Plant Water-Stress Response Mechanisms

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Abstract

Water, the central molecule of life, plays a profound role in a number of plant life processes ranging from photosynthesis to macromolecular interaction through hydrophobic bond. Due to imbalances in natural status of the different physiological, environmental conditions and during natural calamities, plants are exposed to either deficit of water (i.e. drought) or excess of water (i.e. flooding). Both of these conditions lead to water stress on plants which in turn results in disruption of agriculture and food supply in different parts of the world. In this chapter, a brief idea on the causes, indicators, responses and adaptation processes to the water stress in plants and the associated molecular mechanisms has been presented. In this chapter, the stresses related to water are expressed as "drought". The cellular and molecular responses of plants to water stress have been studied intensively throughout the world. Understanding the mechanisms by which plants perceive water stress and transmit the subsequent signals to cellular machinery and modulate expression of genes and their products to activate adaptive responses is of fundamental importance to plant biology. Knowledge about water-stress signal transduction is therefore vital for continued development of rational breeding and transgenic strategies to improve stress tolerance in crops. Factors controlling water-stress conditions alter the normal equilibrium and lead to a series of morphological, physiological, biochemical and molecular changes in plants which adversely affect their growth and productivity. However, plants also have developed innate adaptations to water-stress conditions

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with an array of biochemical and physiological interventions that involve the function of many stress-associated genes. Water-stress-associated hormones like ABA are found to play a central role in orchestrating the molecular and physiological responses leading protective responses in plants. Overall, this chapter provides a systemic glimpse of integrated cellular and whole plant responses to water stress.

Keywords
Water stress • Drought • Signal transduction • Water-stress resistance • Stress tolerance

Abbreviations

ABA	Abscisic acid
ABREs	Abscisic acid responsive elements
APX	Ascorbate peroxidase
AtHD6	Histone deacetylase 6
ATP	Adenosine triphosphate
BapA	Boiling staple protein
bZIP	Basic leucine zipper domain
CBL	Calcineurin B-like protein
CDSP	Chloroplast drought-stress protein
CIPKs	CBL-interacting protein kinases
CO_2	Carbon dioxide
COR	Cold regulated
CPKs/CDPKs	Calcium-dependent protein kinases
DAG	Diacylglycerol
DREs	Dehydration-responsive elements
ERD	Early response to dehydration
ET	Electron transport
ETR	Electron transport rate
Fs	Steady state of chlorophyll fluorescence
GL	Glycolipids
GRase	Glutathione reductase
HSP	Heat-shock protein
IP3	Inositol 1,4,5-trisphosphate
KIN	Cold inducible
LEA	Late embryogenesis abundant
LEAPs	Late embryogenesis abundant proteins
MAPK	Mitogen-activated protein kinase
MYC	Myelocytomatosis oncogene
NAADP	Nicotinic acid adenine dinucleotide phosphate
NAD	Nicotinamide adenine dinucleotide
NADP	Nicotinamide adenine dinucleotide phosphate
NFYA5	Nuclear factor Y, subunit A5
PL	Phospholipids
PLC	Phospholipase C
PS	Photosystem
RAB	Responsive to ABA
RC	Reaction centre
RD	Responsive to dehydration
RNA	Ribonucleic acid
ROS	Reactive oxygen species
RuBisCO	Ribulose-1,5-bisphosphate carboxylase oxygenase
RWC	Relative water content
SOD	Super oxide dismutase
WD	Water deficit

Introduction

Plants in nature are constantly exposed to various abiotic stresses resulting from unfavourable environmental conditions which adversely affect their growth and development (Atkinson and Urwin 2012). Water stress is one of the main abiotic stresses to which crops are exposed in India. Plant water stress, often caused by drought, can have major impact on plant growth and development (Jaleel et al. 2009). When drought occurs, then it can be the cause of lower yields and possible crop failure. The effects of plant water stress vary between the plant species. Early recognition of water-stress symptoms can be critical to maintain the growth of a crop. The most common symptom of plant water stress is wilt. As the plant undergoes water stress, the water pressure inside the leaves decreases and the plant wilts. Drying to a condition of wilt will reduce the growth of any plant (Kaur and Gupta 2005).

From an irrigator's perspective, managing water to minimise stress means knowing plant water availability, recognising symptoms of water stress and planning ahead. This chapter outlines how water stress impacts plant growth and development and how to anticipate plant water stress to minimise negative consequences. Drought (water stress) is one of the main abiotic stress factors that affect all organisms' lives. Drought occurs when soil moisture level and relative humidity in air are low, while temperature is also high. Almost every plant process is affected directly or indirectly by water supply (Akıncı 1997; Lobell et al. 2013). Plants, as one of the basic food sources, either in nature or in cultivations, in their growing period, require water or at least moisture for germination. It is obvious that most land plants are exposed to short- or long-term water stresses at some times in their life cycle and tend to develop some adaptive mechanisms for adapting to changing environmental conditions. The extent and duration of the water deprivation determines the magnitude of stress response (Pugnaire et al. 1999). Some plants may adapt more easily than others giving them an advantage over competitors. Water stress may range from moderate, and of short duration, to extremely severe and prolonged summer drought (Pereira and Chaves 1993, 1995; Bottner et al. 1995). At the whole plant level, the effect of water stress is usually perceived as a decrease in photosynthesis and growth and is associated with alteration in carbon and nitrogen metabolism (Cornic and Massacci 1996; Mwanamwenge et al. 1999). It is observed that within a few seconds following the onset of water stress, short-term responses which are primarily linked to stomatal regulation appeared. Short-term responses lead to reduction in water loss by transpiration and maximising CO_2 intake. Optimum efficiency of these initial responses is found to be responsible for maintenance of constant ratio of transpiration to photosynthesis (Kozlowski et al. 1991). Midterm responses also known as acclimation comprise of the fine-tuning of the osmotic potential by accumulation of solute, modifications in cell wall elasticity and morphological variations. Long-term adaptation to drought is characterised by variation in gene responses, anatomical modifications of specific organs and acquisition of modified physiological mechanisms with an aim to reduce the overall growth to balance resource utilisation (Chapin 1980, 1991) (Fig. 1). Under field conditions, these responses can be synergistically or antagonistically modified by the superimposition of other stresses.

The most severe form of water deficit is desiccation – when most of the protoplasmic water is lost and only a very small amount of tightly bound water remains in the cell. It is reported that water stress encompasses both destructive and constructive elements and acts as a determining factor as well as a driving force for improving resistance and adaptive evolution (Larcher 1987). Plant resistance to water stress which leads to adaptation results from either tolerance or a mechanism that supports avoidance. Whole plant can contribute to the avoidance of water deficit through an array of mechanisms during the plant's life cycle, and evasion to water stress can also occur at the cellular level. The important determinants of these adaptive responses include the species and genotype, the extent and severity of water loss, the age and phase of development, the organ and cell type and the subcellular compartment. An example of avoidance at the cellular level is the process of osmotic adjustment where the osmotic potential of the cell is lowered in order for the water potential gradient to favour water uptake and maintenance of turgor (Bray 1997) (Fig. 1).

In response to water stress, a plethora of modification occurred in the intracellular milieu of the plant cells. The changes include the

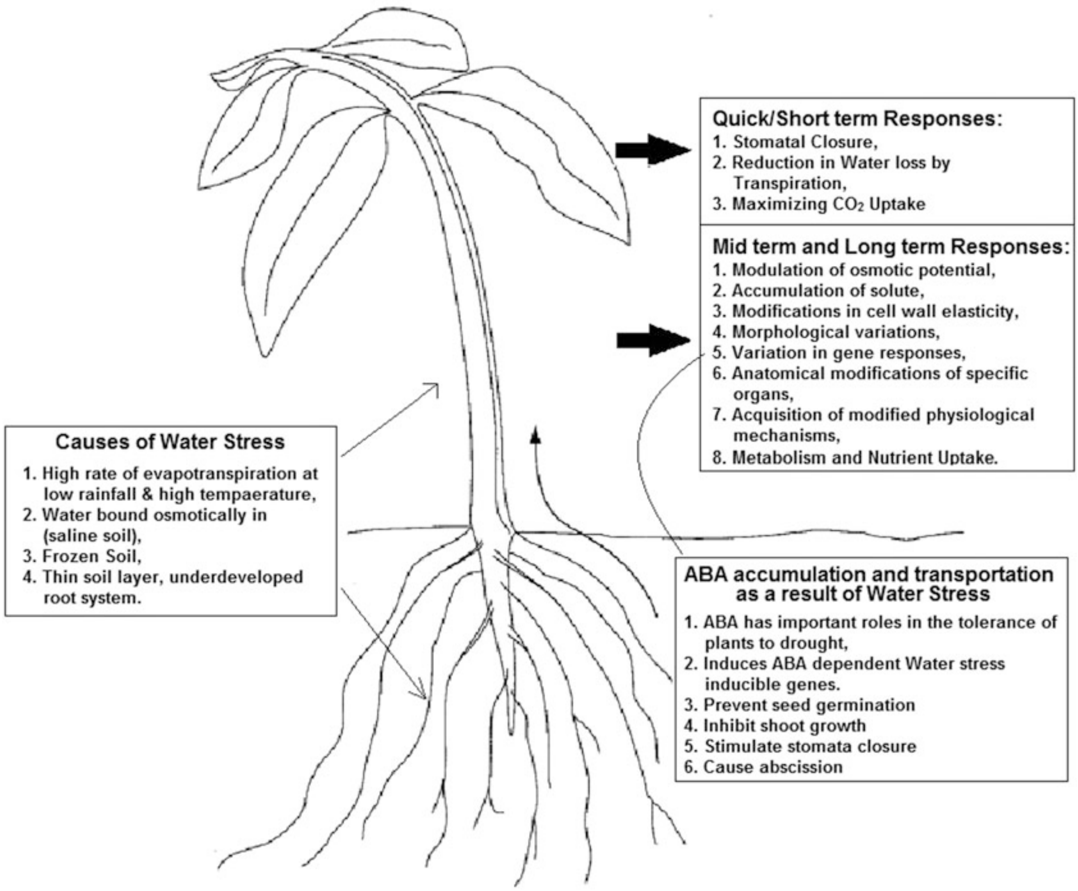

Fig. 1 Causes of water stress and variable responses shown by plants against drought

modification of different intracellular metabolic pathways, changes in the nutrient and ion uptake, synthesis of new proteins, modulation of free radical generation and all these changes found to be preceding the induction of signal transduction pathways. Water stress induces a multiple signal transduction pathway which follows the generation of second messengers (e.g. inositol phosphates, lipid mediators and reactive oxygen species). These second messengers in turn modulate intracellular Ca^{2+} level and activate kinases to initiate protein phosphorylation cascades. These events lead to activation of target proteins which are directly involved in cellular protection or acting as transcription factors controlling genes explicitly involved in regulation of water stress. The activation of these genes is found to be involved in the generation of the plant hormones like abscisic acid (ABA), ethylene and salicylic acid (SA) which in turn initiate a second round of signalling which may be responsible for the adaptive and tolerance responses associated with water stress (Xiong et al. 2002). Specificity in water-stress responses in plants is further determined by a complex regulatory network of molecular mechanisms which include the interaction between transcription factors, kinase cascades, production of reactive oxygen species as well as involvement of heat-shock factors and small RNAs (Atkinson and Urwin 2012).

One of the important adaptive features acquired by the plants to water stress includes sun-type or shade-type chloroplast adaptation which is also induced by many other stress factors including drought (Lichtenthaler et al. 1981). Regions with adequate but non-uniform precipitation also experience water-limiting environments. The general effects of drought on plant growth are fairly well known. However, the primary effect of water deficit at the biochemical and molecular levels is not considerably understood yet, and such understanding is crucial. Knowledge of the biochemical and molecular responses to drought is essential for a holistic perception of plant resistance mechanisms to water-limited conditions in higher plants. The response to abiotic stress results in a dramatic change of the whole plant transcriptome. It is reported that the transcriptomic response to drought can vary with the time of day. These responses seem to interact with hormonal and other stress pathways that naturally vary during the course of the day (Wilkins et al. 2010; Cramer et al. 2011). Sometimes a comparison between cellular response and whole plant response may reveal the level of organisation where the adaptation operates (Kar 2011). In this chapter, we provide an overview of the current understanding of plant responses to drought. In addition, we will describe the cellular signalling mechanisms leading to protect the plant from the deleterious effects of drought.

Origin of Plant Water Stress

Water stress in plants results either from restricted water supply to their roots or due to increased rate of transpiration. Plants growing under arid and semiarid environments frequently experienced the water stress associated with drought. It is reported that high temperatures act as an indirect driver of plant water stress (Lobell et al. 2013). Roots are the primary site of water intake in plants. The extent of force required for a plant to absorb water from the soil is known as the matric potential. In conditions of low soil moisture, more energy is required by the plants to remove water from the soil; thus, the matric potential is greater. Symptoms of water stress have been experienced by plants when the soil is dry and the matric potential is strong (Glyn Bengough et al. 2011). This condition is recognised as the matric effect. It has also been shown that heat is an indirect driver of reduced crop yield through increased plant evapotranspiration (Lobell et al. 2013) (Fig. 1).

Measurement of Water Stress in Plants

The extent of water stress experienced by plants in their habitat can be assessed by measuring the soil moisture and analyses of the distribution of precipitation. Measurement of water potential (ψ) in plants is found to be the most fundamental indicator of water stress. No water stress (small negative water potential values) was found in soils with high water-holding capacity. On the other hand, moderate to high water stress was recorded at the end of the season in those sites with low water-holding capacity. A linear relationship between predawn leaf water potential and stem water potential is also reported (McCutchan and Shackel 1992). Another commonly used indicator of plant water status is relative water content or RWC which at one time had been less accurately termed as relative turgidity. Tissue water content (percent of fresh weight) and fresh weight have also been used as indicators of water status. Unfortunately, water content or fresh weight of tissue at full turgor is normally not given as a reference. Water content can be very misleading because of its superficial resemblance to RWC (Hsiao 1973). In some studies, visual wilting is considered as the sole indicator of water status. Although wilting is dependent on turgor pressure, it is also a function of the mechanical properties of cell wall and tissue (Hsiao 1973; Joly 1985) (Fig. 2).

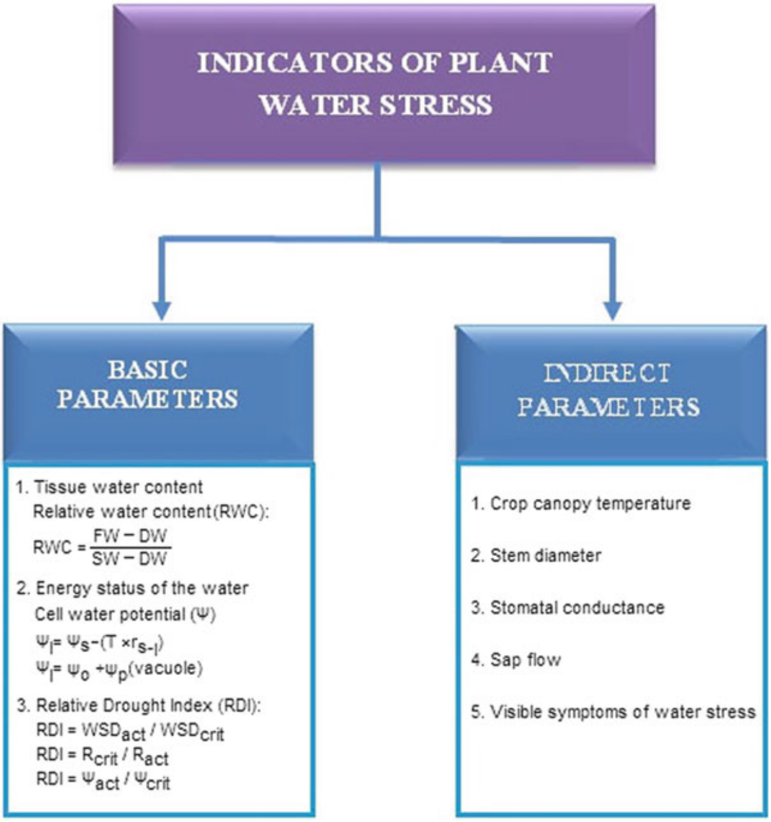

Fig. 2 Indicator of plant water stress

Plant Responses to Water Stress

Photosynthetic Responses to Drought

Reduced rate of photosynthesis is a usual effect of water stress in plants. Water stress reduces photosynthesis by decreasing both leaf area and photosynthetic rate per unit leaf area (McCree 1986). Photosynthesis is severely inhibited and may cease altogether as water deficits increase in crop plants. Water deficiency in plants generates metabolic changes along with functional and structural rearrangements of photosynthesising apparatus. The decrease in leaf growth or increasing senescence of leaves under drought conditions may also inhibit photosynthesis in existing leaves (Boyer 1976). Decreasing water content is accompanied by loss of turgor and wilting, cessation of cell enlargement, closure of stomata, alteration of photosynthesis and interference with many other basic metabolic processes (Kramer and Boyer 1995).

The inhibition of photosynthesis during water stress could be explained as the cause of the stomata closure and the internal CO_2 concentration decrease. Stomatal limitation is more severe when a plant is stressed than when it is not. Therefore, it is rather surprising that photosynthesis often decreases in parallel with or more than stomatal conductance. Limitation of carbon uptake during water stress might be associated with stomatal control of water (Chaves 1991; Cornic and Massacci 1996). Stomata close in response either to a decline in leaf turgor and/or water potential or to a low-humidity atmosphere (Maroco et al. 1997).

The photosynthetic rate in higher plants decreases more rapidly than respiration rate with increased water stress. A nearly effect of water reduction in leaves is usually partial or complete stomatal closures which markedly decrease the movement of carbon dioxide into the assimilating leaves and reduce the photosynthetic rate up to ten times depending on the amount of water removal and the sensitivity of the plant (Ghannoum 2009; Akıncı and Lösel 2012; Chaves et al. 2003).

In C_4 plants, stomatal closure is found to be a major determinant in the inhibition of photosynthesis under water stress, while non-stomatal factors like metabolic impairments are also reported to play the major role in this inhibition. In both C_3 and C_4 plants, the rate of photosynthesis decreases under the drought conditions. It is evidenced that the rate of photosynthesis is more affected in C_4 plants (like corn) than C_3 plants (such as wheat) in conditions of water deficits. This explains the fact that hot arid areas with prevalence of C_4 plants are more susceptible to frequent drought. A number of cofactors like (a) low CO_2 uptake due to stomatal closure and resistance, (b) qualitative and quantitative changes in photosynthesising pigments and (c) poor assimilation rates in photosynthetic leaves are found to be affected under water stress which in turn decreases the rate of photosynthesis in plants. Water stress is also found to inhibit chlorophyll synthesis and subsequently decrease chlorophyll content of leaves. In severe stress, photosynthesis may be more controlled by the chloroplast's capacity to fix CO_2 than by the increased diffusive resistance (Faver et al. 1996; Herppich and Peckmann 1997).

Unlike chlorophyll, other plant pigments like xanthophyll are found to be less sensitive to water stress. During water stress, the synthesis of xanthophyll pigment is shown to be upregulated which supports the finding that xanthophyll pigments have a protective role in plants under stress and also are found to play an inhibitory role on reactive oxygen species (ROS) production (Lisar et al. 2012). The photosynthetic enzymes have been shown to be significantly affected by water stress. In case of C_4, it is difficult to draw a conclusion regarding the specific pattern in the modulation of enzyme activity in response to drought stress, whereas in C_3 cycle enzymes are found to be consistently inhibited in response to water stress. Activity of RuBisCO, the key enzyme for carbon metabolism in leaves, is reported to be strikingly decreased in conditions of water stress. Inhibition of the RuBisCO activity during water stress is found to be associated with acidification of the chloroplast stroma. Furthermore, water-stress-associated suppression in RuBisCO activity is also related to the alterations of the chloroplast structure, conformational change of the RuBisCO, lack of the substrate and reduction in the activity of the coupling factor – ATPase – and sometimes due to damage, the plastids may lose RuBisCO. Activity of other photosynthetic enzymes like NAD-dependent malate dehydrogenase, phosphoenolpyruvate carboxylase, fructose-1,6-bisphosphatase and other related enzymes also is found to be inhibited to different extents (Ramachandra et al. 2004; Lisar et al. 2012) (Fig. 3).

Water stress also disrupts the cyclic and non-cyclic types of electron transport during the light reaction of photosynthesis. The disruption is clear in the oxygen-releasing complex and electron transfer from protochlorophyllide to P_{700}. Lower electron transport rate negatively affects photophosphorylation process and decreases ATP synthesis as well as $NADP^+$ reduction. ATPase inhibition under water deficiency is also responsible for the reduction in ATP levels in chloroplasts. All these factors cumulatively affect the intensity of photo-assimilation and the stability of the photosynthetic apparatus under the conditions of water stress. Both of the PSs in chloroplasts are affected by water deficiency; however, PS1 of some plants is more severely damaged compared to PS2, though there is an opposite concept as well (Ramachandra et al. 2004; Lisar et al. 2012).

Transpiration and Stomata

Stomatal closure is commonly the principal mechanism responsible for restricting transpiration rates in plants during exposure to water stress. Transpiration is directly proportional to the gradient of water vapour concentration from the internal evaporation surface to the bulk air outside the leaf and inversely proportional to the

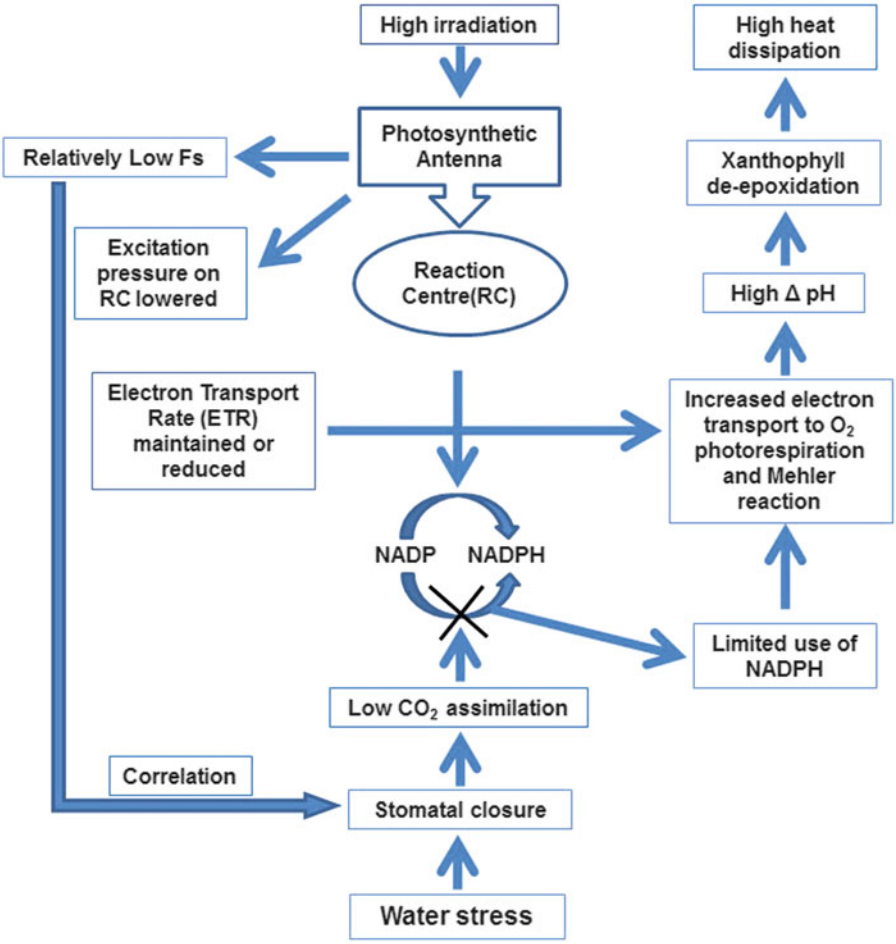

Fig. 3 Schematic presentation of photosynthetic control mechanisms under water stress. *ETR* electron transport rate, *RC* reaction centre, *Fs* steady state of chlorophyll fluorescence

total resistance to water vapour transport of the air boundary layer and of the leaf. In addition, increased stomatal resistance may not cause proportional decreases in transpiration rate because diminished dissipation of heat by vaporisation and the consequent rise in leaf temperature increase the water vapour concentration inside the leaf. In most situations, the rise in leaf temperature accompanying substantial reduction in transpiration has been calculated or measured to be only a few degrees (Hsiao 1973; Chaves et al 2003). Therefore, it would be reasonable to assume that elevation in leaf temperature does not play a general role in water-stress effects. Some other non-stomatal factors in the leaf like "mesophyll" or "wall" resistance cause significant reductions in transpiration as water stress develops. The "wall" resistance is small in turgid leaves and tends to rise with moderate water deficits to a significant level which is nevertheless still minor compared with the expected stomatal resistance (Crafts 1968). Adaxial and abaxial stomata have been observed to differ in response to water stress in some cases but apparently not in others (Wang et al. 1998). The above results indicate that stomata are somewhat insensitive to mild water stress. However, this conclusion probably cannot be generalised, since there are direct or indirect indications that stomata of other species may be sensitive to small water deficits. The stomatal response is found to be dependent on threshold water status. It is observed that the optimum water content for stomatal opening can be actually something less than the tissue water content at full turgor. Full turgor can cause some stomatal closure, presumably because of excessive back pressure from the epidermal cells surrounding the guard cells. Once the threshold water status for stomatal closure is reached, leaf resistance increases sharply, rising 20- or 30-fold. Such large increases in leaf resistance may be taken as indicative of almost complete stomatal closure. Aside from leaf water status, there is some evidence that water vapour content of the air may be very important in determining stomatal opening. In case of maize leaves it is reported that at the same water deficit the diffusive resistance is upto several times as great in dry air (nearly zero humidity) as in moist air. Light may also modify stomatal response to water deficit. At higher light levels, more water deficit seemed to be required to induce closure. It has also been reported that stomatal response to water stress was attenuated by oxygen-free air (Hsiao 1973; Yokota et al. 2006).

Stomatal opening and closing result from turgor differences between guard cells and the surrounding subsidiary or epidermal cells. Stomatal interactions with environmental factors such as light and CO_2 are complex and appear to be mediated by a net gain or loss of guard cell potassium and turgor with the consequent stomatal movement. As the opening of the stomata is turgor dependent, water deficits by reducing leaf turgor would directly reduce opening. It has also been reported that mild water deficit is associated with marked loss of solutes from guard cells which is concurrent with stomatal closure. Thus, a part of the water-stress effect on stomatal closure and associated decrease in the rate of transpiration may not be direct but is linked to the regulation of osmotic solutes in guard cells. Another important determinant in modulating the stomatal opening during water stress is found to be abscisic acid (ABA). It is reported that ABA rises markedly in leaves subjected to water stress and that exogenous ABA is a potent and fast-acting inhibitor of stomatal opening; it is also being hypothesised that stress affects stomata via its effect on ABA levels or on plant hormonal balance, specifically the balance between ABA and cytokinins. It was reported that the rapidity and ready reversibility of the action of ABA on stomata would make it a good modulator of stomatal behaviour. Although stomatal opening is reduced during stress by a concerted effect of depressed cytokinin level and rise in ABA but kinetin, a member of cytokinin family, can promote stomatal opening within a few hours of application. Unfortunately, the stomatal response to kinetin is dependent on the duration of exposure and age of the plants. Stomata of many species and apparently of younger leaves do not respond to kinetin. It is also observed that kinetin is unable to reverse the ABA-mediated inhibition of stomata (Xiong and Zhu 2003; Hsiao 1973; Yokota et al. 2006).

Respiration

Water stress exerts a variable response on plant respiration which ranges from inhibition to stimulation under different water-stress conditions. In different plant organs like leaves, shoots, roots, flowers or whole plants, a decreased rate of respiration in response to water stress has been reported. In contradiction, some other reports have shown that in water-stressed plants the rate of respiration is almost unaffected or even increased. Leaf respiration shows a biphasic response to relative water content (RWC), decreasing in the initial stages of water stress (RWC > 60 %) and increasing as RWC decreases below 50 % (Flexas et al. 2005). Under this hypothesis, the initial decrease in respiration would be related to the immediate inhibition of leaf growth and, consequently, the growth of respiration component. The increase of respiration at lower RWC would relate to an increasing metabolism as the plant triggers acclimation mechanisms to resist water stress. These mechanisms would increase the maintenance component of respiration and, as such, the overall respiration rate. In case of root, the changes in rate of respiration in response to water stress are found to be age dependent. Respiration in the established root and rain root is shown to respond differentially in response to water stress. In established root, the rate of respiration never reached zero in response to water stress and rapidly recovers upon direct rewatering, whereas it has been shown that in rain root the rate of respiration rapidly reached zero and did not recover upon rewatering (Graham and Nobel 1999). It is hypothesised that the differential rate of respiration in response to water stress occurs at a certain threshold of water-stress intensity. It has been reported that dark respiration is generally suppressed, more or less proportionately but not very markedly, by moderate to severe water stress. Similar kind of response was observed in light respiration. It is observed that the effects might be due to plasmolysis rather than water stress. The biphasic response of respiration in whole plants against water stress has also been observed. The initial tendency is for the rate of respiration to decrease probably as a consequence of decreased energy demand for growth. A second trend that appears at severe water stress is the increase of respiration rates, possibly as a consequence of enhanced metabolism (osmoregulation, water-stress-induced senescence processes). It has been reported that the fast-growing plant species show a more pronounced biphasic response than slow-growing species (Flexas et al. 2005) (Fig. 5).

Osmotic Adjustment Mechanisms Under Water Stress

Water is essential in the maintenance of the turgor which is essential for cell enlargement and growth and for maintaining the form of herbaceous plants. Turgor is also important in the opening of stomata and the movements of leaves, flower petals and various specialised plant structures (Kramer and Boyer 1995). The turgor measurements on the lamina have often appeared to show declining rates of leaf growth with decreasing turgor (Kramer and Boyer 1995; Meyer and Boyer 1972; Michelena and Boyer 1982; Westgate and Boyer 1985). The turgor decrease may or may not occur during soil drying, and this is believed to be due to osmotic adjustment, the process in which solutes accumulate in growing cells as their water potential falls of osmotic potential arising from the net accumulation of solutes in response to maintain turgor in tissues (Turner and Jones 1980; Morgan 1984). Osmotic adjustment may allow growth to continue at low water potential. Osmotic adjustment usually depends mainly on photosynthesis to supply compatible solute. Osmotic adjustment has been defined as "the lowering water deficits or salinity" (Turner and Jones 1980). With continued water limitation, osmotic adjustment delays, but cannot completely prevent, dehydration (Kramer and Boyer 1995). Osmotic adjustment has been found in many species and has been implicated in the maintenance of stomatal conductance, photosynthesis, leaf water volume and growth (Turner and Jones 1980; Morgan 1984). In wheat and other cereals, osmotic adjustment leads to rapid responses for decreasing the effect of water stress (Richter and Wagner 1982). It is reported that water stress increases the osmotic pressure of the cell sap, increasing the percentage of sugar in sugar cane and often in sugar beet, although the yield per acre may be reduced (Russel 1976). Solutes known to accumulate with water stress and contribute to osmotic adjustment in non-halophytes include inorganic cations, organic acids, carbohydrates and free amino acids. In some plants, potassium is the primary inorganic cation accumulating during water stress, and it is often the most abundant solute in a leaf (Jones et al 1980; Ford and Wilson 1981). Osmotic adjustment is usually not permanent, and plants often respond rapidly to increased availability of water. Morgan and Condon (1986) showed that such increase in solute concentration gives tissues a temporary advantage, enabling turgor to be maintained at low water potentials by decreasing their osmotic potentials (Morgan and Condon 1986).

Cell Growth and Cell Division

Because plant growth is the result of cell division and enlargement, water stress directly reduces growth by decreasing CO_2 assimilation and reducing cell division and elongation. The effect of water stress is more evident on cell wall expansion because cell enlargement involves the extensibility of the cell wall under turgor pressure. Therefore, any loss in turgor pressure as a consequence of the imbalance in the plant water content could result in reduced growth and even in the total absence of growth under dry environmental conditions.

Cell growth rate, Gr, can be expressed as a function of turgor pressure, P, and the extensibility coefficient, Φ, by the equation $Gr = \Phi (P - Y)$ where Y is the yield threshold pressure. The equation shows that growth rate decreases as P decreases, but it could also be maintained if either Φ increases or Y decreases. Therefore, reduced growth rate may not rely only on reduced turgor caused by desiccation. There is some evidence of reduced growth without loss of turgor in plants subjected to desiccation stress, but this reduction may be part of the osmotic adjustment process. Some mechanism may control cell wall extensibility through the perception of soil dryness, giving rise to smaller plants and hence lower water requirements and higher survival (Hsiao 1973).

Plant Metabolic Response to Water Stress

Plant adaptations to dry environments can be expressed at four levels: phenological or developmental, morphological, physiological and metabolic. The metabolic response is least known where the metabolic or biochemical adaptations are involved (Hanson and Hitz 1982). Physiological and biochemical changes including carbohydrates, proteins and lipids are observed in many plant species under various water-stress levels which may help in better understanding survival mechanisms in drought.

Carbohydrate Changes Under Water Stress

The available reports stated that the content of soluble sugars and other carbohydrates in the leaves of various water-stressed plants is altered and may act as a metabolic signal in the response to drought (Akıncı and Lösel 2009, 2010; Chaves et al. 2003; Koch 1996; Jang and Sheen 1997). Munns et al. (1979) and Quick et al. (1992) showed that sugars are major contributors to osmotic adjustment in expanding wheat leaves (Munns et al. 1979; Quick et al. 1992). The increase of sugar in various plant tissue responses to water stress supports the idea of contribution of solutes while the plants are exposed to different stress levels. The studies have shown that soluble sugars accumulate in leaves during water stress and have suggested that these sugars might contribute to osmoregulation, at least under moderate stress (Morgan 1984; Quick et al. 1992; Jones et al. 1980; Munns and Weir 1981; Ackerson 1981; Kameli and Losel 1993, 1996; Al-Suhaibani 1996).

Increase in total carbohydrate is recorded in cotton by Timpa et al. (1986) and Evans et al. (1992). Total soluble sugar is found to be increased in wheat, alfalfa, lupins, bean and cucumber (Kameli and Losel 1996, 1993; Irigoyen et al. 1992; Quick et al. 1992; Al-Suhaibani 1996; Akıncı and Lösel 2009). But depletion of sucrose and starch content is also recorded in soya bean, grapevine, lupins, bean and cucumber by Westgate et al. (1989), Rodriguez et al. (1993), Quick et al. (1992), Steward (1971) and Akıncı and Lösel (2009).

Plant Proteins: Responses to Water Stress

Many specified proteins synthesised under water scarcity have been isolated and characterised by researches (Singh et al. 1987; Close 1997; Pelah et al. 1997; Claes et al. 1990). The water-stress-specific proteins (stress induced) have been described as dehydrins (polypeptide) and LEA (late embryogenesis abundant), RAB (responsive to ABA) and storage proteins (in vegetative tissues) (Artlip and Funkhouser 1995). Under water-stress conditions, plants synthesise alcohols, sugars, proline, glycine, betaine and putrescine and accumulate that of those molecular weights which are low (Chopra and Sinha 1998; Galston and Sawhney 1990). Dehydrins have been the most observed group among the accumulated proteins in response to loss of water and increased in barley, maize, pea and *Arabidopsis*. Under water stress, LEA proteins play an important role as protection of plants. Osmotin is also an accumulated protein under water stress in several plant species such as tobacco, triplex, tomato and maize (Ramagopal 1993).

Heat-shock proteins (HSPs) and late embryogenesis abundant (LEA)-type proteins are two major types of stress-induced proteins during different stresses including water stress. Protection of macromolecules such as enzymes, lipids and mRNAs from dehydration is the well-known function of these proteins. LEA proteins accumulate mainly in the embryo. The exact functions and physiological roles of these proteins are unknown. HSPs act as molecular chaperones and are responsible for protein synthesis, targeting, maturation and degradation in many cellular processes. They also have important roles in stabilisation of proteins and membranes and in assisting protein refolding under stress conditions. Expression of LEA-type genes under osmotic stress is regulated by both ABA-dependent and independent signalling pathways. Genes encoding LEA-type proteins are diverse – RD (responsive to dehydration), ERD (early response to dehydration), KIN (cold inducible), COR (cold regulated) and RAB (responsive to ABA) genes (Lisar et al. 2012; Wang et al. 2004; Singh et al. 2005).

Changes of amino acids and protein have been mentioned in many reports which have stated that water stress caused different responses depending on the level of stress and plant type. Water stress has a profound effect upon plant metabolism and results in a reduction in protein synthesis. Several protein contents were reduced by stress in maize mesocotyls (Bewley and Larsen 1982; Bewley et al. 1983). Dasgupta and Bewley (1984) pointed out water stress reduced protein synthesis in all regions of barley leaf. Vartanian et al. (1987) mentioned the presence of drought-specific proteins in taproot in *Brassica*.

Various water-stress-induced proteins like dehydrins, LEAs, RABs, osmotins, boiling staple proteins, Beta alanine amino peptidase A (BapA, 87 kDa proteins) and chloroplast proteins (CDSP32 and CDSP 34) are recorded by many scientists. Protein content decrease has been recorded in *Avena* coleoptiles (Xu et al. 1996; Artlip and Funkhouser 1995; Ramagopal 1993; Sinha et al. 1996; Bray 1995; Naot et al. 1995; Pareek et al. 1997; Pelah et al. 1997; Mantyla et al. 1995; Pruvot et al. 1996).

Inhibition and/or decrease in protein synthesis has been recorded in *Avena* coleoptiles (Dhindsa and Cleland 1975), in sugar beet (Shah and Loomis 1965) and in *Pisum sativum* L. nodules (Gogorcena et al. 1995). Water stress inhibits cell division and expansion, consequently leaf expansion, and also halts protein synthesis. The direct significance of the inhibition of protein synthesis by stress to growth and leaf expansion is difficult to assess. Free proline accumulation in response to drought in many plant species tissues is well documented (Andrade et al. 1995; Aspinall and Paleg 1981; Chandrasekhar et al. 2000; Tholkappian et al. 2001; Nair et al. 2006). The functions of many of these proteins have not been established (Hughes et al. 1989). However, water stress may inhibit the synthesis of different proteins equally while inducing the synthesis of a specific stress protein (Dasgupta and Bewley 1984).

Treshow (1970) concluded that water stress inhibits amino acid utilisation and protein synthesis (Treshow 1970). Due to unutilisation of amino acids, they are accumulated, giving a 10–100-fold accumulation of free asparagine, valine and glutamic acid, but alanine levels decreased. Barnett and Naylor (1966) found no significant differences in the amino acid and protein metabolism of two varieties of Bermuda grass during water stress. They have also reported that during water deficit, amino acids were continually synthesised but protein synthesis was inhibited followed by decrease in protein content.

Plant Lipid–Water-Stress Interactions

Along with proteins, lipids are the most abundant component of membranes, and they play a role in the resistance of plant cells to environmental stresses (Kuiper 1980; Suss and Yordanov 1986). Strong water deficit leads to a disturbance of the association between membrane lipids and proteins as well as to a decrease in the enzyme activity and transport capacity of the bilayer (Caldwell and Whitman 1987). In plant cell, polar acyl lipids are the main lipids associated with membranous structures (Harwood 1979; Bishop 1983). Glycolipids (GL) are found in chloroplast membranes (more than 60 %), and phospholipids (PL) are thought to be the most important mitochondrial and plasma membrane lipids (Harwood 1980). Many workers have investigated the effect of different levels of water stress on lipid content and composition in different parts of plants (Kameli 1990; Al-Suhaibani 1996; Pham Thi et al. 1982, 1985, 1987; Navari-Izzo et al. 1989, 1990, 1993; Douglas and Paleg 1981; Liljenberg and Kates 1982). Fatty acid, phospholipid, total lipid, etc., are recorded to be increased in soya bean, cotton, wheat, alfalfa and maize by various workers (Navari-Izzo et al. 1990; Pham Thi et al. 1982; Kameli 1990; Al-Suhaibani 1996; Douglas and Paleg 1981; Quartacci et al. 1994; Poulson et al. 2002). It is observed that for Arabidopsis, polyunsaturated trienoic fatty acids may be an important determinant of responses of photosynthesis and stomatal conductance to environmental stresses such as vapour pressure deficit. When *Vigna unguiculata* plants are submitted to drought, the enzymatic degradation of galacto- and phospholipids increased. The stimulation of lipolytic activities is greater in the drought-sensitive than in drought-tolerant cvs (Sahsah et al. 1998).

Phospholipid and glycolipid decline is recorded in cotton (Wilson et al. 1987; Ferrari-Iliou et al. 1984; El-Hafid et al. 1989), wheat and barley (Chetal et al. 1981), sunflower and maize (Quartacci and Navari-Izzo 1992). Total lipid content decrease is recorded in cucumber and squash by Akıncı (1997). Linoleic, linolenic acid, galactolipid, hexadecenoic acid and diacylglycerol are found to be decreased in cotton (Pham Thi et al. 1982, 1985) and in maize (Navari-Izzo et al. 1989). Investigations on various crop species record a general decrease in phospholipid, glycolipid and linoleic acid contents and an increase in the triacylglycerol of leaf tissues exposed to long periods of water deficits. Enzyme activity and transport capacity are affected by the composition and phase properties of the membrane lipids (Kuiper 1985; Gronewald et al. 1982; Whitman and Travis 1985). Wilson et al. (1987) observed that water deficit caused a significant decline in the relative degree of acyl unsaturation (i.e. FA unsaturation) in phospholipids and glycolipids in two different drought-tolerant cotton plants (Wilson et al. 1987). Pham Thi et al. (1987) pointed out that changes in oleic and linoleic acid during water stress resulted in desaturation and water stress markedly inhibited the incorporation of the precursors into the leaf lipids (Pham Thi et al. 1987).

The study of Navari-Izzo et al. (1989) revealed the responses of maize seedling to field water deficits and found that the diacylglycerol, free fatty acid and polar lipid contents decrease significantly with stress (Navari-Izzo et al. 1989). The dry land conditions induced a decrease of more than 50 % in phospholipid levels, and triacylglycerols increased by about 30 % over the control. Pham Thi et al. (1982) have shown that the most striking effects are a decrease of total fatty acids especially trans-hexadecenoic acid. Water deficits inhibit fatty acid desaturation resulting in a sharp decrease of linoleic and linolenic acid biosynthesis. Wilson et al. (1987) and Navari-Izzo et al. (1993) found that in plasma membranes isolated from sunflower seedlings grown under water stress, there is a reduction of about 24 % and 31 % in total lipids and phospholipids, respectively, and also significant decreases in glycolipids and diacylglycerols.

Drought and Nutrient Uptake

The capacity of plant roots to absorb water and nutrients generally decreases in water-stressed plants, presumably because of a decline in the nutrient element demand (Alam 1999). It is well documented that essential plant nutrients are known to regulate plant metabolism even the plants exposed to drought by acting as cofactor or enzyme activators (Nicholas 1975).

Many reports stated that water stress mostly causes reduction in uptake of nutrients (Levitt 1980), for instance, phosphorus, K^+, Mg^{2+} and Ca^{2+} in some crops (Foy 1983; Abdalla and El-Khoshiban 2007; Bie et al. 2004); Ca^{2+}, Fe^{3+}, Mg^{2+}, nitrogen and phosphorus and potassium in *Spartina alterniflora* (Brown et al. 2006); Fe^{3+}, Zn^{2+} and Cu^{2+} in sweet corn (Oktem 2008); and Fe^{3+}, K^+ and Cu^{2+} in *Dalbergia sissoo* leaves (Nambiar 1977). Gerakis et al. (1975) and Kidambi et al. (1990) stated that nutrient elements increased in forage plant species and alfalfa. An increase in some specific elements such as K^+ and Ca^{2+} was reported in maize (Tanguilig et al. 1987) and K^+ in drought-tolerant wheat varieties (Sinha 1978). In leaves of *Dalbergia sissoo*, nitrogen, phosphorus, Ca^{2+}, Mg^{2+}, Zn^{2+} and Mn^{2+} increased with increasing water stress (Singh and Singh 2004).

It is generally accepted that the uptake of phosphorus by crop plants is reduced in dry soil conditions (Pinkerton and Simpson 1986; Simpson and Lipsett 1973). According to Singh and Singh (2004), availability of soil nutrients decreases with increasing soil drying, with K^+, Ca^{2+}, Mg^{2+}, Zn^{2+}, Fe^{3+} and Mn^{2+} decreasing by 24 %, 6 %, 12 %, 15 %, 25 % and 18 %, respectively.

Drought Perception, Signal Transduction and Response

Plant response to water stress depends on their ability to sense the extent or severity of drought they are exposed. It has been reported that water stress can be sensed by a membrane-bound two-component histidine kinase which is activated by high osmolarity. The increase of a cell osmolarity upon water loss during drought therefore triggers the signal transduction in response to drought. The active signal receptor activates phospholipase C (PLC) which hydrolyses phosphatidylinositol 4,5-bisphosphate to yield the second messengers inositol 1,4,5-trisphosphat (IP3) and diacylglycerol (DAG) (Mahajan and Tuteja 2005). IP3 releases calcium from internal stores, and the Ca^{2+} sensor (calcineurin B-like protein, CBL) activates downstream protein kinases and phosphatases. Drought-inducible genes display characteristic promoter cis-acting elements, the dehydration-responsive elements (DREs) which at least partially resemble those of the cold-induced genes (Bray 1997). Abscisic acid triggers a major signalling pathway in drought-stress response. Activation of the abscisic acid responsive elements (ABREs) by several transcription factors such as the DRE-binding factors and bZIP proteins leads to the expression of drought-stress tolerance effectors such as dehydrins or enzymes catalysing low molecular weight osmolytes. The signal transduction pathway of ABA involves cADP ribose, NAADP and Ca^{2+} as second messenger (Quatrano et al. 1997). Calcium appears as a prime candidate in drought-stress signal transduction resulting in a metabolic or structural mitigation of the effect of the stressor. Therefore, proteins, which sense changes in the cytoplasmic calcium concentrations, are important components of the signal transduction chain. Calcium-dependent protein kinases (CDPKs or, in Arabidopsis, CPKs) act as sensor responders by combining Ca^{2+}-binding and kinase activity in the same polypeptide. CPK4 and CPK11 have also been identified as positive transducers of Ca^{2+}-dependent ABA signalling. Strong ABA insensitivity in stomata closure and increased drought sensitivity were reported in the cpk4 and cpk11 single and double mutants, with opposite phenotypes observed in CPK4 and CPK11 overexpression lines. Calcineurin B-like proteins (CBLs) are sensor relay proteins that, upon Ca^{2+} binding, interact with and modulate the activity of CBL-interacting protein kinases (CIPKs). CBL1 an isoform of CBL was identified as a relay for ABA-mediated responses and can act as a positive regulator of drought signalling. CBL1-overexpressing plants exhibit enhanced drought tolerance and constitutive expression of stress genes. Although not only CBL single mutant is ABA hypersensitive in guard cells but also the cbl1cbl9 double mutant was reported to be more drought tolerant in wilting assays and the stomatal closure response in the double mutant was hypersensitive to ABA. It has been shown that in the vasculature and in guard cells, luciferase reporter expression under the control of ABA-responsive AtHD6 (histone deacetylase 6) promoter was detected in response to drought, suggesting a role for tissue autonomous ABA synthesis in addition to long-distance root-to-shoot movement of ABA in response to water stress. It has been observed that the transcription factors like NFYA5 (nuclear factor Y, subunit A5) in Arabidopsis and the maize NF-YB2 function as positive regulators of drought-stress responses, suggesting a possible role of the CCAAT box element and its binding partner NF-Y in ABA/drought-stress signalling. Besides transcriptional induction by ABA, NFYA5 gene expression is further enhanced by posttranscriptional control of NFYA5 mRNA stability. NFYA5 transcripts contain a target site for the microRNA, miR169, which is downregulated by drought. Furthermore, overexpression of miR169 and a T-DNA insertion mutation in NFYA5 both caused drought sensitivity (Raghavendra et al. 2010; Xiong et al. 2002).

Other intracellular hazards observed in plants in response to drought stress are the generation of reactive oxygen species (ROS), which is being considered as the cause of cellular damage. However, recently, a signalling role of such ROS in triggering the ROS scavenging system that may confer protection or tolerance against stress is emerging. Such scavenging system consists of antioxidant enzymes like SOD, catalase and peroxidases and antioxidant compounds like ascorbate and reduced glutathione; a balance between ROS generation and scavenging ultimately determines the oxidative load. As revealed in case of defences against pathogen, signalling via ROS is initiated by NADPH oxidase-catalysed superoxide generation in the apoplastic space (cell wall) followed by conversion to hydrogen peroxide by the activity of cell wall-localised SOD. Wall peroxidase may also play role in ROS generation for signalling. Hydrogen peroxide may use Ca^{2+} and MAPK pathway as downstream signalling cascade. Plant hormones associated with stress responses like ABA and ethylene play their role possibly via a crosstalk with ROS toward stress tolerance, thus projecting a dual role of ROS under drought stress (Kaur and Gupta 2005; Xiong et al. 2002; Raghavendra et al. 2010).

DNA Elements Controlling Gene Expression During Water Deficit

The most comprehensive information about the mechanism of regulation of gene expression in response to water deficit has been obtained from the investigation of DNA elements and sequence-specific DNA-binding proteins. Presently, two classes of DNA elements have been identified: the ABA-responsive element (ABRE) and the dehydration-responsive element (DRE). The ABRE has been shown to be sufficient for ABA-regulated gene expression during water deficit, but in some genes it must be associated with a coupling element. The dehydration-responsive element from the rd29A gene from Arabidopsis, TACCGACAT, has been shown to be involved in the regulation of this gene by an ABA-independent pathway induced by water deficit. It has been shown that these are insufficient for controlling the genes that are induced by water deficit, and new additional DNA elements and several of these elements are beginning to be defined. In the Arabidopsis gene rd22, which requires protein synthesis for expression, there is a DNA element, CACATG, that is similar to the element bound by the transcription factor MYC (Kaur and Gupta 2005; Xiong et al. 2002).

Mechanisms of Acclimation to Water Deficit and Stress Tolerance

Plants have developed multiple mechanisms in order to protect PSA against different kinds of stresses. At the cellular level, plants attempt to alleviate the damaging effects of stress by altering their metabolism to cope with the stress. Many plant systems can survive dehydration but to a different extent. According to Hoekstra et al. (2001) on the basis of the critical water level, two types of tolerance are distinguished:

1. Drought tolerance can be considered as the tolerance of moderate dehydration, down to moisture content below which there is no bulk cytoplasmic water present – about 0.3 g $H_2O\ g^{-1}$ DW.

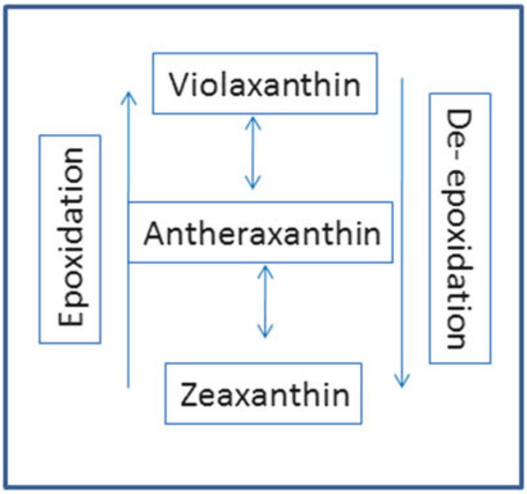

Fig. 4 Water stress induced the synthesis of accessory photosynthetic pigments like zeaxanthin and antheraxanthin

2. Desiccation tolerance refers to the tolerance of further dehydration, when the hydration shell of the molecules is gradually lost. Desiccation tolerance includes also the ability of cells to rehydrate successfully.

According to Bohnert and Shen (1999), a nearly universal reaction under stress conditions, including WD, is the accumulation of “compatible solutes”, many of which are osmolytes (i.e. metabolites whose high cellular concentration increases the osmotic potential significantly) considered to lead to osmotic adjustment. These observations indicate that “compatible solutes” may have other functions as well, namely, in the protection of enzyme and membrane structure and in scavenging of radical oxygen species. One of the principal mechanisms employed by plants to prevent or to alleviate damage to the PSA is non-photochemical chlorophyll fluorescence quenching (qN) (Ruban and Horton 1995). In this mechanism, excess light energy is dissipated as heat in the light-harvesting antenna of PS2. This dissipation is primarily controlled by the trans-thylakoid pH gradient (pH) (Gounaris et al. 1984).

When CO_2 fixation and therefore ATP consumption are decreased at low RWC, the functioning electron flow gives rise to an acidification of the thylakoid lumen that induces Zx and Ax synthesis. It has been proposed that the photoprotective process results in the diversion of energy away from the reaction centres (Ruban and Horton 1995; Medrano et al. 2002). According to Tambussi et al. (2002), the non-photochemical fluorescence quenching (qN), as well as the content of zeaxanthin and antheraxanthin after moderate WS, increased significantly. However, at severe WS, a further rise in these xanthophylls was not associated with any increase in qN. In addition, the β-carotene content rose significantly during severe WD, suggesting an increase in antioxidant defence. Besides the above-mentioned mechanisms of energy dissipation, there are also other ways. For example, the energy dissipation in closed stomata can occur via ATP and NADPH, which are used for other metabolic processes, and they are obviously important mechanisms of tolerance and protection against water stress and photooxidative damage (Lichtenthaler 1996) (Fig. 4).

During dehydration, anhydrobiotes pass through hydration ranges that also necessitate protection against drought. The desiccation tolerance programme can be switched on by dehydration and the plant hormone ABA (Ingram and Bartels 1996). Upon water loss, the cellular volume decreases and cell content becomes increasingly viscous and the chance for molecular interactions rises. The danger of protein denaturing and membrane fusion increases. But a range of compatible solutes which do not interfere with cellular structure and function hinder this process. It is considered that at lower water contents, molecular oxidants (glutathione, ascorbate, tocopherol) play a preponderant role in elevating oxidative stress. Hoekstra et al. (1997) showed that desiccation may increase the transfer of these amphiphiles from the polar cytoplasm into the lipid phase of membranes. They thought that this partitioning into membrane might be extremely effective in automatically inserting amphiphilic antioxidant into membranes upon dehydration.

Reduction of metabolism coincides with survival of desiccation (Leprince et al. 1999). In vegetative tissues, genes encoding enzymatic

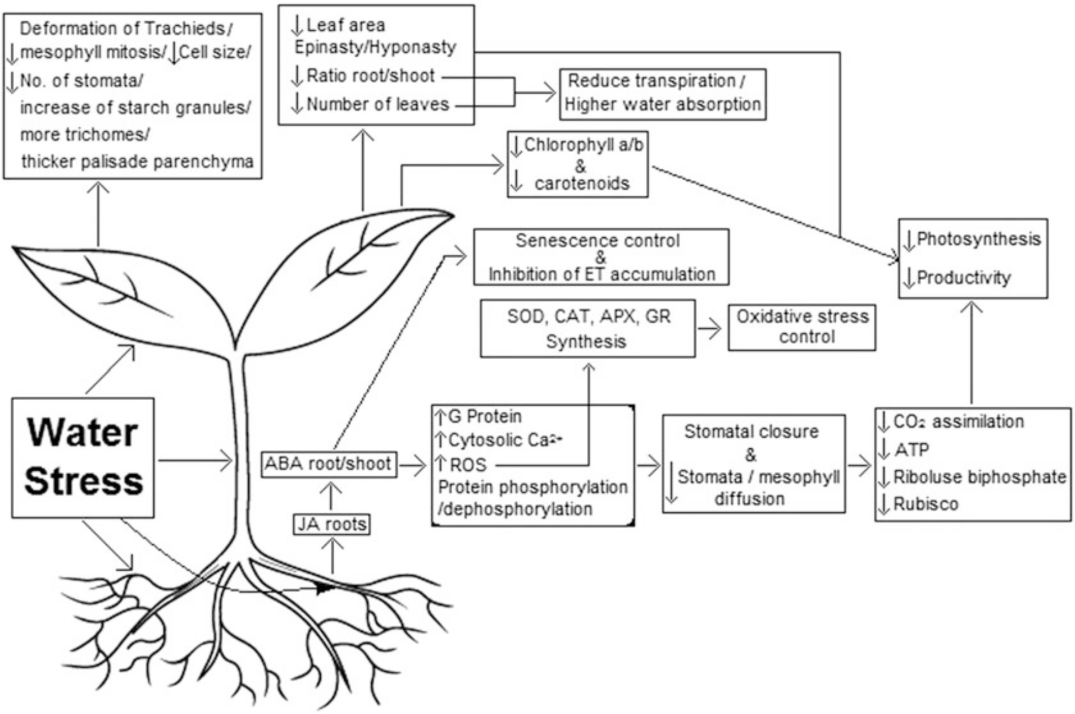

Fig. 5 Schematic presentation showing integrated approach of acclimation to water stress

antioxidants such as APX, SOD and GRase are upregulated during drying or rehydration (Fig. 5). When the bulk water is removed (below 0.3 g H_2O g^{-1} DW), the mechanism keeping the macromolecules preferentially hydrated through amphiphiles fails to work, because there is no water left for preferential hydrations (Crowe et al. 1990). It has been established that during desiccation, soluble sugars interact with the polar head groups and replace the water molecules. Phospholipid molecules largely retain the original spacing between one another. When water dissipates from the water shell of macromolecules at moisture contents below 0.3 g H_2O g^{-1} DW, the hydrophobic effect responsible for structure and function is lost. After bulk water is lost, the hydrogen bonding and glass formation are the mechanisms by which membranes and proteins are structurally and functionally preserved.

Sugars are special in that they allow the removal of the closely associated water from protein without this leading to conformational changes and loss of enzymatic function. According to the water replacement hypothesis, sugars act as a water substitute by satisfying the hydrogen-bonding requirement of polar groups of the dried protein surface (Carpenter and Growe 1988; Wolkers et al. 1998). At around 0.3 g H_2O g^{-1} DW, the cytoplasm vitrifies and exists in a so-called glassy state, an amorphous metastable state, retaining the disorder and physical properties of the liquid state (Franks et al. 1991). This state decreases the probability of chemical reactions and is indispensable for surviving the dry state. A very important role in this process is played by late embryogenesis abundant proteins (LEAPs), especially their Group 1 – dehydrins, in stabilisation and protecting during desiccation. It was observed that their accumulation coincides with the acquisition of desiccation tolerance (Bartels et al. 1988). Group 1 proteins have very high potential for hydration – several times greater than that for “normal” cellular proteins (McCubbin et al. 1985). Because of these special features, LEAPs potentially bind to intracellular macromolecules coating them with a cohesive water layer and preventing their coagulation during desiccation (Close 1996). Upon removal of their own hydration shell, these proteins would still be capable of playing a role in stabilising macromolecular structures. They could provide a layer of their own hydroxylated residues to interact with surface groups of other proteins, acting as "replacement water" (Cuming 1999; Buitink et al. 2002). Wolkers et al. (1999) suggested that LEAPs embedded in the glassy matrix might confer stability on slowly dried carrot somatic embryos.

Another class of proteins associated with desiccation tolerance are low molecular weight HSPs. Coordinated expression of LEAPs and sHSP transcripts is observed during embryo development in response to ABA, indicating the existence of common regulatory elements of LEAPs, sHSPs and desiccation tolerance (Wehmeyer et al. 1996). But so far, there is no direct experimental evidence for a specific role of sHSPs in desiccation tolerance. Satoh et al. (2002) followed recovery of the photosynthetic system during rewatering in a terrestrial, highly drought-tolerant cyanobacterium *Nostoc commune*. With absorption of water, the weight of the Nostoc colony increased. Fluorescence intensities of phycobiliproteins and PS1 complexes recovered almost completely within 1 min, suggesting that their functional forms were restored very quickly. PS1 activity and cyclic ET flow around PS1 recovered within 2 min, while the PS2 activity recovered after a time lag of 5 min. Photosynthetic CO_2 fixation was restored almost in parallel with the first recovery phase of PS2 reaction centre activity (Fig. 5).

There is need to search for valuable approaches in order to identify those metabolic steps that are most sensitive to drought and to elucidate which metabolites and gene products are of primary importance for increasing drought tolerance of plants. Many proteins are involved in damage limitation or the removal of toxic compounds which are induced during water deficit. For example, ubiquitin, chaperones and proteases may all be involved in the recovery of proteins or their building blocks. Genes encoding enzymes that detoxify reactive oxygen species are also induced. It is difficult to ascertain whether the induction of these genes is to repair damage caused directly by reduced water content or if they accumulate to ameliorate damage caused by a secondary stress or to restrict pathogen invasion. The characterisation of genes induced by water deficit has greatly improved our understanding of plant responses to the environment.

Conclusion

The multitude of different stressors, their spatial and temporal character, their variation in intensity and dose and their potential interaction yield an abundance of scientific questions. One of the most interesting aspects of water-stress physiology is how mild or moderate stress is transduced into alterations in metabolism. The foregoing considerations make it seem unlikely that mild stress could, by any of the mechanisms mentioned, damage biochemical components or organelles of the cell; yet mild stress does have pronounced effects. It is more probable that changes in metabolism elicited by mild stress represent plant regulatory responses rather than damage. This in turn implies that many of the changes in plant processes brought about by stress arise indirectly. Among all the changes, the most important aspect of water stress proven to be results reduced cell growth. Inhibition of cell growth during water stress is found to corroborate with inhibition of protein synthesis, cell wall synthesis, membrane proliferation, etc. For maintaining balance of metabolites, the plant has probably evolved controls which slow down synthesis of cell building blocks when low turgor prevents expansion. This may be a likely explanation for the susceptibility of cell wall synthesis and polyribosomes (hence protein synthesis) in growing tissue to very mild water stress. It has also been reported that water stress is associated with impaired lipid synthesis in such tissue. These explain how cell wall synthesis is impaired during water stress, and it may be coupled with suppression of plant growth. Various other changes may also be expected in growing cells under mild to moderate water stress, on the basis of suppressed enlargement of cell volume, for the alteration in volume can be marked. Therefore, a slowing or cessation of growth should result in a quick accumulation of many metabolites, which in turn could affect various processes. Another interesting fact is that water stress affects metabolic processes in a variable fashion. A clear differentiation is made between the changes in metabolism in growing and nongrowing tissue and in the case of young tissue when they are exposed to water stress. There seems to be little doubt that in nongrowing or slowly growing tissue, some metabolic parameters, such as protochlorophyll formation and nitrate reductase levels, are also susceptible to water stress. Regarding possibilities other than turgor changes, the lowering of water activity is the least likely to be a mechanism underlying water-stress effects. Changes in molecular and ionic concentrations and spatial relations may mediate water-stress effects within the limitations.

All the results from research focusing on explaining the mechanism of resistance to water stress of plants have important applications for other fields, such as ecology, forestry, biology and agriculture. At the same time the expanding human population is facing acute food shortage. Therefore, the study of the mechanisms of stress resistance of plants has assumed practical importance over and above academic interest. The greater our understanding of plant response to stressors and stress tolerance, the greater will be our ability to manage natural and human-made ecosystems.

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