyamines in response to stress, resulting in a two- to three fold rise in endogenous polyamine levels over the unstressed ones (Kasukabe et al., 2004). Recent studies suggested that rice has a great capacity to enhance polyamine biosynthesis, particularly spermidine and spermine in free form and putrescence in insoluble-conjugated form, in leaves earlier in response to drought stress. This was considered as an important physiological trait of drought tolerance in rice (Yang et al., 2007).

3.2.5. Compatible solutes and osmotic adjustment

One of the most common stress tolerance strategies in plants is the overproduction of different types of compatible organic solutes (Serraj and Sinclair, 2002). Compatible solutes are low-molecular-weight, highly soluble compounds that are usually nontoxic even at high cytosolic concentrations. Generally they protect plants from stress through different means such as contribution towards osmotic adjustment, detoxification of reactive oxygen species, stabilization of membranes, and native structures of enzymes and proteins (Fig. 8).

Osmotic adjustment is a mechanism to maintain water relations under osmotic stress. It involves the accumulation of a range of osmotically active molecules/ions including soluble sugars, sugar alcohols, proline, glycinebetaine, organic acids, calcium, potassium, chloride ions, etc. Under water deficit and as a result of solute accumulation, the osmotic potential of the cell is lowered, which attracts water into the cell and helps with the maintenance of turgor. By means of osmotic adjustment, the organelles and cytoplasmic activities take place at about a normal pace and help plants to perform better in terms of growth, photosynthesis and assimilate partitioning to grain filling (Ludlow and Muchow, 1990; Subbarao et al., 2000). As

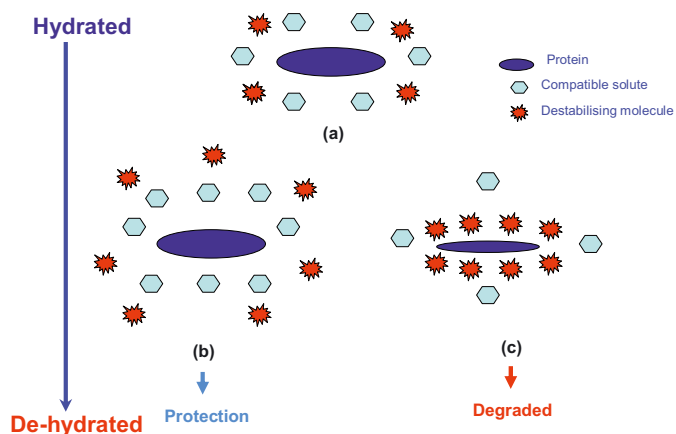


Figure 8. Role of compatible solutes in drought tolerance. In the hydrated state, the presence of water reduces the interaction of destabilizing molecules (a), in tolerant cells the synthesis of compatible solutes preferentially excludes the binding of destabilizing molecules and stabilizes native protein conformation (b) and in sensitive cells the lack of compatible solutes results in the preferential binding of destabilizing molecules to the protein surface, leading to degradation (c). (Adapted from Hoekstra et al., 2001).

a mechanism, osmotic adjustment has been suggested as an important trait in postponing the dehydration stress in water-scarce environments (Morgan, 1990). Variation in osmotic adjustment among chickpea cultivars in response to soil drought has been observed, and seed yield of chickpea was correlated with the degree of osmotic adjustment when grown under a line-source irrigation system in the field (Moinuddin and Khannu-Chopra, 2004). Contrarily, Serraj and Sinclair (2002) found no yield advantage from osmotic adjustment in any crop. Nevertheless, further investigations are imperative to establish this controversy.

As mentioned above, osmotic adjustment is accomplished with the accumulation of compatible solutes. Of these, proline is one amongst the most important cytosolutes and its free accumulation is a widespread response of higher plants, algae, animals and bacteria to low water potential (Zhu, 2002; Wahid and Close, 2007). Its synthesis in leaves at low water potential is caused by a combination of increased biosynthesis and slow oxidation in mitochondria. Despite some controversy, many physiological roles have been assigned to free proline including stabilization of macromolecules, a sink for excess reductant and a store of carbon and nitrogen for use after relief of water deficit (Zhu, 2002). Proline contents were increased under drought stress in pea cultivars (Alexieva et al., 2001). Drought-tolerant petunia (*Petunia hybrida*) varieties were reported to accumulate free proline under drought that acted as an osmoprotectant and induced drought tolerance (Yamada et al., 2005).

Glycinebetaine (N, N, N-trimethyl glycine) is one of the most extensively studied quaternary ammonium compounds and compatible solutes in plants, animals and bacteria (Wahid et al., 2007). Many studies demonstrate that glycinebetaine plays an important role in enhancing plant tolerance under a

range of abiotic stresses including drought (Quan et al., 2004). The introduction of genes synthesizing glycinebetaine into non-accumulators of glycinebetaine proved to be effective in increasing tolerance to various abiotic stresses (Sakamoto and Murata, 2002). Naidu et al. (1998) reported that cotton cultivars adapted to water stress conditions accumulated higher glycinebetaine than the non-adapted ones under drought. In addition to direct protective roles of glycinebetaine either through positive effects on enzyme and membrane integrity or as an osmoprotectant, glycinebetaine may also protect cells from environmental stresses indirectly by participating in signal transduction pathways (Subbarao et al., 2000).

Citrulline, named after *Citrullus*; a Latin name of watermelon, from which it was isolated, is an amino acid. Although not built into proteins during their synthesis, and not encoded by a nuclear gene, several proteins are known to contain citrulline (Kawasaki et al., 2000). Wild watermelon (*Citrullus lanatus*) has the ability to adapt to severe drought stress despite carrying out normal C₃-type photosynthesis, which seem to be correlated with citrulline accumulation (Akashi et al., 2001). Wild watermelon primarily accumulated citrulline followed by glutamate and arginine, in place of proline and glycinebetaine (Kawasaki et al., 2000). Yokota et al. (2002) reported a higher citrulline accumulation in the wild watermelon leaves assuming that citrulline is located only in the cytosol and constitutes 5% of the total volume of the mesophyll cells. Citrulline is a novel and the most effective OH⁻ scavenger among compatible solutes examined so far. Moreover, it can effectively protect DNA and enzymes from oxidative injuries (Akashi et al., 2001; Bektaşoğlu et al., 2006).

Rapid accumulation of the non-protein amino acid γ -aminobutyric acid was identified in plant tissues upon exposure to stress many years ago. γ -aminobutyric acid acts as a zwitterion, exists in free form, and has a flexible molecule that can assume several conformations in solution, including a cyclic structure that is similar to proline. At physiological pH, γ -aminobutyric acid is highly water-soluble (Shelp et al., 1999), and may function as a signaling molecule in higher plants under stress (Serraj et al., 1998). The physiological roles of γ -aminobutyric acid in drought tolerance entail osmotic regulation (Shelp et al., 1999), detoxication of reactive oxygen radicals, conversion of putrescine into proline and intracellular signal transduction (Kinnersley and Turano, 2000).

Drought stress initiates a signal transduction pathway, in which increased cytosolic Ca²⁺ activates Ca²⁺/calmodulin-dependent glutamate decarboxylase activity, leading to γ -aminobutyric acid synthesis (Shelp et al., 1999). Elevated H⁺ and substrate levels can also stimulate glutamate decarboxylase activity, leading primarily to γ -aminobutyric acid accumulation. Experimental evidence supports the involvement of γ -aminobutyric acid in pH regulation, nitrogen storage, plant development and defense, as well as a compatible osmolyte and an alternative pathway for glutamate utilization (Shelp et al., 1999; Wahid et al., 2007). After drought stress the content of proline was more than 50% and at the end of recovery the γ -aminobutyric acid content reached 27% (Simon-sarkadi et al., 2006).

Trehalose is a non-reducing disaccharide of glucose that functions as a compatible solute in the stabilization of biological structures under abiotic stress (Goddijn et al., 1997). In nature, trehalose is biosynthesized as a stress response by a variety of organisms including bacteria, fungi, algae, insects, invertebrates and lower plants (Wingler, 2002). Capacity to produce trehalose, earlier thought to be absent from higher plants, has now been reported to accumulate in high amounts in some drought-tolerant ferns, the resurrection plant *Selaginella lepidophylla* (Penna, 2003) and desiccation-tolerant angiosperm *Myrothamnus flabellifolia* (Drennan et al., 1993). The presence of low amounts of trehalose was demonstrated even in tobacco (Goddijn et al., 1997) and many higher plants (Kosmas et al., 2006). Its metabolism may be channelized to enhance drought tolerance in plants (Pilon-Smits et al., 1998; Penna, 2003). Physiological roles of trehalose include efficient stabilization of dehydrated enzymes, proteins and lipid membranes, as well as protection of biological structures under desiccation stress (Wingler, 2002) rather than regulating water potential (Lee et al., 2004). Karim et al. (2007) reported that enhanced drought tolerance by trehalose depends on improved water status and expression of heterologous trehalose biosynthesis genes during *Arabidopsis* root development.

At a molecular level, exogenously applied trehalose may trigger the abscisic acid-insensitive 4 gene expression but decrease sucrose induction, providing a possible molecular mechanism for the trehalose effect on plant gene expression and growth (Ramon et al., 2007). Trehalose-accumulating organisms produce this sugar in a two-step process by the action of the enzymes trehalose-6-phosphate synthase and trehalose-6-phosphate phosphatase when exposed to stress. Improved drought tolerance has been reported in the transgenic plants overproducing trehalose-6-phosphate synthase in spite of minute accumulation of trehalose (Karim et al., 2007).

In fact, plants can withstand drought stress by conserving cell and tissue water principally by osmotic adjustment, maintenance of the antioxidant defense system for the scavenging of reactive oxygen species, and keeping the cell membranes stabilized. Plant growth regulators and polyamines, γ -aminobutyric acid, free amino acids and sugars also play a vital role in drought tolerance by scavenging the reactive oxygen species, stomatal regulation and protection of vital macromolecules, and maintenance of the cell water balance.

3.3. Molecular mechanisms

Plant cellular water deficit may occur under conditions of reduced soil water content. Under these conditions, changes in gene expression (up- and down-regulation) take place. Various genes are induced in response to drought at the transcriptional level, and these gene products are thought to function in tolerance to drought (Kavar et al., 2007). Gene expression may be triggered directly by the stress conditions or result from secondary stresses and/or injury responses. Nonetheless, it is well established that drought tolerance is a complex phenomenon involving the concerted action of many genes (Agarwal et al., 2006; Cattivelli et al., 2008).

3.3.1. Aquaporins

Aquaporins have the ability to facilitate and regulate passive exchange of water across membranes. They belong to a highly conserved family of major intrinsic membrane proteins (Tyerman et al., 2002). In plants, aquaporins are present abundantly in the plasma membrane and in the vacuolar membrane. The structural analysis of aquaporins has revealed the general mechanism of protein-mediated membrane water transport. Although the discovery of aquaporins in plants has resulted in a prototype shift in the understanding of plant water relations (Maurel and Chrispeels, 2001), the relation between aquaporins and plant drought resistance is still elusive (Aharon et al., 2003). Nevertheless, it is believed that they can regulate the hydraulic conductivity of membranes and potentiate a ten- to twenty-fold increase in water permeability (Maurel and Chrispeels, 2001).

Studies on aquaporins and plant water relations have been carried out for many years. Mercury is a potential inhibitor of aquaporins. This was evident from a number of reports on mercury-induced decline in root hydraulic conductivity, which substantiated that aquaporins play a major role in overall root water uptake (Javot and Maurel, 2002), and play a role in cellular osmoregulation of highly compartmented root cells (Maurel et al., 2002; Javot et al., 2003). Reverse genetics provides an elegant approach to explore aquaporin roles in plant water relations (Kaldenhoff et al., 1998). The overexpression of the plasma membrane aquaporin in transgenic tobacco progressively improved plant vigor under favorable growth conditions, but the prolactin-inducible protein 1b gene overexpression had retrogressive influence under salinity, and caused fast wilting under water stress (Aharon et al., 2003). Phosphorylation (Johansson et al., 1998), calcium and pH (Tournaire-Roux et al., 2003) are important factors modulating aquaporin activity.

Recently, efforts have been concentrated on investigating the function and regulation of plasma membrane intrinsic protein aquaporins. The aquaporins play a specific role in controlling transcellular water transport. For instance, they are abundantly expressed in roots where they mediate soil water uptake (Javot and Maurel, 2002) and transgenic plants down-regulating one or more prolactin-inducible protein genes had lower root water uptake capacity (Javot et al., 2003).

3.3.2. Stress proteins

Synthesis of stress proteins is a ubiquitous response to cope with prevailing stressful conditions including water deficit. Most of the stress proteins are soluble in water and therefore contribute towards the stress tolerance phenomena by hydration of cellular structures (Wahid et al., 2007). Synthesis of a variety of transcription factors and stress proteins is exclusively implicated in drought tolerance (Taiz and Zeiger, 2006).

Dehydration-responsive element-binding genes belong to the ν -ets erythroblastosis virus repressor factor gene family of transcription factors consisting of three subclasses, dehydration-responsive element-binding gene1 and

dehydration-responsive element-binding gene2, which are induced by cold and dehydration, respectively (Choi et al., 2002). The dehydration-responsive element-binding genes are involved in the abiotic stress signaling pathway. It was possible to engineer stress tolerance in transgenic plants by manipulating the expression of dehydration-responsive element-binding genes (Agarwal et al., 2006). Introduction of a novel dehydration-responsive element-binding gene transcriptional factor effectively improved the drought tolerance ability of groundnut (Mathur et al., 2004) and rice (Yamaguchi-Shinozaki and Shinozaki, 2004). After successful cloning of dehydration-responsive element-binding gene1 (Liu et al., 1998), many capsella bursa-pastoris-like genes have been reported to be synthesized in response to drought stress in various plant species including rye and tomato (Jaglo et al., 2001), rice (Dubouzet et al., 2003), wheat (Shen et al., 2003), cotton (Huang and Liu, 2006), brassica (Zhao et al., 2006) and soybean (Chen et al., 2007). Introduction of dehydration-responsive element-binding gene1A genes in transgenic tall fescue (*Festuca arundinacea*) showed increased drought resistance with the accumulation of a high level of proline. This indicated the ability of capsella bursa-pastoris 3 to induce drought tolerance (Zhao et al., 2007). Drought stress causes many changes in the expression levels of late embryogenesis abundant/dehydrin-type genes and molecular chaperones that protect the cellular proteins from denaturation (Mahajan and Tuteja, 2005).

Heat shock proteins belong to a larger group of molecules called chaperones. They have a role in stabilizing other proteins' structure. Low-molecular-weight heat shock proteins are generally produced only in response to environmental stress, particularly high temperature (Wahid et al., 2007). But many heat shock proteins have been found to be induced by different stresses such as drought, anaerobic conditions and low temperatures (Coca et al., 1994). They are reported to serve as molecular chaperones that participate in adenosine triphosphate-dependent protein unfolding or assembly/disassembly reactions and prevent protein denaturation during stress (Gorantla et al., 2006).

Membrane-stabilizing proteins and late embryogenic abundant proteins are another important protein group responsible for conferring drought tolerance. These increase the water-binding capacity by creating a protective environment for other proteins or structures, referred to as dehydrins. They also play a major role in the sequestration of ions that are concentrated during cellular dehydration (Gorantla et al., 2006). These proteins help to protect the partner protein from degradation and proteinases that function to remove denatured and damaged proteins. Dehydrins, also known as a group of late embryogenesis abundant proteins, accumulate in response to both dehydration and low temperature (Close, 1997). In addition to their synthesis at the desiccating stage of seed, they also accumulate during periods of water deficit in vegetative tissues. These proteins are easily identifiable from their particular structural features such as the highly conserved Lysine-rich domain predicted to be involved in hydrophobic interactions, leading to macromolecule stabilization (Svensson et al., 2002).

3.3.3. Signaling and drought stress tolerance

General responses to stress involve signaling stress detection via the redox system, checkpoints arresting the cell cycle and deoxyribonucleic acid repair processes stimulated in response to deoxyribonucleic acid damage. The complexity of signaling events associated with the sensing of stress and the activation of defense and acclimation pathways is believed to involve reactive oxygen species, calcium, calcium-regulated proteins, mitogen-activated protein kinase cascades, and cross-talk between different transcription factors (Kovtun et al., 2000; Chen et al., 2002).

Chemical signals, e.g., reactive oxygen species, calcium and plant hormones are involved in inducing stress tolerance by acting via transduction cascades and activate genomic re-programing (Fig. 7; Joyce et al., 2003). Mitogen-activated protein kinases are important mediators in signal transmission, connecting the perception of external stimuli to cellular responses. Mitogen-activated protein kinase cascades are involved in signaling various stresses, including drought (Wrzaczek and Hirt, 2001). Calcium has been established as a ubiquitous intracellular second messenger in plants. Calcium-based signaling systems comprise a receptor, a system for generating the increase in cytosolic calcium, downstream components that are capable of reacting to increased cytosolic calcium, and other cellular systems responsible for returning cytosolic calcium to its pre-stimulus level (Alistair and Brownlee, 2004). More recently, it is reported that calcium can improve water stress tolerance in *Catharanthus roseus* by increasing γ -glutamyl kinase and reducing the proline oxidase activities (Abdul Jaleel et al., 2007).

The calcium-dependent protein kinases in higher plant cells are an important group of calcium sensors that decode calcium ion signals in plant cells (Cheng et al., 2002). As a family of unique serine/threonine kinases in higher plants, they perform diverse and important functions in plant signal transduction (Mori et al., 2006). Drought stress increases the cytoplasmic calcium level in living plant cells (Knight, 2000). A number of potential calcium sensors, such as salt overly-sensitive 3-like proteins (Zhu, 2002) or Casitas B-lineage Lymphoma (Luan et al., 2002) and calcium-dependent protein kinases may further transduce stress-induced calcium signals (Harmon et al., 2000). Mishra et al. (2006) also reported that signaling for cell division and stress responses in plants is mediated through monoammonium phosphate kinases, and even auxins also utilize a monoammonium phosphate kinase pathway for its action.

A number of phospholipid systems are activated by osmotic stress, generating an array of messenger molecules, some of which may function upstream of the osmotic stress-activated protein kinases. Abscisic acid biosynthesis is regulated by osmotic stress at multiple steps. Both abscisic acid-dependent and - independent osmotic stress signaling first modify constitutively expressed transcription factors, leading to the expression of early response transcriptional activators, which then activate downstream stress tolerance effector genes (Zhu, 2002). Recently, Wan et al. (2007) reported that amongst the 29 calcium-dependent protein kinase genes identified so

far, all contained multiple stress-responsive *cis*-elements upstream in the promoter region (1 kb). Sucrose non-fermenting 1-related protein kinase 2 has also been reported to be capable of mediating signals initiated during drought stress, resulting in appropriate gene expression (Umezawa et al., 2005).

In fact, various chemical signals transduced under drought stress activate an array of genes, leading to the synthesis of proteins and metabolites, conferring drought tolerance in a number of plant species.

4. MANAGING DROUGHT STRESS

Drought stress effects can be managed by production of the most appropriate plant genotypes together with adjustment of agronomic practices (sowing time, plant density and soil management). This is done to ensure that sensitive crop stages occur at the time when likelihood of drought is minimal. Various strategies of paramount importance to accomplish this objective may entail production of appropriate plant varieties and improvement of the existing high-yielding varieties. Efforts have been made to produce drought-tolerant genotypes using the knowledge of responses of plants to drought stress and mechanisms involved as elaborated above. The two most important strategies may include: (a) selecting the desired materials as in traditional breeding using molecular and biotechnological means, including production of genetically modified or transgenic plants (Fig. 9) and (b) inducing drought tolerance in otherwise susceptible plants by priming and hormonal application. An account of these efforts is elaborated below.

4.1. Selection and breeding strategies

Conventional breeding has been based on empirical selection for yield (Atlin and Lafitte, 2002). However, this approach is far from being optimal, since yield is a quantitative trait and characterized by a low heritability and a high genotype \times environment interaction (Babu et al., 2003). It is strongly believed that understanding of a physiological and molecular basis may help target the key traits that limit yield. Such an approach may complement conventional breeding programs and hasten yield improvement (Cattivelli et al., 2008). Moreover, even the power of molecular biology for locating important gene sequences and introgressing quantitative trait loci or even for selecting or genetically transforming important quantitative trait loci strongly depends upon our understanding of yield-determining physiological processes (Araus et al., 2002; Kirigwi et al., 2007).

Screening under natural drought stress conditions in the target environments is difficult because of the irregular and erratic drought response. But screening under controlled stress environments and rain-out shelters is more manageable. Selection response in the target population of environments under natural stress can be considered a correlated response to selection in the managed stress environment (Venuprasad et al., 2007). On the other hand, classical breeding is a good approach for developing drought tolerance, which relies upon

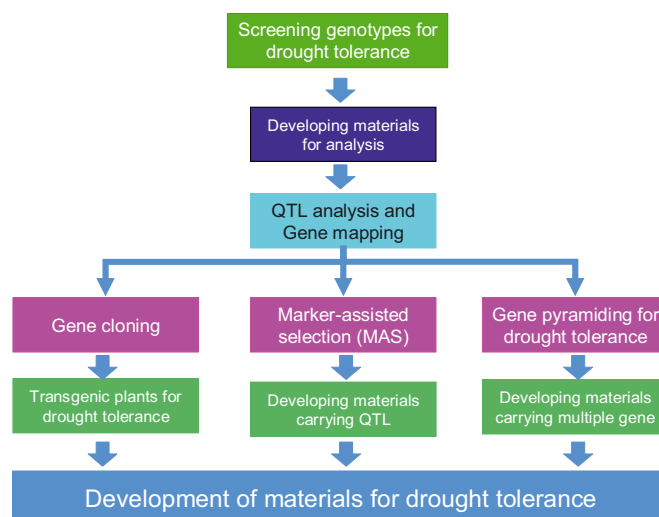


Figure 9. Developing materials for drought tolerance. Under drought stress conditions, the genotypes showing drought tolerance are selected. To analyze the genotypes for drought tolerance, the materials for analysis are developed. Using developed materials, QTL analysis and gene mapping are conducted. For gene cloning, identified genes or major QTL are analyzed in detail using a large size population. A cloned gene for drought tolerance is transferred into widely adapted varieties. To develop the materials carrying the gene or QTL for drought tolerance, DNA markers which linked to the gene or QTL are used for marker-assisted selection. Similarly, marker-assisted selection is used for developing the materials of gene pyramiding. Gene cloning, marker-assisted selection and gene pyramiding are useful for developing the materials for drought tolerance. QTL: quantitative trait locus.

multi-location testing of progenies in environments representing a random selection of the variation in drought stress in the target environment (Babu et al., 2003). A modification to this strategy involves selection for putative drought-adaptive secondary traits (Ludlow and Muchow, 1990), either alone or as part of a selection index. Selection for low-transpiration types, at unchanged water-use efficiency, would result in lower yields under optimum conditions.

In recent studies on unselected populations of doubled-haploid lines, broad-sense heritability of grain yield under reproductive-stage drought stress was comparable with that of grain yield estimated in non-stressed conditions (Atlin and Lafitte, 2002; Babu et al., 2003; Venuprasad et al., 2007). Considerable efforts have been targeted at the genetic analysis of secondary traits such as root system architecture, leaf water potential, panicle water potential, osmotic adjustment and relative water content (Jongdee et al., 2002). A suitable secondary trait is: (1) genetically associated with grain yield under drought; (2) highly heritable; (3) stable and feasible to measure and (4) not associated with yield loss under ideal growing conditions (Edmeades et al., 2001). However, such traits rarely have high broad-sense heritability like yield under drought stress and are often not highly correlated with it (Atlin and Lafitte, 2002).

Hampered water-use efficiency is an initial and the most common plant response to drought stress and plant species/varieties show great variations for this trait. Thus, it is a genetically linked trait. Available reports show that drought-tolerant species reduce the water loss either by reducing the leaf area or restricting stomatal opening or both (Lazaridou et al., 2003; Abbate et al., 2004; Lazaridou and Koutroubas, 2004) simultaneously with less effect on the biomass production (Lazaridou et al., 2003; Abbate et al., 2004; Lazaridou and Koutroubas, 2004). In the genotypes, which are either unable to adjust their organ size and reduce water loss or sustain the biomass production under water-limited conditions, water-use efficiency is substantially reduced (Costa et al., 1997). Condon et al. (2004) described three key processes in breeding to improve water-use efficiency in crop plants. These include (1) increasing the uptake of available water; (2) improving biomass production per unit transpired water and (3) partitioning of produced biomass towards the harvested product.

4.2. Molecular and functional genomics approaches

For more than two decades, molecular and biochemical studies have identified many of the abscisic acid- and stress-responsive genes and a few of the transcription factors responsible for their induction in crop plants (Buchanan et al., 2005; Poroyko et al., 2005). The products of certain stress-responsive genes could function in alleviating stress damage through still elusive mechanisms (Shinozaki et al., 2003).

Many laboratory and field studies have shown that transgenic expression of some of the stress-regulated genes results in increased tolerance to drought and other stresses. These transgenic approaches are currently the mainstream method to bioengineer drought tolerance in crop plants (Bahieldina et al., 2005). However, enhanced expression of these genes is frequently associated with retarded growth and thus may limit its practical applications. Arising from breeding or bioengineering, the next generation of drought-tolerant crop plants requires better understanding of the molecular and genetic basis of drought resistance (Xiong et al., 2006). In this regard, rice, a submerged plant, offers an excellent model for the precise understanding of drought tolerance phenomena. An increasing number of studies witnesses that rice displays early morphological changes upon exposure to drought at various growth stages (Manikavelu et al., 2006). Since drought tolerance is a genetically controlled phenomenon, many quantitative trait loci for membrane stability and other functionally related phenomena genes have been characterized using bioinformatics tools (Tripathy et al., 2000; Fu et al., 2007).

To identify the less obvious genetic networks that respond to stress, more straightforward and sensitive methods are necessary. The advent of whole genomics and related technologies is providing the necessary tools to identify key genes that respond to drought stress and relating their regulation to adaptive events occurring during stress (Bruce et al., 2002). Differential display was one of the earliest methods of parallel screening for differences in the levels of complementary DNA frag-

ments generated from messenger RNA isolated from samples between experimental treatments (Liang and Pardee, 1992).

The progressive cloning of many stress-related genes and responsive elements, and the proof of their association with stress-tolerant quantitative trait loci suggests that these genes may represent the molecular basis of stress tolerance (Cattivelli et al., 2002, 2008). On the other hand, the identification of quantitative trait loci associated with drought tolerance is also an important tool for marker-assisted selection of desirable plants (Fig. 9). In a recent study, mapping of quantitative trait loci for grain yield and its components using a simple sequence repeat/expressed sequence tag marker map explained considerable variation in chromosome 4A of wheat (Kirigwi et al., 2007). It makes clear that the combination of traditional and molecular breeding, marker-assisted selection and genetic engineering may allow a more rapid way to improve abiotic stress tolerance in crops (Chaves and Oliveira, 2004).

In summary, to be able to prove that a transgenic plant is more resistant to water stress than the wild type, one would need a rigorous evaluation of the physiological performance as well as water status of transformed plants. This will avoid ambiguous interpretations of the genetic effects on drought resistance of plants (Chaves and Oliveira, 2004).

4.3. Induction of drought resistance

Drought resistance can be induced by adopting various strategies. Of these, exogenous use of various growth regulating and other chemicals has proven worthwhile in producing drought resistance at various growth stages in a number of plants. An account of these strategies is given below.

4.3.1. Seed priming

One of the short-term and most pragmatic approaches to overcome the drought stress effects is seed priming. Seed priming is a technique by which seeds are partially hydrated to a point where germination-related metabolic processes begin but radicle emergence does not occur (Farooq et al., 2006). Primed seeds usually exhibit increased germination rate, greater germination uniformity, and sometimes greater total germination percentage (Kaya et al., 2006; Farooq et al., 2007). This approach has been applied to overcome the drought stress effects in a range of crop species.

Improvement of rice and other crops for growing in water-scarce areas is of current interest. In the newly introduced aerobic rice culture, the frequency and intensity of drought may increase manifold. Du and Tuong (2002), while testing the effectiveness of different osmotica to improve the performance of direct-seeded rice, noted that osmopriming with 4% KCl solution and saturated CaHPO₄ solution was successful in improving the seedling emergence, crop stand establishment and yield under stress. In drought-prone areas primed rice seeds germinated well and seedlings emerged faster and more uniformly, leading to increased yield (Harris et al., 2002). A germination trial of 11 varieties of upland rice under limited soil moisture

conditions revealed early and synchronized emergence owing to seed priming (Harris and Jones, 1997).

Seed priming improved performance of wheat seeds under drought stress in terms of germination and water-use efficiency of drought-stressed plants by 44% compared with unprimed seeds (Ajouri et al., 2004). The beneficial effects of priming included faster emergence of crop seedlings, early flowering and higher grain yield even under drought stress (Kaur et al., 2005). In sunflower, osmopriming with KNO_3 and hydropriming improved the germination and stand establishment under stress conditions (Kaya et al., 2006).

4.3.2. Use of plant growth regulators

Foliar application of plant growth regulators, both natural and synthetic, has proven worthwhile for improving growth against a variety of abiotic stresses. Drought stress alone inhibited increases in length and fresh weight of the hypocotyl, while applied levels of gibberellic acid reversed this effect. In this case, gibberellic acid partially increased the water status of the seedlings and partially sustained protein synthesis (Taiz and Zeiger, 2006). Exogenous application of gibberellic acid increased the net photosynthetic rate, stomatal conductance and transpiration rate in cotton (Kumar et al., 2001), and stimulated pollen and seed cone production in Sitka spruce (*Picea sitchensis*) under drought stress (Philipson, 2003).

Among other hormones, exogenous application of 1-aminocyclopropane-1-carboxylic acid also improves drought tolerance by delaying senescence (Todd et al., 2004). In another study, exogenously applied uniconazole, brassinolide and abscisic acid increased soybean yields both under well-watered and water deficit conditions. Under water stress conditions, plant growth regulator treatments significantly increased water potential, and improved chlorophyll content (Zhang et al., 2004). Jasmonates, including jasmonic acid and its related compounds, are a group of naturally occurring growth regulators rather recently discovered in higher plants (Creelman and Mullet, 1995). Jasmonates play an essential role in the signaling pathway, triggering the expression of plant defense genes in response to various stresses (Koda, 1997). Exogenously applied jasmonic acid induced drought tolerance by increasing the betaine level in pear (Gao et al., 2004). Exogenous application of brassinolide, uniconazole and methyl jasmonate in maize improved drought tolerance owing to increased activities of superoxide dismutase, catalase and ascorbate peroxidase, abscisic acid and total carotenoid contents (Li et al., 1998). Benzyladenine is an active cytokinin, which can increase the drought resistance of different plants (Shang, 2000).

Salicylic acid can also effectively improve plant growth under drought conditions (Senaratna et al., 2000). In a recent study, exogenous application of salicylic acid improved the drought tolerance of winter wheat, which was correlated with an increased catalase activity (Horváth et al., 2007). Both salicylic acid and acetyl-salicylic acid (a derivative of salicylic acid), applied at various concentrations through seed soaking or foliar spray protected muskmelon (*Cucumis melo*)

seedlings, subjected to drought stress. However, the best protection was obtained from seedlings pretreated with lower concentrations of salicylic acid (Korkmaz et al., 2007).

The fact that seed imbibition with salicylic acid or acetyl-salicylic acid confers stress tolerance in plants is more consistent with signaling for gene expression rather than their direct effects (Senaratna et al., 2000). The endogenous salicylic acid content was increased in drought-stressed *Phillyrea angustifolia* (Munné-Bosch and Penuela, 2003), suggesting that salicylic acid might have a role in the drought stress response. In wheat, salicylic acid was shown to increase the abscisic acid content, leading to the accumulation of proline (Shakirova et al., 2003). Pretreatment with 0.5 mM salicylic acid for 1 day limited the drought tolerance of 2-week-old maize plants by increasing their polyamine content (Németh et al., 2002). However, soaking grains in acetyl-salicylic acid improved the drought tolerance of wheat.

4.3.3. Use of osmoprotectants

Osmoprotectants are involved in signaling and regulating plant responses to multiple stresses, including reduced growth that may be part of the plant's adaptation against stress (Fig. 7). In plants, the common osmoprotectants are proline, trehalose, fructan, mannitol, glycinebetaine and others (Zhu, 2002). They play adaptive roles in mediating osmotic adjustment and protecting subcellular structures in stressed plants (Fig. 8). However, not all plants accumulate these compounds in sufficient amounts to avert adverse effects of drought stress (Penna, 2003). Ashraf and Foolad (2007) outlined three approaches to increase the concentrations of these compounds in plants grown under stress conditions to increase their stress tolerance: (1) use of traditional protocols of plant genetics and breeding to develop cultivars with natural abilities to produce high levels of these compounds under stress conditions, (2) engineering genetically modified plants capable of producing sufficient amounts of these compounds in response to environmental stresses and (3) as a short-cut method, exogenous use of these osmolytes on plants to enhance their stress tolerance ability.

Exogenously applied glycinebetaine improves the growth and production of some plants under stress (Naidu et al., 1998; Chen et al., 2000; Hussain et al., 2008). In many crop plants the natural accumulation of glycinebetaine is lower than sufficient to ameliorate the adverse effects of dehydration caused by various environmental stresses (Subbarao et al., 2000). Exogenous application of glycinebetaine has been reported to improve drought tolerance in this regard (Hussain et al., 2008). Foliar-applied glycinebetaine improved the growth of plants subjected to water deficit by the maintenance of leaf water status due to improved osmotic adjustment and enhanced photosynthesis, primarily due to a greater stomatal conductance and carboxylation efficiency of Rubisco (Sakamoto and Murata, 2002). Exogenous application of glycinebetaine effectively diminished the drought effects in terms of greater number of achenes per capitulum in sunflower (Azam et al., 2005). However, pre-soaking of seeds with glycinebetaine was not

effective in preventing the adverse effects of water stress on yield components. Glycinebetaine application at the vegetative stage was more effective in ameliorating the adverse effects of drought (Azam et al., 2005). Glycinebetaine also increased anti-oxidative enzyme activities under water deficit (Ma et al., 2007). Exogenously applied proline enhanced the endogenous accumulation of free proline and improved the drought tolerance in petunia (Yamada et al., 2005).

Inhibitors of polyamine biosynthetic enzymes limit stress tolerance of wheat but the concomitant exogenous application of polyamines restores it (Liu et al., 2004). Exogenous spermidine application before the drought stress significantly improved the stress tolerance in barley (Kubiś, 2003). In a recent review, Liu et al. (2007) concluded that though there was variation in effects between polyamines and plant species, exogenous polyamine application to stressed cells or tissues could lead to injury alleviation and growth promotion. Yang et al. (2007) suggested that for rice, to perform well under drought stress, it should have higher levels of free spermidine/free spermine and insoluble-conjugate putrescine.

4.3.4. Silicon

Silicon is the second most abundant element in soils and a mineral substrate for most of the world's plant life. Ample evidence is available indicating that when silicon is readily available to plants, it plays a significant role in their growth, mineral nutrition, mechanical strength and resistance to several stresses (Epstein, 1994). It has not been considered an essential element for higher plants yet, partly because its role in plant biology is less well understood (Gong et al., 2003). Nevertheless, numerous studies demonstrate that silicon is an important element, and plays an important role in tolerance of plants to environmental stresses (Savant et al., 1999).

With respect to drought stress, relevant work is limited on silicon. Sorghum (*Sorghum bicolor*) plants grown in pots in the presence of silicon had higher relative water content and dry materials by improving shoot water uptake (Hattori et al., 2001, 2005). Wheat plants applied with silicon could maintain better water status and higher content of dry materials compared with non-silicon treatment under drought (Gong et al., 2003). Exogenously applied silicon lowered the shoot to root ratio, indicating the facilitation of root growth and maintenance of a higher photosynthetic rate and stomatal conductance compared with plants grown without silicon application under drought stress (Hattori et al., 2005). In another study, Gong et al. (2005) opined that the silicon-triggered improvement in drought tolerance of wheat plants was associated with an increase in antioxidant defense, thereby alleviating oxidative stress on functional molecules of cells. Silicification endodermal tissue was found to play an important role in water transport across the root of rice (Lux et al., 1999) and sorghum (Lux et al., 2002). These data, together with the rate of silicon uptake and deposition by sorghum roots (Lux et al., 2003), and the effects of losing root cell walls in sorghum (Hattori et al., 2003), suggested an important role of silicon in water transport and maintenance of root growth under drought stress.

5. CONCLUSION

Water deficit reduces plant growth and development, leading to the production of smaller organs, and hampered flower production and grain filling. A diminution in grain filling occurs due to a decrease in the accumulation of sucrose and starch synthesis enzymes. Timing, duration, severity and speed of development undoubtedly have pivotal roles in determining how a plant responds to water deficit. Following drought, stomata close progressively with a parallel decline in net photosynthesis and water-use efficiency. Stomatal conductance is not controlled by soil water availability alone, but by a complex interaction of intrinsic and extrinsic factors. Depending upon the availability of moisture, activities of the enzymes of carbon assimilation and those involved in adenosine triphosphate synthesis are decreased and sometimes inhibited. One of the major factors responsible for impaired plant growth and productivity under drought stress is the production of reactive oxygen species in organelles including chloroplasts, mitochondria and peroxisomes. The reactive oxygen species target the peroxidation of cellular membrane lipids and degradation of enzyme proteins and nucleic acids.

Being very complex, the drought tolerance mechanism involves a number of physiological and biochemical processes at cell, tissue, organ and whole-plant levels, when activated at different stages of plant development. Examples of these mechanisms are reduction in water loss by increasing stomatal resistance, increased water uptake by developing large and deep root systems, accumulation of osmolytes and osmoprotectant synthesis. Amongst plant growth substances, salicylic acid, cytokinin and abscisic acid have been reported to play an important role in drought tolerance. Scavenging of reactive oxygen species by enzymatic and non-enzymatic systems, cell membrane stability, expression of aquaporins and stress proteins are also vital mechanisms of drought tolerance. Drought stress effects can be managed by production of most appropriate plant genotypes, seed priming, plant growth regulators, use of osmoprotectants, silicon and some other strategies.

Although physiological mechanisms of drought tolerance are relatively well understood, further studies are essential to determine the physiological basis of assimilate partitioning from source to sink, plant phenotypic flexibility which leads to drought tolerance, and factors that modulate plant drought-stress response. Like most other abiotic stresses, foliar plant parts are more directly impinged upon by drought than roots. However, an understanding of root responses to drought stress, most likely involving root-shoot signaling, is a preferred area of research. Investigations that seek to improve crop performance by increasing osmotic adjustment need to focus on meristematic regions of roots. For effective application and commercial use of exogenous glycinebetaine, proline and other compatible solutes as inducers of drought tolerance, their mechanisms of action, the most optimal concentrations, and appropriate plant developmental stages must be carefully determined. The role of H₂O₂ as a signaling molecule as well as the identification of regulatory components in the pathway that leads to plant responses to drought stress are fundamental clues for future research. Applications of genomics,

proteomics and transcriptomic approaches to a better understanding of the molecular basis of plant drought tolerance and improved water-use efficiency under drought are also imperative. Mutants or transgenic plants exhibiting differential capabilities for reactive oxygen species formation and elimination could be useful to elucidate this fundamental point. Molecular knowledge of response and tolerance mechanisms is likely to pave the way for engineering plants that can withstand and give satisfactory economic yield under drought stress.

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