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Introductory Chapter

Water Stress in Plants: Causes, Effects and Responses

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1. Introduction

Biosphere's continued exposure to abiotic stresses, for example, drought, salinity, extreme temperatures, chemical toxicity, oxidative stress, etc., cause imbalances in the natural status of the environment. Each year, stresses on arable plants in different parts of the world disrupt agriculture and food supply with the final consequence - famine. Factors controlling 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. The average yields from the major crop plants may reduce by more than 50% owing to stresses. However, plants also have developed innate adaptations to stress conditions with an array of biochemical and physiological interventions that involves the function of many stress-associated genes. In this chapter, we aim at the stresses related to water and the expression 'drought' which is derived from the agricultural context, is used as equal to water stress throughout the article.

Water, comprising 80-90% of the biomass of non-woody plants, is the central molecule in all physiological processes of plants by being the major medium for transporting metabolites and nutrients. Drought is a situation that lowers plant water potential and turgor to the extent that plants face difficulties in executing normal physiological functions. However, a few groups of animals and a wide variety of plants are known for their tolerance to desiccation during the adult stages of their life cycle. Though our knowledge on plant's drought tolerance is ancient, the modern scientific study of drought tolerance started in 1702 with Anthony von Leeuwenhoek's discovery of the survival of rotifers without water for months.

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2. Water stress – Why and how?

Plants experience water stress either when the water supply to their roots becomes limiting or when the transpiration rate becomes intense. Water stress is primarily caused by the water deficit, *i.e.* drought or high soil salinity. In case of high soil salinity and also in other conditions like flooding and low soil temperature, water exists in soil solution but plants cannot uptake it – a situation commonly known as ‘physiological drought’. Drought occurs in many parts of the world every year, frequently experienced in the field grown plants under arid and semi-arid climates. Regions with adequate but non-uniform precipitation also experience water limiting environments.

Since the dawn of agriculture, mild to severe drought has been one of the major production-limiting factors. Consequently, the ability of plants to withstand such stress is of immense economic importance. 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 are not considerably understood yet and such understanding is crucial. All plants have tolerance to water stress, but the extent varies from species to species. 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.

3. Effects of water stress on plants

Drought, as an abiotic stress, is multidimensional in nature, and it affects plants at various levels of their organization. In fact, under prolonged drought, many plants will dehydrate and die. Water stress in plants reduces the plant-cell’s water potential and turgor, which elevate the solutes’ concentrations in the cytosol and extracellular matrices. As a result, cell enlargement decreases leading to growth inhibition and reproductive failure. This is followed by accumulation of abscisic acid (ABA) and compatible osmolytes like proline, which cause wilting. At this stage, overproduction of reactive oxygen species (ROS) and formation of radical scavenging compounds such as ascorbate and glutathione further aggravate the adverse influence. Drought not only affects plant water relations through the reduction of water content, turgor and total water, it also affects stomatal closure, limits gaseous exchange, reduces transpiration and arrests carbon assimilation (photosynthesis) rates. Negative effects on mineral nutrition (uptake and transport of nutrients) and metabolism leads to a decrease in the leaf area and alteration in assimilate partitioning among the organs. Alteration in plant cell wall elasticity and disruption of homeostasis and ion distribution in the cell has also been reported. Synthesis of new protein and mRNAs associated with the drought response is another outcome of water stress on plants. Under the water stress cell expansion slows down or ceases, and plant growth is retarded. However, water stress influences cell enlargement more than cell division. Plant growth under drought is influenced by altered photosynthesis, respiration, translocation, ion uptake, carbohydrates, nutrient metabolism, and hormones.

3.1 Photosynthesis

Photosynthesis is particularly sensitive to the effects of water deficiency. Plants’ resistance to water deficiency yields metabolic changes along with functional and structural rearrangements of photosynthesizing apparatus. Photosynthesis of higher plants decreases with the reduction in the relative water content (RWC) and leaf water potential. Lower

photosynthesis rate is a usual effect of water stress in plants and has been attributed primarily to stomatal limitation and secondarily to metabolic impairment. However, metabolic impairment is the more complex phenomenon than the stomatal limitation though the relative importance of stomatal or metabolic inhibitions is unclear. Some studies blamed stomatal closure for the inhibition of C_4 photosynthesis under water stress while others concluded that non-stomatal factors play the major role.

The photosynthesis rate of leaves in both C_3 and C_4 plants decrease under the drought conditions. Evidence indicates that C_4 photosynthesis is more sensitive to water stress and C_4 plants, such as corn (*Zea mays* L.) are more susceptible to water deficiency than C_3 plants, such as wheat. It explains the predominance of C_4 plants in hot, arid regions - areas prone to frequent drought. C_3 and C_4 plants are alike in the basic process of photosynthesis like Calvin cycle and electron transport chain components, yet significant differences exist between them, which make their responses to water stress differ at a number of levels.

There are some co-factors, which decrease plants' photosynthesis under water stress. Of them, qualitative and quantitative changes in the pool of photosynthesizing pigments, low CO_2 uptake due to stomatal closure and resistance, poor assimilation rates in photosynthetic leaves are prominent. Assimilation rates in photosynthetic leaves decreases due to reduced photosynthetic metabolites and enzymes activity, low carboxylation efficiency and inhibition of chloroplast activity at low water potential. Among other co-factors of water stress, the damage of the photosynthetic apparatus through the production of ROS such as superoxide and hydroxyl radicals, worth special mention.

Decrease in chlorophyll content of leaves under water stress is well known. Water stress inhibits chlorophyll synthesis at four consecutive stages: (I) the formation of 5-aminolevulinic acid (ALA); (II) ALA condensation into porphobilinogen and primary tetrapyrrol, which is transformed into protochlorophyllide; (III) light-dependent conversion of protochlorophyllide into chlorophyllide; and (IV) synthesis of chlorophylls a and b along with their inclusion into developing pigment-protein complexes of the photosynthetic apparatus. In the majority of cases, carotenoids are less sensitive to water stress than chlorophyll, which has been demonstrated for several species of agricultural plants. However, unlike chlorophyll, increase in xanthophyll pigments such as zeaxanthin and antheraxanthin in plants under water stress have been reported. Xanthophyll pigments have a protective role on plants under stress, and some of these pigments are involved in the xanthophyll cycle which has inhibitory role on ROS production.

RuBisCO, the key enzyme for carbon metabolism in leaves, acts as a carboxylase in the Calvin cycle and as an oxygenase in the photorespiration which, however, frequently is viewed as an adverse process. RuBisCO is the most critical player influencing the physiology of plants under water-stressed conditions. Under the conditions of water stress, a rapid decrease in the amount of RuBisCO takes place in most plants which in turn leads to lower activity of the enzyme. This effect is evident in all plants studied though the extent is species-dependent. Water deficiency reduces the supply of carbon dioxide from the environment due to the closure of stomata. Consequently, photorespiration increases which ensure partial substrate replenishment and maintain the carboxylating function of RuBisCO. The end result is the utilization of excess reducing equivalents in chloroplast that causes a reduction in the oxygen-free radicals' production leading to the oxidative damage in chloroplasts. The reduction in chloroplast volume can also be linked to the desiccation within the chloroplast that leads to the conformational changes in RuBisCO. Moreover,

drought stress conditions acidify the chloroplast stroma causing inhibition to the RuBisCO activity. In addition, decline in RuBisCO activity is also caused by the lack of the substrate for carboxylation, reduction in the amount and/or activity of the coupling factor - ATPase, loss of RBP recognition sites in RuBisCO, structural alterations of chloroplasts and RuBisCO, and release of RuBisCO from damaged plastids. In addition to RuBisCO, water stress can reduce activity of other photosynthetic enzymes to different extents such as NADP-dependent glyceraldehyde phosphate dehydrogenase, phosphoenolpyruvate carboxylase, NAD-dependent malate dehydrogenase, phosphoribulos kinase, fructose-1,6-bisphosphatase and sucrose phosphate synthase.

In addition to its negative effects on dark reactions of photosynthesis, water stress also disrupts the cyclic and non-cyclic types of electron transport during the light reaction of photosynthesis. The disruption is clearer in the oxygen-releasing complex and electron transfer from protochlorophyllide to P700. Lower electron transport rate negatively affects photophosphorylation process and decrease 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, PS I of some plants are more severely damaged compared to PS II, though there is an opposite conclusion as well.

3.2 Protein synthesis

Drought conditions bring about quantitative and qualitative changes in plant proteins. In general, proteins in the plant leave decrease during water deficiency due to the suppressed synthesis, more pronouncedly in C₃ than in C₄ plants. Water stress alters gene expression and consequently, the synthesis of new proteins and mRNAs. The main proteins those synthesized in response to water stress are LEA, desiccation stress protein, proteins those respond to ABA, dehydrins, cold regulation proteins, proteases, enzymes required for the biosynthesis of various osmoprotectants, the detoxification enzymes (SOD, CAT, APX, POD, GR). In addition, protein factors involved in the regulation of signal transduction and gene expression, such as protein kinases and transcription factors are also synthesized. The majority of these stress response proteins are dehydrin-like proteins, which accumulate during seed production and embryo maturation of many higher plants as well as in water stressed seedlings. These proteins have highly conserved domain that linked to hydrophobic interactions needed for macromolecular stabilization.

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 are well known functions 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 stabilization 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 signaling 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.

3.3 Lipids

Water stress can lead to a disturbance of the association between membrane lipids and proteins as well as enzymes activity and transport capacity of membranes. Drought results in the variation of fatty acid composition, for example, an increase in fatty acids having less than 16 carbons in chloroplasts. Lipid peroxidation is the well-known effect of drought and many other environmental stresses via oxidative damage.

3.4 Morphological, anatomical and cytological changes

In the majority of the plant species, water stress is linked to changes in leaf anatomy and ultrastructure. Shrinkage in the size of leaves, decrease in the number of stomata; thickening of leaf cell walls, cutinization of leaf surface, and underdevelopment of the conductive system - increase in the number of large vessels, submersion of stomata in succulent plants and in xerophytes, formation of tube leaves in cereals and induction of early senescence are the other reported morphological changes.

The root-to-shoot ratio increases under water-stress conditions to facilitate water absorption and to maintain osmotic pressure, although the root dry weight and length decrease as reported in some plants like sugar beet and *Populus*. Higher root-to-shoot ratio under the drought conditions has been linked to the ABA content of roots and shoots. Water stress is linked to decrease in stem length in plants such as *Albizia*, *Erythrina*, *Eucalyptus* and *Populus* with up to 25% decrease in plant height in citrus seedling. Decreased leaf growth, total leaf area and leaf-area plasticity were observed under the drought conditions in many plant species, such as peanut and *Oryza sativa*. Although water saving is the important outcome of lower leaf area, it causes reduced crop yield through reduction in photosynthesis. Decrease in plant biomass consequences from the water deficit in crop plants, mainly due to low photosynthesis and plant growth and leaf senescence during the stress conditions. However, in some plants, higher yield was reported under-water deficit condition.

3.5 ABA accumulation

The plant hormone ABA accumulates under-water deficit conditions and plays a major role in response and tolerance to dehydration. Closure of stomata and induction of the expression of multiple genes involved in defense against the water deficit are known functions of ABA. The amount of ABAs in xylem saps increases substantially under reduced water availability in the soil, and this results in an increased ABA concentration in different compartments of the leaf. Another well-known effect of drought in plants is the decrease in PM-ATPase activity. Low PM-ATPase increases the cell wall pH and lead to the formation of ABA⁻ form of abscisic acid. ABA⁻ cannot penetrate the plasma membrane and translocate toward the guard cell by the water stream in the leaf apoplasm. High ABA concentration around guard cell results in stomata closure and help to conserve water.

3.6 Mineral nutrition

Water stress also affects plant mineral nutrition and disrupts ion homeostasis. Calcium plays an essential role in structural and functional integrity of plant membrane and other structures. Decrease in plant Ca²⁺ content was reported in many plants, for example,

approximately 50% decrease in Ca^{2+} in drought stressed maize leaves, while in roots Ca^{2+} concentration was higher compared to control. Potassium is an important nutrient and plays an essential role in water relation, osmotic adjustment, stomatal movement and finally plant resistance to drought. Decrease in K^{+} concentration was reported in many plant species under water deficient condition, mainly due to membrane damage and disruption in ion homeostasis. K^{+} deficient plant has lower resistance to water stress. Nitrogen metabolism is the most important factor that influences plant growth and performance. Disruption in N-metabolism is a crucial in-plant injury under the water deficit conditions. Some studies showed the reduction of nitrate uptake and decrease in nitrate reductase activity under water stress.

4. Drought and oxidative stress in plants

Oxidative stress, which frequently accompanies many abiotic stresses like high temperature, salinity, or drought stress, causes a serious secondary effect on cells. Oxidative stress is accompanied by the formation of ROSs such as O_2^- , $^1\text{O}_2$, H_2O , and OH^- . ROSs damage membranes and macromolecules affect cellular metabolism and play a crucial role in causing cellular damage under drought stress.

Drought creates an imbalance between light capture and its utilization, which inhibits the photosynthesis in leaves. In this process imbalance between the generation and utilization of electrons is created. Dissipation of excess light energy in photosynthetic apparatus results in generation of reactive oxygen species (ROS). Denaturation of functional and structural macromolecules is the well-known results of ROS production in cells. DNA nicking, amino acids, protein and photosynthetic pigments oxidation, and lipid peroxidation are the reported effects of ROS. As a consequence, cells activate some responses such as an increase in the expression of genes for antioxidant functions and production of stress proteins, up-regulation of anti-oxidants systems, including anti-oxidant enzymes and accumulation of compatible solutes. All these responses increase scavenging capacity against ROSs.

5. Plant responses to water stress

Plants adapt themselves to drought conditions by various physiological, biochemical, anatomical, and morphological changes, including transitions in gene expression. The physiology of plants' response to drought at the whole plant level is highly complex and involves deleterious and/or adaptive changes. This complexity is due to some factors such as plant species and variety, the dynamics, duration and intensity of soil water depletion, changes in water demand from the atmosphere, environmental conditions, as well as plant growth and the phenological state in which water deficit is developed.

Plants' strategies to cope with drought normally involve a mixture of stress avoidance and tolerance strategies. Early responses of plants to drought stress usually help the plant to survive for some time. The acclimation of the plant to drought is indicated by the accumulation of certain new metabolites associated with the structural capabilities to improve plant functioning under drought stress. The main aspects of plant responses to water involve the maintenance of homeostasis (ionic balance and osmotic adjustment),

counter action to resulted damages and their quick repair such as scavenging of ROS and decrease oxidative stress and the regulation and recovery of growth.

The complex plant response to water stress, alike other abiotic stresses, involves many genes and biochemical and molecular mechanisms. Sequentially, they are: signal sensing, perception and transduction by osmosensors like AtHK1, kinases and phospholipases as well as secondary messengers; transcriptional control by transcription factors such as DREB (dehydration-responsive transcription factors); and activation of stress responsive mechanisms such as detoxification of ROS by enzymes such as SOD and CAT; osmoprotection by compatible solutes and free radicals scavengers such as glutathione and proline; and water and ion homeostasis by aquaporins and ion transporters. The results of these responsive pathways are the re-establishment of cellular homeostasis and functional and structural protection and finally stress resistance or tolerance.

Stomata closure is the well-known first responsive event of plants to water deficiency. Stomatal closures are more closely related to soil moisture content than leaf water status, and it is mainly controlled by chemical signals such as ABA produced in dehydrating roots. A direct correlation between the xylem ABA content and stomatal conductance has been demonstrated. Changes in plant hydraulic conductance, plant nutritional status, xylem sap pH, farnesyl tranferase activity, leaf-to-air vapor pressure deficit and decrease in relative water content are other factors working in stomatal regulation plants. Although CO₂ assimilation and net photosynthesis decreases due to stomatal closure but attainment of low transpiration rate and prevention of water losses from leaves is a good tradeoff for survival in exchange of growth. Stomata can completely close in mild to severe stress depending on plant species, and tolerant species control stomata opening to allow some carbon fixation and improving water-use efficiency. The increased stomatal resistance under stress levels indicates the efficiency of a species to conserve water.

6. Plants resistance to water stress

Plants optimize the morphology, physiology and metabolism of their organs and cells in order to maximize productivity under the drought conditions. The reactions of the plants to water stress differs significantly at various organizational levels depending upon intensity and duration of stress as well as plant species and its stage of development. Stress resistance in plant is divided into two categories, including stress tolerance and stress avoidance. Drought avoidance is the ability of plant to maintain high tissue water potential under drought conditions, while drought tolerance is a plant's stability to maintain its normal functions even at low tissue water potentials. Drought avoidance is usually achieved through morphological changes in the plant, such as reduced stomatal conductance, decreased leaf area, development of extensive root systems and increased root/shoot ratios. On the other hand, drought tolerance is achieved by cell and tissue specific physiological, biochemical, and molecular mechanisms, which include specific gene expression and accumulation of specific proteins. The dehydration process of drought-tolerant plants is characterized by fundamental changes in water relation, biochemical and physiological process, membrane structure, and ultrastructure of sub cellular organelles. Some plants are able to cope with arid environments by mechanisms that mitigate drought stress, such as stomatal closure, partial senescence of tissues, reduction of leaf growth, development of

water storage organs, and increased root length and density, in order to use water more efficiently. Water flux through the plant can be reduced or water uptake can be increased by several physiological adaptations. Many lichens, bryophytes, and a few ferns can survive in a dried state. Resistant dried structures like seeds and pollen grains are frequently present in most plant species. Among vascular plants, a small group of angiosperms known as poikilohydric or resurrection plants, such as *Craterostigma plantagineum* can tolerate extreme dehydration at the whole plant level. This suggests that the genetic properties required for drought tolerance are present in flowering plant.

6.1 Accumulation of compatible solutes

Osmolytes have some important role in plant responses to water stress and resistance. Many studies indicated that the accumulation of compatible solutes in plant's causes resistance to various stresses such as drought, high temperature and high salinity. Osmotic adjustment and turgor regulation are the well-illustrated functions of these compounds in plants and algae since their high solubility in water acts as a substitute for water molecules released from leaves. The primary function of compatible solutes is to prevent water loss to maintain cell turgor and to maintain the gradient for water uptake into the cell. These metabolite accumulations in cells leads to increase in the osmotic potential and finally resulted in higher water uptake capacity by roots and water saving in the cells. Natural osmolytes concentrations in plant cells can reach 200 mM or more, and such concentrations are osmotically significant. For example, under water stress the proline concentration can reach up to 80% of the total amino acid pool in some plants.

In addition to osmoregulation function, compatible solutes have some other functions in plants such as, protecting of enzymes and membrane structures and integrity, maintain protein conformation at low water potentials, scavenging free oxygen radicals and stabilizing cellular macromolecule's structures such as membrane components. A study also indicated the involvement of glycinebetaine in the protection of the transcriptional and translational machinery under stress conditions. Hydroxyl radicals are the most dangerous of all active oxygen species, but no enzyme has been shown to decompose hydroxyl radicals. Some compatible solutes function as scavengers of hydroxyl radicals such as proline, citrulline and mannitol.

Some aspects of these functions of compatible solutes are related to their extremely hydrophilic property, and hence might also replace water molecules around nucleic acids, proteins and membranes during water shortages. Cell water deficits cause an increase in the concentration of ions that destabilize macromolecules. Compatible solutes might prevent interaction between these ions and cellular components by replacing the water molecules around these components, thereby, protecting against destabilization during drought. For example, protection of RuBisCO by betaine and proline and stabilization of PSII super complex by betaine were shown in pervious works.

Osmolyte's accumulation in plants is caused, not only by the activation of biosynthesis, but also by the inactivation of degradation. Transformed plants with the higher ability in compatible solutes' production showed a significant increase in plant's tolerance to osmotic stress. All known compatible solutes was not accumulated in all plant species, for example, accumulation of GlyBet occurs in some, but not in all, higher plant species such as xerophytes and halophytes. Citrulline accumulates in leaves of wild watermelon plants

under drought. Organisms other than plants also accumulate compatible solutes; for example, glycerol in yeast and phytoplanktons, ectoine in *Halomonas*, trimethylamine *N*-oxide and urea in shallow-sea animals, and di-*myo*-inositol-1,1'-phosphate and related compounds in thermophilic and hyperthermophilic bacteria and Archea.

Compatible solutes are divided into three major groups - amino acids (e.g. proline), polyamins and quaternary amines (e.g. glycinebetaine, dimethylsulfoniopropionate), polyol (e.g. mannitol, trehalose) and sugars like sucrose and oligosaccharids. Free proline is believed to play a key role in cytoplasmic tolerance in many species and, therefore, in the resistance of the whole plant to severe drought. Sugars can play a role in osmoregulation under a drought condition in many plants such as alfalfa and *Ziziphus mauritiana*. Many studies indicated that solute accumulation under water stress contributes to inhibition of shoot growth. It is clear because compatible solute synthesis and accumulation need high energy level.

6.2 Activation of antioxidant systems

Free oxygen radicals, produced as the usual secondary consequence of environmental stresses, are very dangerous for cell components and must be precisely regulated. All plants have developed several antioxidant systems, both enzymatic and non-enzymatic, to scavenge these toxic compounds. Among antioxidant enzymes are catalases (CAT), superoxide dismutase (SOD), peroxidases (POD), ascorbate peroxidases (APX), glutathione reductase (GR) and monodehydroascorbate reductase (MDAR) are prominent. Besides, there are antioxidant molecules such as ascorbic acid (AA), glutathione, tocopherols, flavanones, carotenoids and anthocyanins. Some other compounds like osmolytes (e.g. proline), proteins (e.g. peroxiredoxin) and amphiphilic molecules (e.g. tocopherol) also have ROS scavenging function and may act as the antioxidant. Non-enzymatic plant antioxidants are either AA-like scavengers or they are pigments. Some of these compounds are multifunctional; for example, AA can react with H_2O_2 , O_2 , OH^- and lipid hydroperoxidases, acts as the enzyme co-factor and as a donor/acceptor of electron. The degree of activities of antioxidant systems under drought stress is extremely variable. The defining factors include variation in plant species, in the cultivars of the same species, development and the metabolic state of the plant, and the duration and intensity of the stress, etc.

7. Biotechnology and water stress

Various approaches have been so far been tested to produce stress tolerant plants using classical genetic methods as well as improved plant breeding techniques. One approach to improve plant resistance and crop performance in water-limited environments is to select genotypes that have improved yield in dry environments. The approach is proven partially successful, but it is difficult to accomplish due to the variability of rainfall and the polygenic nature of drought tolerance. The strategy of gene transfer to crop plants from their more tolerant wild relatives using classical genetic methods has also been of limited success. A partial list of potentially important traits for plant breeding might include water-extraction efficiency, water-use efficiency, hydraulic conductance, osmotic and elastic adjustments, and modulation of leaf area.

Plant modification for enhanced tolerance is mostly based on the manipulation of genes that protect and maintain the function and structure of cellular components. The genetically complex responses to abiotic stress conditions are more difficult to control and engineer. Present engineering strategies rely on the transfer of one or several genes associated with stress responsive pathways. Although the current efforts to improve plant stress tolerance by gene transformation have resulted in important achievements; the nature of the genetically complex mechanisms of abiotic stress tolerance, and the potential detrimental side effects, make this task extremely difficult.

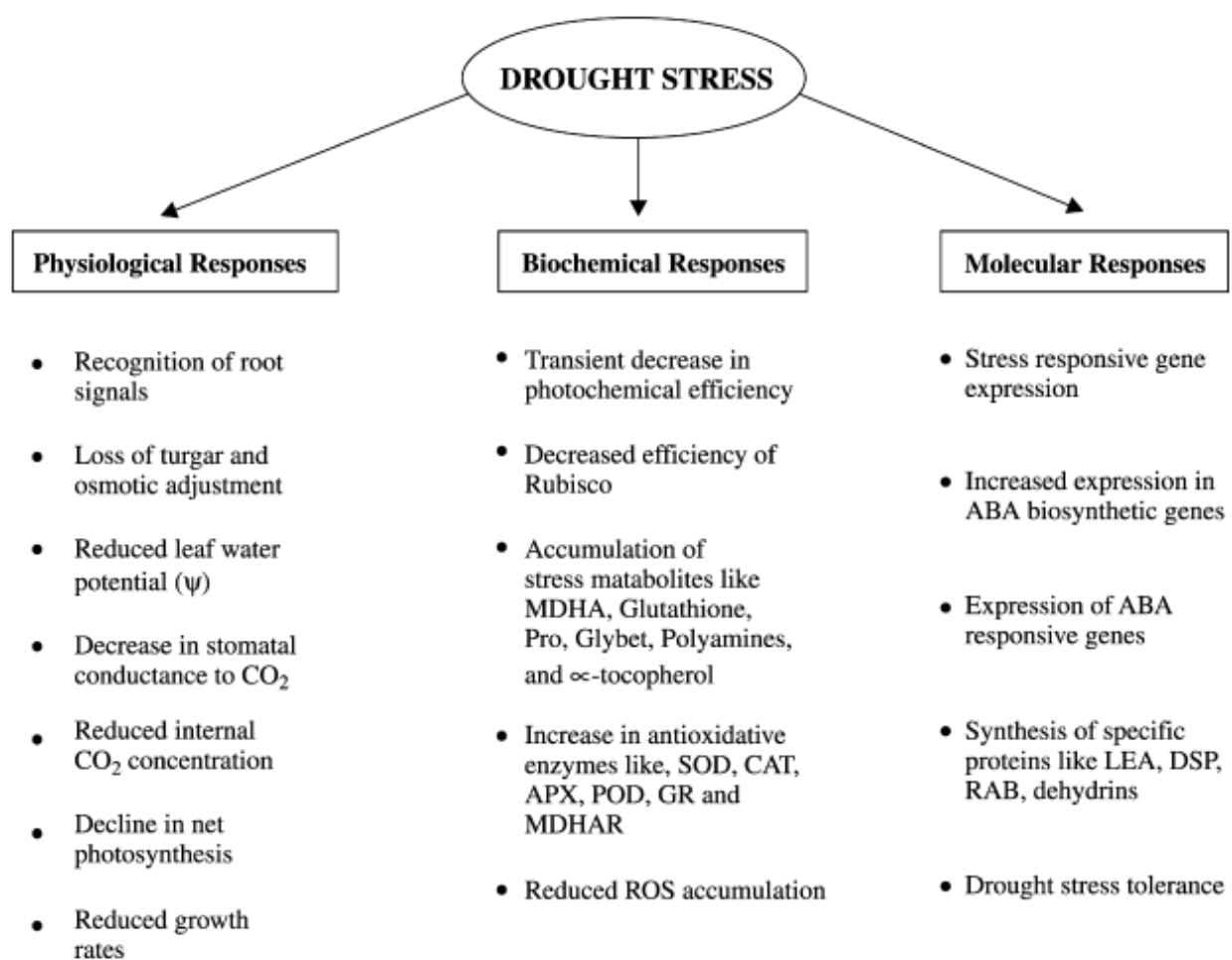


Fig. 1. Physiological, biochemical and molecular basis of drought stress tolerance in plants [Reprinted with permission from 'Shao *et al.* (2008). *Comptes Rendus Biologies*, 331:215-225.' ©2008, Elsevier Limited, UK]

Genetic engineering has allowed the introduction of new pathways for the biosynthesis of various compatible solutes into plants, resulting in the production of transgenic plants with improved stress tolerance. Overexpression of compatible solutes in transgenic plants also resulted in improved stress tolerance. Proline and betaine are well known compatible solutes, synthesized in plants. Genetic engineering of the proline biosynthesis pathways led to increased osmotolerance and salinity stress tolerance in transgenic plant. Proline is synthesized from glutamate via glutamic- γ -semialdehyde (GSA) and Δ^1 -pyrroline-5-carboxylate (P5C). P5C synthase (P5CS) catalyzes the conversion of glutamate to P5C, followed by P5C reductase (P5CR), which reduces P5C to proline. Transgenic tobacco (*Nicotiana tabacum*) and rice plants overexpressing the *p5cs* gene that encodes P5CS produced more proline and exhibited better performance, reduced free radical levels and higher biomass under osmotic stress.

Betaine occurs naturally in a wide variety of plants and other organisms to help them better respond to water stress. Glycinebetaine is synthesized in the chloroplast. Choline is converted to betaine aldehyde by the choline mono oxygenase (CMO) under drought, and salinity stresses. Betaine aldehyde is then catalyzed into glycine betaine by betaine aldehyde dehydrogenase. Many important crops, such as rice, potato and tomato, do not naturally accumulate glycinebetaine and are therefore, potential candidates for the engineering of betaine biosynthesis to make them perform better under the drought conditions. Transformed plants like *Arabidopsis*, tobacco and Brassica that overexpressing choline oxidase (involved in glycinebetaine synthesis) gene (*CodA/cox*), showed higher tolerance to drought and salt stress. *Arabidopsis* that expressed N-methyltransferase genes, accumulated glycinebetaine in roots, stems, leaves, and flowers and showed improved seed yield under stress conditions. Transgenic cyanobacteria and other plants engineered to synthesize higher glycinebetaine have shown better resistance to drought, salinity and cold.

On the other hand, polyamines accumulate in plants under a variety of abiotic stresses including drought. Over expression of spermidine synthase in *Arabidopsis* enhanced its tolerance to multiple stresses including the water deficit. Besides, a number of sugar alcohols like mannitol, trehalose, *myo*-inositol, D-ononitol and sorbitol have been targeted for the engineering of compatible solute overproduction. For example, transgenic tobacco plants carrying a cDNA encoding *myo*-inositol O-methyltransferase (IMT1) accumulated D-ononitol and, as a result, acquired enhanced photosynthesis protection and increased recovery under drought and salt stress. Trehalose overproducing transgenic rice plants showed high tolerance to different abiotic stresses and maintained optimal K^+/Na^+ ratios necessary for cellular functions. Transgenic tobacco plants expressing alfalfa aldose aldehyde reductase, a stress-activated enzyme, showed reduced damage when exposed to oxidative stress and increased tolerance to some stresses like dehydration.

Ion homeostasis in cells is critical for plant resistance and growth under many stress conditions like drought and salinity. Proton pumps such as P-ATPase, V-ATPase and H⁺-PPase have the more important role in this function. *Arabidopsis* plants, transformed with a vacuolar H⁺-PPase pump (*AVP1* gene), expressed higher levels of *AVP1* and were more resistant to salt and drought than wild-type plants.

LEA protein accumulates in plants in response to water stress and have several functions in plant resistance to drought. Constitutive over expression of ABF3 (ABRE binding factor) in

Arabidopsis enhances expression levels of target LEA- type genes (RAB18 and RD29) and these transgenic plants are drought tolerant during seedling stage. Over expression of a barley group 3 LEA protein gene, HAV1 in transgenic rice, showed better stress tolerance under salt and drought stress than wild-type plants.

8. Conclusion

The changes in the climatic condition all over the world under the influence of global warming is creating unusual weather phenomena often in the form of water deficit or in the form of floods and waterlogging. Drought is severe of these two due to the prolonged exposure of plants to a water deficient condition. Through the evolutionary mechanism, plants have developed their innate mechanism to combat water stress. All the plants are not equally capable in withstanding water stress and their response to the stress also varies. Even in the highly tolerant species of plants, tolerance comes through changes in the molecular and physiological mechanisms that make plants morphologically adaptable to water deficits. However, they have to pay the price of such tolerance in the form of reduced photosynthesis and resulting in lower biomass yields often caused by the conservative water management scheme adopted by plants. It helps plants to reduce water loss and to maximize available water uptake while making sure the maximum utilization of physiologically available water. The adaptation in this form came from genetic machineries that help plants to produce enzymes, proteins and synthesize molecules suitable in various means to combat water shortages. The drought related oxidative stress is also addressed by biomolecules synthesized by plants. Our knowledge on the causes and effects of water stress on plants along with the understanding of plant's responses in different forms to become tolerant to such stress has already created biotechnological intervention to enhance the drought adaptability of fewer adaptive plants. However, our knowledge about causes and consequences of the water stress in plants still has many dark areas, and we need to enhance our efforts in furthering our appreciation of the issue.

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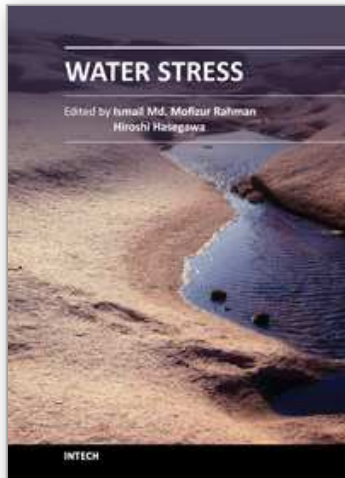
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Water Stress

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Plants experience water stress either when the water supply to their roots becomes limiting, or when the transpiration rate becomes intense. Water stress is primarily caused by a water deficit, such as a drought or high soil salinity. Each year, water stress on arable plants in different parts of the world disrupts agriculture and food supply with the final consequence: famine. Hence, the ability to withstand such stress is of immense economic importance. Plants try to adapt to the stress conditions with an array of biochemical and physiological interventions. This multi-authored edited compilation puts forth an all-inclusive picture on the mechanism and adaptation aspects of water stress. The prime objective of the book is to deliver a thoughtful mixture of viewpoints which will be useful to workers in all areas of plant sciences. We trust that the material covered in this book will be valuable in building strategies to counter water stress in plants.

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