Journal of Pharmacognosy and Phytochemistry

Available online at www.phytojournal.com

Vara Prasad KVGK
Regional Research Unit, Crop physiology, Regional Agricultural Research Station, Lam Guntur, Acharya NG Ranga Agricultural University, Andhra Pradesh India

Rama Rao G
Regional Research Unit, Crop physiology, Regional Agricultural Research Station, Lam Guntur, Acharya NG Ranga Agricultural University, Andhra Pradesh India

Various plant's responses and strategies to cope with the water deficit: A review

Vara Prasad KVGK and Rama Rao G

Abstract
When plants themselves get exposed to water stress especially water deficit, plants have to face the negative consequences on their morpho-physiological traits in various ways. In the light of Climate Change phenomenon across the world, drought is the most frequently occurring natural disaster in the tropical regions especially in the arid and semi-arid belts and substantially decline the yield of crops. Plants too have evolved various strategies at morphological, physiological, biochemical and molecular levels to encounter other abiotic stresses as well. Some species are better able to adapt than others and various anatomical, structural and biochemical mechanisms account for acclimation. Therefore, this review is confined to effect of water stress i.e., deficit stress on the plants and the mechanism of drought resistance in plants on a morphological, physiological and molecular basis and also on recent studies which suggest that changes in gene expression at the level of transcriptional and translational control of protein synthesis are involved [1].

Keywords: Water stress, drought resistance, phenotypic plasticity, osmotic adjustment, signal transduction, ABA role

Introduction

Water is the very essential component of all living beings for their survival. However, either excess water available to the plants or water deficit stress causes the strain in the plant's life. Plants grow and reproduce in harsh environments containing a variety of abiotic factors that vary both temporally and spatially. The primary abiotic environmental parameters that effect plant growth are light (intensity, quality, & duration), water (soil availability and humidity), carbon dioxide, oxygen, soil nutrients, temperature and toxins. But any considerable fluctuations in these factors i.e., stress, plants are subject to negative biochemical and physiological consequences i.e., strain. Owing to sessile nature, plants have to face these abiotic stresses. Stress can be defined as any environmental condition that prevents the plant from achieving its full genetic potential.

Water deficit stress triggers a wide variety of plant responses. Plant responses to water deficit can be a part of the mechanisms that permit the plant to withstand the stress. Alternatively, such responses may be a manifestation of injury that has occurred in response to the water deficit stress. The response depends on the severity and duration of this stress, the developmental stage of the affected plant, the tissue type, and the interaction of a multitude of stresses. Features of the plant, including organ or tissue identity, developmental age and genotype also influence plant's responses to the water stress. Mechanisms that permit water stress survival are termed as drought resistance mechanisms although the term 'drought' is related to Meteorology. These mechanisms can allow plants either to avoid or tolerate water deficit stress.

Water deficit and its effects

Water deficit in plants can be induced by many environmental conditions. Periods of little or no rainfall can lead to a meteorological condition called drought. Transient or prolonged drought conditions reduce the amount of water available for plant growth. However, water deficit also occurs sometimes due to salinity or cellular dehydration caused by freezing temperatures. Water status of the plant can be described by two parameters viz., water potential and Relative Water Content (RWC). The water potential of plant organs such as roots or leaves can be measured by using a pressure chamber or a thermocouple psychrometer [2]. Thus, measuring the water status of the plant is an important parameter for determining the impact of the environmental condition.

Water deficit can affect plants differently during vegetative versus reproductive growth. When plant cells experience water deficit, cell dehydration occurs.

Correspondence
Vara Prasad KVGK
Regional Research Unit, Crop physiology, Regional Agricultural Research Station, Lam Guntur, Acharya NG Ranga Agricultural University, Andhra Pradesh India

Cell dehydration adversely affects many basic physiological processes. Reduction of water potential, cell dehydration and hydraulic resistance are the primary effects whereas reduced cell/ leaf expansion, reduced cellular and metabolic activities, stomatal closure, photosynthetic inhibition, leaf abscission, altered carbon partitioning, cytorrhysis, cavitation, membrane and protein destabilization, Reactive Oxygen Species (ROS) production, ion cytotoxicity, cell death etc., are the secondary effects [1].

Drought resistance
Drought resistance mechanisms have been divided into several types. Drought tolerance at high water potential i.e., ability to maintain tissue hydration is called desiccation postponement whereas drought tolerance at low water potential i.e., ability to function while dehydrated is called desiccation tolerance. Among desiccation postponers, plants can be further categorised into water spenders and water savers. In fact, the terms 'drought avoidance' and 'drought tolerance' that appear in old literature are misnomers because, drought is a meteorological condition. A drought avoidance mechanism provides another class of plants called "Phreatophytes" characterised by deep roots with improved access to ground water, so that they can survive long periods without rain. Contrary to this, desert ephemerals developed a third category strategy called, 'drought escape' that comprises plants completing their life cycles during the wet season, before the onset of drought. These are the only true drought avoiders. The water-limited productivity of plants will depend on the total amount of water available and the water use efficiency of the plant. Drought resistance strategies vary with climatic or soil conditions. A plant that is capable of acquiring more water or that has higher water use efficiency will have greater stress resistance to drought.

Acclimation
In addition to these, plants posses another kind of strategies called, acclimation mechanisms that are activated in response to water stress. The adjustment of individual organisms in response to changing environmental factors is achieved by acclimation. Individual plants respond to changes in the environment by directly altering their physiology or morphology to enhance survival and reproduction. Moreover, physiological adjustment to abiotic stress involves trade-offs between vegetative and reproductive development. Such responses do not require new genetic modifications. Acclimation represents a non-permanent change in the physiology or morphology of the individual plant that can be reversed if the prevailing environmental conditions change. Epigenetic mechanisms that alter the expression of genes without changing the genetic code of an organism can extend the duration of acclimation responses and make them heritable. During acclimation an organism alters its homeostasis, its steady-state physiology, to accommodate shifts in its external environment [2].
Acclimation allows plants to respond to environmental fluctuations. In addition to genetic changes in entire populations, individual plants may acclimate to periodic changes in the environment by directly altering their morphology or physiology. The physiological changes associated with acclimation require no genetic modifications, and many are reversible. Hardening off process of gardening plants is one example of it. Acclimation strategies also vary with the growth habit be it determinate or indeterminate one.

Acclimation to stress also involves transcriptional regulatory networks called regulons. Transcrptional regulators or transcription factors are proteins that bind specific DNA sequences and activate or suppress the expression of different genes. Combination of different transcription factors can generate a gene network responding to a particular abiotic stimulus, with some genes being activated and some suppressed. Such transcriptional regulatory networks responding to abiotic stress have been termed stress response regulons [2].

Adaptations
When genetic changes in an entire plant population have been fixed over many generations by selective environmental pressure, those changes are referred to as adaptations. Drought Resistance mechanisms constitute adaptations, evolutionary improvements that enhance the environmental fitness of a population of organisms. Some plants possess adaptations such as the C4 and CAM modes of metabolism, that allow them to exploit more arid environments. Besides, sunken stomata, light reflective spines and deep roots are among the constitutive, genotypically determined traits for stress resistance that are expressed whether the plants are stressed or not. Adaptations to stress involves genetic modifications over many generations [1].

Plants Responses
Phenotypic plasticity
Plants show a wide variety of responses at different levels when they are subject to water deficit. Decreased leaf area is an early response to water deficit. The earliest responses to this stress appear to be mediated by biophysical events rather than by changes in chemical reactions due to dehydration. The lower hydrostatic pressure or turgor occurs due to decrease in cell volume by cell shrinkage. As cells contract further, the solutes in the cells become more concentrated. The plasma membrane also becomes thicker. As cell expansion, a turgor dependent process, is inhibited, the leaf expansion also slows down. Thus, leaf area is limited and it results in decline in transpiration. Water stress not only limits the size of individual leaves, but also limits the number of leaves on an indeterminate plant because it decreases both the number and the growth rate of branches. Water deficit also stimulates leaf abscission [1].

Changes in the root system architecture
Plant growth is greatly affected by deficit. At a morphological level, the shoot and root are most affected and both are key components of plant adaptation to drought. Plants generally limit the number and area of leaves in response to drought stress just to cut down the water budget at the cost of yield loss [3]. Since roots are the only source to acquire water from soil, the root growth, its density, proliferation and size are key responses of plant to drought stress [4].
Plants constantly obtain water (and nutrients as well) from the soil through the roots. Hence, the root system plays a critical role in response to water deficit stress. Some plants have robust ability to increase root growth at the early stage of drought stress to absorb the water in deep soil [5] A positive correlation have been found between penetration ability of roots and the degree of drought resistance in *Phaseolus acutifolius* [6]. The length, weight, volume, and density of plant roots were also reported to be associated with the drought resistance in crops [7, 8]. Nevertheless, other research showed a lack of perceptible association between root traits

with single plant and plot yield under reproductive stage stress in rice [9]. In dry areas, woody plant seedlings have vertical roots with ten times the length of the above ground height [10]. With this extensive root system and rooting depth, plants are able to maintain a higher water potential and a longer duration of transpiration under drought conditions, which provides further advantages for their growth and development [11]. Rooting depth, volume, and distribution are mainly influenced by the depth and range of soil moisture. In cases of soil water deficit, plant dynamically adapt and modify their root system architecture by changing their root growth in diverse manners depending on the species [12, 13]. It is evident that severe soil water deficit can reduce root elongation, branching, and the formation of the cambium layer, and root tips of plant growing in arid soil become suberized [14].

Altered Root-Shoot Ratio
Root growth is also influenced by the water or nutrient status of the aerial portion of the plant [15]. Increased root/shoot ratios are often observed under water stress conditions [16, 17]. For a long time, the root/shoot ratio has been used as a criterion to describe the plant capacity for drought resistance [18, 19]. Roots are the key plant organ for adaptation to drought. If tolerance is defined as the ability to maintain leaf areas and growth under prolonged vegetative stage stress, the main basis of variation appears to be constitutive root system architecture that allows the maintenance of more favourable plant water status [20]. The possession of a deep and thick root system allowed access to water deep in the soil, which was considered important in determining drought resistance in upland rice [4]. Evidence suggests that it is quality, i.e., the distribution and structure and not quantity of roots that determines the most efficiency strategy for extracting water during the crop-growth season. The drought tolerance of tea, onion and cotton was increased by improved root growth and root functioning. Selection for a deep and extensive root system has been advocated to increase productivity of food legumes under moisture-deficit conditions as it can optimize the capacity to acquire water [21].

Leaf traits
The morphological and physiological responses of leaves to drought stress are crucial to reduce water loss and promote water use efficiency. When plums sense severe water deficiency, their leaves droop or roll because of the loss of cell turgor pressure, this phenomenon is called wilting [22]. High rates of transpiration temporarily induce an insufficient water supply, and some plums wilt around the middle of the day, while a decline in transpiration relieves the water deficit at night, and the rolled leaves slowly re-expand. Wilting is a passive movement of plant leaves to prevent excess water consumption under drought stress Conditions. Apart from this, some plants can actively adjust the orientation of leaf blades to keep them parallel to the direction of incident solar radiation rolling. The phototropic movement of plant leaves can regulate the interception of solar radiation [23, 24], when the leaf blades expand in a direction perpendicular to the direction of solar radiation. The single blade receives the largest amount of radiation, while deviation from the vertical direction will reduce the amount of radiation. Upright leaves under water mess conditions will receive less radiation, resulting in reduced water loss and better overall water status, indicating that erect leaves are an effective mechanism of drought avoidance [25, 26, 27]. Leaf rolling is a common

response of plants to water deficit and it is a mechanism to reduce water consumption when water stress is present [23]. Leaf rolling is a drought-adaptive trait induced by turgor pressure, and osmotic adjustment can delay leaf rolling [28]. Both passive and active leaf movements have a role in reducing incident solar radiation and thus reducing leaf surface temperature, protecting plants from excess water loss. Plants with increased drought resistance often have xeromorphic structures such as smaller and thicker leaves, more epidermal trichomes, smaller and denser stomata, a thicker cuticle on the epidermis, thicker palisade tissue, a higher ratio of palisade to spongy parenchyma thickness, and more developed vascular bundle sheath [29]. Leaf epidermal trichomes reduce plant transpiration under intense light conditions and help to reflect light [30]. Lipids accumulate in the epidermis to form wax and increase the reflectivity of sunlight to prevent plants from excessive transpiration and high leaf surface temperatures [31]. The fortified sclerenchyma (mechanical tissue) can reduce the damage from wilting and protect the plants from direct light irradiation [32]. Palisade tissues and vascular bundles ensure transportation and retention of water and nutrients [33]. These features effectively reduce excess water loss and enhance the water-holding ability to avoid damage from exposure to drought stress conditions.

Role of the Stomata
Stomata are the pores which formed in the leaves of terrestrial plants during a long-term evolutionary process. As the vital organs for exchanging gas and water between the plants and the external environment, stomata play critical role in the activities of plant life by ensuring maximum absorption of CO_2 for photosynthesis, and meanwhile controlling the optimal transpiration. The stomatal density and aperture are closely related to plant drought resistance [34]. Guard cells which in pairs surround the stomatal pores are extremely sensitive to environmental conditions. After receiving the environment stimuli, changes of water potential and turgor movement in guard cells control the opening and closure of stomata, further regulate pivotal physiological processes in plants such as transpiration and photosynthesis. Under water-liming conditions, the function of stomata in adjusting transpiration is particularly important. Stomata of water-saving plants (Which avoid dehydration by reducing transpiration) are sensitive to water deficit, and the leaf stomata close before the leaf water status approaches wilting, thereby exerting a DA function. Stomata respond to water stress mainly in two ways: [1] as a direct response to the air humidity in which guard cells and adjacent epidermal cells directly evaporate moisture to include stomatal closure and prevent leaf water deficit, and [2] stomata respond to the water potential changes in the leaves in which stomata close when the leaf water potential falls below a certain threshold.
Stomatal movement is controlled by osmatic potential changes in guard cells, and k+ is one of the major ions affecting the osmatic potential in guard cells [35]. The influx of efflux of k+ from the guard cells play a critical role in changing the osmatic potential and the turgor pressure, which leads to the opening or closure of the stomata [36]. The outward and inward K+ channels on the plasma membrane of guard cells are vital to the transmembrane transport of K+. There are various specific proteins such as substrate-binding proteins (including ABA-binding proteins, acetylcholine receptors, GTP-binding proteins, and light receptors), Pumps, and channels on the plasma membrane of guard cells which

are involved in the control of stomata movement [37, 40]. These proteins are crucial for receiving and transducing stress signals in guard cells. And continue the fundamental basis of the opening and closure of the stomata under drought stress conditions. Furthermore, numerous studies suggest that stomatal movement is also controlled by the ABA signaling which is triggered by roots in drying soil profile [41, 42].

Stomatal closure is an important strategy to support water consideration by plants during drought stress. Thus, better understanding of the stomatal movement mechanisms is crucial for optimizing water use efficiency related to drought resistance in plants. Besides, other leaf-associated traits such as epidermal hairs, cuticular wax, along with leaf water potential, relative water content, water loss rate, and canopy temperature are also used as criteria for appraisal of DA [5]. It has long been established that plant bearing small leaves are typical to xeric environments. Such plants withstand drought very well, albeit their growth rate and biomass are relatively low [43]. Leaf pubescence is a xeromorphic trait that helps protect the leaves from excessive heat load. Hairy leaves have reduced leaf temperatures and transpiration [44] whilst inter and intra-specific variation exists for the presence of this trait. Under high temperature and radiation stress, hairiness increases the light reflectance and minimizes water loss by increasing the boundary layer resistance to water vapor movement away from the leaf structure. Although drought stress also includes the production of trichomes on both sides of wheat leaves, they had no significant influence on boundary layer resistance.

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

Role of Phytohormones in Signal Transduction
Phytohormones such as auxins, gibberellins, cytokinins, ethylene, abscisic acid, polyamines, brassinosteroids, jasmonates and strigolactones when applied externally or produced internally, influence physiological processes of plants at very low concentrations. Under drought conditions, among these hormones like ethylene, abscisic acid play a key role in coping with these adverse conditions.

Auxins induce new root formation by breaking root optical dominance induced cytokinins. As a prolific root system is vital for drought tolerance, auxins have an indirect but key role in this regard. Drought stress limits the production of endogenous auxins, usually when contents of abscisic acid and ethylene increase [45]. Nevertheless, exogenous application of indole-3-butyric acid synthetase from Arabidopsis is also drought-inducible [46]. Experiments with indole-3-yl-acetic acid and ethylene glycol tetra-acetic acid suggested that calcium and auxin participate in signaling mechanisms of drought- induced proline accumulation [47].

Drought rhizogenesis is an adaptive strategy that occurs during progressive drought stress and is reported from Brasicaceae and related families by the formation of short, tuberized, hairless roots. These roots are capable of withstanding a prolonged drought period and give rise to a new functional root system upon rehydration. The drought rhizogenesis was highly increased in the gibberelic acid biosynthesis mutant ga5, suggesting that some gibberrelic acid might also participate in this process [48].

Abiscisic acid is a growth inhibitor and produced under a wide variety of environmental stresses, including drought. All plants respond to drought and many other stresses by accumulating abscisic acid. Abiscisic acid is ubiquitous in all flowering plants and is generally recognized as a stress hormone that regulates gene expression and acts as a signal for the initiation of processes involved in adaptation to drought and other environmental stresses. It has been proposed that abscisic acid and cytokinin have opposite roles in drought stress. Increase closure and limit water loss through transpiration under water stress [49]. When plants wilt, abscisic acid levels typically rise as a result of increased synthesis [50]. Increased abscisic acid concentration leads to many changes in development, physiology and growth. Abscisic acid alters the relative growth rates of various plants parts such as increase in the root-to-shoot dry weight ratio, inhabitation of leaf area development and production of prolific and deeper roots [51]. It triggers the occurrence of a complex series of events leading to stomatal closure, which is as important water-conservation response [52]. In a study on generic variation for abscisic acid accumulation in rice, a consistent negative relationship between the ability of detached and partially dehydrated leaves to accumulate abscisic acid and leaf weight was established [43]. By its proposed cellular events and signaling cascades in a plant cell responding to drought stress. Drought stress is perceived by an unknown mechanism, which then activates the signaling cascades, plausibly by abscisic acid (ABA), hydrogen peroxide (H_2O_2) and calcium (Ca^{+2}). These cascades then activate the synthesis of specific protein kinases which activate main downstream responses such as changes in gene expression. The response to these signaling cascades also result in changes in plant metabolism including activation and synthesis of antioxidants, synthesis and accumulation of osmoprotectants and solutes, and stomatal closure under acute drought stress. Effect in closing stomata, abscisic acid can control the rate of transpiration And, to some extent, may be involved in the mechanism conferring drought tolerance in plants.

Abscisic acid includes expression of various water stress related genes. In a recent study, [53] reported a regulatory role of telomeric repeat binding factor gene 1 in abscisic acid sensitivity and drought response during seedling development [54]. Suggested the existence of abscisic acid-dependent and abscisic acid-independent transduction cascades and pathways to act as a signal of drought stress and expression of specific water stress-induced genes. Abscisic acid produces such changes that confer an ability to maintain cellular turgor to withstand dehydrative forces.

Ethylene has long been considered a growth inhibitory hormone, although it is involved in environmentally driven growth inhabitation and stimulation [1]. He response of cereals to drought includes lo0ss of leaf function and premature onset of senescence in older leaves. Ethylene may serve to regulate leaf performance throughout its life span as well as to determine the onset of natural senescence and metabolic drought-induced senescence [57]. Recent studies suggest that growth promotion is a common feature in ethylene responses. To escape this adversity, plants can option this response also involves ethylene synthesis [58].

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

promotes the generation of Reactive Oxygen Species (ROS) in photosynthetic tissues of Arabidopsis thaliana during osmotic stress [59].

Polyamines are known to have profound influence on plant growth and development. Being cationic, polyamines can associate with anionic components of the membrane, such as phospholipids, thereby protecting the lipid bi-layer from deteriorating effects of stress [60]. There has been a growing interest in the study of polyamine participation in the defense reaction of plants against environmental stresses and extensive research efforts have been made in the last two decades [60, 61]. Many genes for enzymes involved in polyamine metabolism have been cloned from several species, and their expression under several stress conditions has been analyzed. For example, the apple spermidine synthase, which substantially improves abiotic stress tolerance including drought [62].

Among various polyamines, a rise in the putrescence level is generally due to an enhanced arginine decarboxylase activity [60]. Compared with the sensitive plants stress-tolerant plants generally have a greater capacity to synthesize polyamines in response to stress, resulting in a two to three fold rise in endogenous polyamine levels over the unstressed ones [61]. Recent studies suggested that rice has a great capacity to enhance polyamine biosynthesis, particularly spermidine and spermine in free form and putrescence in insoluble-conjugated form, in the leaves earlier in response to drought stress. This was considered as an important physiological trait of drought tolerance in rice [63].

Osmotic adjustment

Major abiotic stress factors such as salt and drought adversely affect important physiological processes and biochemical mechanisms and cause severe loss in crop productivity worldwide. Plants develop various strategies to stand healthy against these stress factors. Osmotic adjustment is a biochemical mechanism that helps plants acclimate to water deficit conditions due to dry or saline soils. Many drought tolerant plants can regulate their potentials to compensate for transient or extended periods of water stress. This process is called osmotic adjustment, results from a net increase in the number of solute particles present in the plant cell. Thus, decrease in plant water potential may be brought about by osmotic adjustment, the accumulation of compatible solutes that promote acclimation to dry or saline soils. Compatible solutes, also known as compatible osmolytes are a small group of chemically diverse organic compounds that are highly soluble and do not interfere with cellular metabolism, even at high concentrations. Synthesis and accumulation of organic osmolytes are widespread in plants, but the distribution of specific compatible solutes varies among plant species.

Substances currently known to be involved in osmatic adjustment encompass several types of organic compounds such as mannitol, proline, glycine, betaine, trehalose, fructan, inositol, and inorganic ions [55, 56]. These organic substances can regulate the plasma membranes. In addition, changes in the ion and water channels control the export and import of ions and moisture for plant cells, which also contributes to osmotic adjustment. The organic ions mainly regulate the osmatic potential of the vacuole to maintain turgor pressure. However, a high concentration of inorganic ions is likely to cause metabolism disorders in plant cells. Hydration of the membrane and the surface layer of intracellular proteins are also important for stabilizing the surface bound water of and sustaining the spatial structure of biological macromolecules.

The accumulation of proline is one of the striking metabolic responses of plants to salt and drought stress. Proline biosynthesis and signaling contribute to the redox balance of cell under normal and stressful conditions. The amino acid proline is accumulated by a taxonomically diverseset of plants, whereas accumulation of the quaternary ammonium compound beta- alanine betaine appears to be confined to representatives of a few genera in Plumbaginaceae (Leadwort family). One mechanism for increasing solute concentrations is the irreversible synthesis of compounds such as glycine betaine. Concentrations of other compatible solutes like proline are maintained through a combination of synthesis and catabolism. Monomeric sugars are also released from polymeric form in response to stress. The role that compatible solutes play in osmotically stressed plants often has been defined as "osmoprotection." Glycine betaine is synthesized and accumulated by many algae and higher plants. Its distribution among plants is sporadic in Chenopodiaceae (Goosefoot family). Glycine betainevis synthesized from Choline in a two-step pathway. It's accumulation is regulated by the rates of it's synthesis and transport. Mannitol, D-Pinitol etc., are polyhydric alcohols. Mannitol is the reduced form of the sugar mannose. This sugar alcohol is broadly distributed among plants. D- Pinitol, a cyclic sugar alcohol is a major solute in members of Pinaceae, Fabaceae and Caryophyllaceae. pinitol is believed to be synthesized by O-methylation of myo-inositol that forms ononitol in Angiosperms sequoyitol in Gymnosperms. In addition to osmotic adjustmen, some compatible solutes may serve other protective functions.

Altered metabolism

Plant production is mainly determined by photosynthesis and plant photosynthesis is governed mainly by stomata for CO_2/water exchange and photosynthesis activity in mesophyll cells. Water stress affects not only the light reactions, but also assimilation efficiency of the dark reactions, thereby reducing the contents of the photosynthesis products (64,65,66).Plants have evolved three photosynthetic pathway including C_3, C_4, and Crassulacean Acid Metabolism (CAM) to assimilate atmospheric CO_2. Generally, plants utilizing C_3 and CAM photosynthetic mechanisms can better adapt to drought-prone climate [67]. C_3 plants open their stomata during the day for CO_2 absorption and fixation and close their stomata at night. This mechanism is deficient when C_3 plants confront water limitation because it doesn't retain moisture under drought stress conditions. C_4 plants have evolved a metabolic pump to concentrate CO_2 in the bundle sheath cells, and perform the fixation of CO_2 in mesophyll cells and the bundle sheath cells separately [68]. This particular mechanism contributes to higher water use efficiency than that of C_3 plants and provides more chances for C_4 plants to survive in arid areas [68]. In the CAM cycle photosynthesis pathway, plants open their stomata for CO_2 absorption and fixation at night, and close their stomata to reduce transpiration of water loss during the day. Therefore, CAM metabolism can dramatically increase the water use efficiency and is proposed to be a plastic photosynthesis adaptation to extremely arid environments [69]. When challenged by water stress, some plants considered as facultative CAM species are capable of switching their photosynthesis pathway from the C_3 cycle to the CAM cycle mode [70, 71]. Researchers have found that the key enzyme in the CAM metabolic pathway, phosphoenolpyruvate

carboxylase is transcriptionally regulated by water stress conditions. [72].

Role of Proteins
Aquaporins and defensive proteins
Effects of water deficit and perturbing ions on the membrane may be minimized by the action of carriers, pumps and channels. Synthesis and activity of aquaporin may be up-regulated in response to drought water movement through aquaporins can be modulated rapidly. In *Arabidopsis,* water deficit strongly induces expression of the *Rd28* gene, which encodes a member of of the MIP (Major Intrinsic Protein) family. The aquaporin RD28 is located in the plasma membrane. A wide range of mechanism and molecules have been studied which play important role in drought tolerance. Under abiotic stress a group of proteins i.e., aquaporins are responsible for water regulation In the plants. Functional characterization of these aquaporins and other protective proteins has proved the importance of their regulation under abiotic stress. Overexpression of the protective genes in transgenic plants not only enhances the drought tolerance in plants but also improve the tolerance against other abiotic stress as well. These genes are responsible either for signaling or activation of some regulatory pathways or encode some enzymes which involves in the synthesis of structural and functional protectants. Under the stress conditions, plants build up some new protective proteins like (HSP) heat shock proteins and late embryogenesis abundant (LEA) proteins. Complete information regarding the regulation of these protective proteins can help biotechnologist to enhance the adaption and drought tolerance ability in plants. HSP are produced by plants in stress conditions especially in response to high temperature [85].

Aquaporins are channel proteins which are responsible for water transportation. Aquaporins form selective water transport channels in plant cells and regulate the rapid transmembrane transport of moisture during the processes of seed germination, cell elongation, stomatal movements, and abiotic stress responses. Aquaporins are divided into three groups according to their subcellular location: plasma-membrance-intrinsic proteins (PIPs), tonoplast-intrinsic proteins (TIPs), and nodulin-26-like major-intrinsic proteins (NLMs), Aquaporins mediate passive water transport along the osmotic pressure gradient inside and outside the membrane, and they are capable of regulating the moisture balance for the entire plant under drought stress conditions. This is achieved by maintaining the water potential balance between the xylem parenchyma cells and the transpiration current, regulating water transport across cells and tissues, as well as adjusting the cell turgor and volume Further, characterization of key genes controlling the biosynthesis and metabolism pathways of these OA substances may provide useful candidate genes for improving drought tolerance by transgenic approach.

LEA Proteins
Additional genes are also induced by water stress. Some seed proteins may protect vegetative tissues from stress called LEA (Late Embryogenesis Abundant) proteins. Amelioration of plant stress may also arise from the function of a set of genes discovered during the investigation of the desiccation stages of seed development. Seven groups of LEA genes have been identified, based on homology among different species. Majority of these proteins are hydrophilic and soluble when boiled. However, not all groups have these characteristics

several LEA encoding genes have been shown to function in stress resistance by using over-expression technology in transgenic plants. They are low-molecular weight proteins which are usually between 10 and 30 KDa and consist of basic amino acids rich in lysine, glycine, and serine and commonly lack cystein and tyrosine residues [73]. LEAs are not only hyper hydrophilic proteins but also have extremely high thermal stability. LEA proteins can protect biological macro molecules, redirect intracellular water distribution, bound to inorganic ions to avoid the damage caused by drought stress and also prevent excessive dehydration of plant tissues and also controls the expression of other genes by binding to nucleic acids [74].

Molecular basis of drought resistance
Abiotic stresses (such as drought) induce the expression of the following transcription factors. They bind to cis-elements, resulting in a change in stress response and tolerance. Various other types of genes also are induced by water deficit, including those that may protect the plant from secondary biotic stresses. Osmotin, a tobacco protein with antifungal activity, accumulates during water deficit. The mechanisms of gene induction are regulated by specific DNA elements: two classes of elements, ABRE and DRE, have been found in many water deficit induced genes.

The molecular control of drought tolerance is also very complex and is influenced other factors such as environment and the developmental stage of the plant. This control consists mainly of transcriptional factors, such as dehydration-responsive element-binding protein (DREB), abscisicacid (ABA)-responsive element-binding factor (AREB), and NAM (no apical meristem). In response to drought conditions, there is an alteration of gene expression, induced by or activated by transcription factors (TFs). These TFs bind to specific cis-elements to induce the expression of targeted stress-inducible genes, allowing for products to be transcribed that help with stress response and tolerance. Some of these include dehydration-responsive element-binding protein (DREB), ABA-responsive element-binding factor (AREB), no apical meristem (NAM), Arabidopsis transcription activation factor (ATAF), and cup-shaped cotyledon (CUC). Much of the molecular work to understand the regulation of drought tolerance has been done in *Arabidopsis*, helping elucidate the basic processes below.

DREB TFs
DREB1/CBF TFs: DREB1A, DREB 1B, and DREB 1C are plant specific TFs which bind to drought responsive elements (DREs) in promoters responsive to drought, high salinity and low temperature in *Arabidopsis.* Over-expression of these genes enhance the tolerance of drought, high salinity, and low temperature in transgenic lines from *Arabidopsis*, rice, and tobacco.DREB2 TFs: DREB proteins are involved in a variety of functions related to drought tolerance. For example, DREB proteins including DREB2A cooperate with AREB/ABF proteins in gene expression, specifically in the DREB2A gene under osmotic stress conditions [6]. DREB2 also induces the expression of heat-related genes, such as heat shock protein. Over-expression of DREB2Aca enhances drought and heat stress tolerance levels in *Arabidopsis*.

AREB/ABF TFs
AREB/ABFs are ABA-responsive bZIP-type TFs which bind to ABA-responsive elements (ABREs) in stress-responsive promoters and activate gene expression [3]. AREB1, AREB2,

ABF3, and ABF1 have important roles in ABA signaling in the vegetative stage, as ABA controls the expression of genes associated with drought response and tolerance. The native form of AREB1 cannot target drought stress genes like RD29B in *Arabidopsis*, so modification is necessary for transcriptional activation. AREB/ABFs are positively regulated by SnRK2s, controlling the activity of target proteins via phosphorylation. This regulation also functions in the control of drought tolerance in the vegetative stage as well as the seed maturation and germination.

Other TFs

TFs like NAC (comprised of NAM, ATAF, and CUC), are also related to drought response in *Arabidopsis* and rice. Over-expression in the aforementioned plants improves stress and drought tolerance. They also may be related to root growth and senescence, two physiological traits related to drought tolerance.

Engineering Drought tolerance in Plants

Functional and regulatory genes directly involved in all stress related responses in drought tolerant plants are being engineered to enhance their function and to introduce these responses in drought non tolerant plants. Arabidopsis is a model plant for studying drought tolerance because of availability of its complete genomic sequence, short term generation times, whole transformation protocols, proteomic data, microarray, EST sequence tags and wide variety of mutants. Potential target gene for drought tolerance is selected in a rational way. Water, cold and salinity stress are treated as being correlated [75]. Microarray gene expression technology is mostly used for identifying target gene. Genome wise responses are analyzed by contribution of gene ontology. Due to complex nature of this drought stress response modification of single component or gene will not be enough. Several regulatory and signaling factors should be manipulated together. Cross tolerant nature of target gene can be checked by additional abiotic stress response expression describing experiments. Microarray experiments also identify co-regulated genes. Up stream promoter sequence is required for knowing cis-elements and transcriptional factors. Several databases serve this purpose. Transcriptional profiles vary between roots and shoot so crude over-expression of selected gene is not sufficient. Drought stress responses are function of tissues specificity and timing and vary widely. It will be beneficial to know about precise transcriptional changes occurring after drought to select and design target [76]. At last mechanism and site of expression of transgene is also necessary to know. Signaling molecule manipulation is a reproducible attempt but can result in unfavorable broad response. It is economical to manipulate stress-activation mediated signaling component instead of using over-expression of target gene. Engineered APETALAL2 transcription factor gene enables alfalfa (*Medicago trancuiata*) to tolerate drought stress through wax production [77]. Members of R2R3 MYB gene of Arabidopsis AtMYBGO and AtMYBBl encode transcriptional factors controlling stomatal movement. Mutant Arabidopsis osml/syp61 leads to impaired ABA mediated stomatal opening. Engineered AtMYBSO gene through null mutation reduces stomatal opening. In *Arabidopsis* post-translationally activation of SRK2C kinase in response to stress enhances tolerance. In transgenic plants with engineered SRch gene this activity was observed much more. Through post-genomic tools transgenic constructs can be evaluated. Recently microRNAs responsive

to drought stress have been discovered and used successfully. Mannitol Dehydrogenase (Mtl D) gene when introduced in wheat increased drought tolerance. In tobacco plant over-expression of transgenic Inositol Methyl Transferase (IMTI) gene originated from the plants enhanced drought tolerance [79]

Conclusion

Plant growth and productivity is adversely affected by nature's wrath in the form of various biotic and abiotic stress factors. Water deficit is one of the major abiotic stresses, which adversely affects crop growth and yield. The drought resistance of plants is quite complex. For a given plant species, plants often combine different categories of mechanisms to confer drought resistance at different developmental stages. At a particular developmental stage, plant drought resistance is associated with a series of events (such as stomatal movement, photosynthesis, cell osmotic regulation, synthesis of protective macromolecules and antioxidants etc.) in every conceivable facet at the morphological, physiological and molecular levels. In addition to this, natural drought stress is dynamic and unpredictable. Therefore, it is rather difficult to comprehensively and accurately evaluate the overall drought resistance of a given plant species. Plants can be subjected to slowly developing water shortages (ie, taking days, weeks, or months), or they may face short-term deficits of water (ie, hours to days). In these situations, plants adapt by responding accordingly, minimizing water loss and maximizing water uptake. Plants are more susceptible to drought stress during the reproductive stages of growth, flowering and seed development. Therefore, the combination of short-term plus long-term responses allow for plants to produce a few viable seeds. Some examples of short-term and long-term physiological responses include: root growth, increased root/shoot, increased absorption. Short-term responses: In the leaf: root-signal recognition, stomatal closure, decreased carbon assimilation. In the stem: inhibition of growth, hydraulic changes, signal transport, assimilation of transport. In the root: cell-drought signaling, osmotic adjustment. Long-term responses: In the above-ground portion of the plant: inhibition of shoot growth, reduced transpiration area, grain abortion, senescence, metabolic acclimation, osmotic adjustment, anthocyanin accumulation, carotenoid degradation, intervention of osmoprotectants, ROS-scavenging enzymes. In the below-ground portion of the plant: turgor maintenance. The mechanisms behind drought tolerance are complex and involve many pathways which allow plants to respond to specific sets of conditions at any given time. Some of these interactions include stomatal conductance, carotenoid degradation and anthocyanin accumulation, the intervention of osmoprotectants (such as sucrose, glycine, and proline), ROS-scavenging Plants usually begin various mechanisms to sustain water in them such as through formation of deep roots, pumping of salts into the vacuole and out of the cells, increase of water resistive diffusion and the formation of small succulent leaves to reduce water loss. Osmolytes including polyols, metabolites, organic acids, glycine betaine, and proline along with many other aminoacids play an important role during drought conditions to sustain the proper functioning of plant cells [80]. There are many enzymes and substances like polyamines and citrulline which work as effective anti-oxidants to limit the effect of drought. Researchers have developed several techniques to make plants resistant towards drought

conditions through breeding and massive screening, application of phytohormones exogenously to the plants subjecting some osmoprotectants to the seeds for germination and good growth genetic engineering, and marker based selection methods [81]. The environmental conditions leading to drought include low precipitation and high rate of evapotranspiration causing reduction in plant cell division, proliferation of roots, closure of stomatal pores, changes in relation between plant and water uptake efficiency and high production of Abscisic acid which further helps decreasing the evapotranspiration by controlling stomatal pores [82]. Since plant growth is a reversible process with myriad metabolic pathways, all the phases such as development, growth differentiation of cells, division, elongation, increase in volume, and intensification of weight are irreversible in it and get affected. [83, 84] In this review paper we have highlighted the advances which are being made to make plants more droughts tolerant: starting from traditional methods gene and regulation, genetic engineering and plant physiology along with numerous essential substances which play an important role in plant metabolism.

References
1. Taiz L, Zeiger E. Plant Physiology, 6th Ed., Sinauer Associates Inc. Publishers, Massachusetts. 2015, 731-761.
2. Bob B Buchannan, Wilhelm Gruissen, Russel L Jones, 1st edi, Biochemistry and Molecular Biology of plants, John Wieley publishes. 2000, 1158-2103.
3. Schuppler U, He PH, John PCL, Munns R. Effects of water stress on cell division and cell-division-cycle-2-like cell-cycle kinase activity in wheat leaves, Plant Physiol. 1998; 117:667-678.
4. Kavar T, Maras M, Kidric M, Sustar-Vozlic J, Meglic V. Identification of genes involved in the response of leave of Phaseolus vulgaris to drought stress, Mol. Breed. 2007; 21:159-172.
5. Hu H, Xiong L. Genetic engineering and breeding of drought-resistant crops. Annu Rev Plant Biol. 2014; 65:715-741.
6. Mohamed MF, Keutgen N, Tawfika AA, Noga G. Dehydration-avoidance responses of tepary bean lines differing in drought resistance. J Plant Physiol. 2002; 159:31-38.
7. Price A, Steele K, Moore B, Jones R. Upland rie grown in soil-filled chambers and exposed to contrasting water-deficit regimes: II. Mapping quantitative trait loci for root morphology and distribution. Field Crops Res. 2002; 76:25-43.
8. Foster B, Thomas W, Chloupek O. Genetic controls of barley root syste4ms and their associations with plant performance. Aspects Appl Biol. 2005; 73:199-204.
9. Subashri M, Robin S, Vinod K, Rajeswari S, Mohanasundaram K, Raveendran T. Trait identification and QT%L validation for reproductive stage drought resistance in rice using selective genotyping of near flowering RILs. Euphytica. 2009; 166:291-305.
10. Larcher W. Physiological plant ecology: ecophysiology and stress physiology of functional groups. Springer, Netherlands, 2003.
11. Dixon R, Wright G, Behrns G, Teskey R, Hinckley T. Water deficits and root growth of ectomycorrhizal white oak seedlings. Can J For Res. 1980; 10:545-548.
12. Den Herder G, Van Isterdael G, Beeckman T, De Smet I. The roots of a new green revolution. Trends Plant Sci. 2010; 15:600-607.
13. Malamy J. Intrinsic and environmental response pathways that regulate root system architecture. Plant Cell Environ. 2005; 28:67-77.
14. Kramner PJ. Plant and soil water relationships: a modern synthesis. Plant and woil water relationships: a modern synthesis. McGraw-Hill Book Company, New York, 1969.
15. Price AH, Cairns JE, Horton P, Jones HG, Griffiths H. Linking drought-resistance mechanisms to drought avoidance in upland rice using a QTL approach: progress and new opportunities to integrate stomatal and mesophyll responses. J Exp Bot. 2002; 53:989-1004.
16. Wu Y. Cosgrove DJ. Adaptation of roots to low water potentials by changes in cell wall extensibility and cell wall proteins. J Exp Bot. 2000; 51:1543-1553.
17. Fulda S, Mikkat S, Stegmann H, Horn R. Physiology and proteomics of drought stress acclimation in sunflower (*Helian – thus annuus* L.). Plant Biol (stuttg). 2011; 13:632-642.
18. Pallardy SG. Physiology of woody plants. Academic Press, London, 2010.
19. Ali MA, Abbas A, Niaz S, Zulkiffal M, Ali S. Morpho – Physiology criteria for drought tolerance in sorghum (*Sorghum bicolor*) at seeding and post – anthesis stages. Int J Agric Biol. 2009; 11:674-680.
20. Nguyen HT, Babu RC, Blum A. Breeding for drought resistance in rice: Physilogy and molecular genetics considerations, Crop Sci. 1997; 37:1426-1434.
21. Subbarao GV, Johansen C, Slinkard AE, Rao RCN, Saxena NP, Chauhan YS. Strategies and scope for improving drought resistance in grain legumes. Crit. Rev. Plant Sci. 1995; 14:469-523.
22. Poorter L, Markesteijn L. Seeding traits determine drought tolerance of tropical tree species. Biotropica. 2008; 40:321-331.
23. Begg J, Turner N, Kramer P. Morphological adaptations of leaves to water stress. Adaptation of plants to water and high temperature stress. Wiley, New York, 1980.
24. Ludlow MM, Bjorkman O. Paraheliotropic leaf movement in Siratro as a protective mechanism against drought-induced damage to primary photosynthetic reactions: damage by excessive light and heat. Planta. 1984; 161:505-518.
25. Stevenson K, Shaw R. Effects of leaf orientation on leaf resistance to water vapor diffusion in soybean (*Glycine max* L. Merr) leaves. Agron J. 1971; 63:327-329
26. Meyer WS, Walker S. Leaflet orientation in water-stres-sed soybeans. Agron J. 1981; 73:1071-1074.
27. Oosterhuis DM, Walker S, Eastham J. Soybean leaflet movements as an indicator of crop water stress. Crop Sci. 1985; 25:1101-1106.
28. Hsiao TC, O'Toole JC, Yambao EB, Tower NC. Indluence of osmotic adjustments on leaf rolling and tissue death in rice (*Oryza sativa* L). Plant Physiol. 1984; 75:338-341.
29. Esau K. Anatomy of seed plants. Soil Sci. 1960; 90:149.
30. Abclulrahaman A, Oladele E. Response of trichomes to water stress in two species of *Jatropha*. Insight bot. 2011; 1:15-21.
31. Mohammadian MA, Watling JR, Hill RS. The impact of epicuticular wax on gas-exchange and photonhibition in

Leu-cadendron lanigerium (Proteaceae). Acta Oecol. 2007; 31:93-101.

32. Terashima I. Anatomy of non-unform leaf photosynthesis Photosyn Res. 1992; 31:195-212.

33. Guha A, Sengupta D, Kumar Ramachandra Reddy A. An integrated diagnostic approach to understand drought tolerance in mulberry (*Morus indica* L.). Flora Morphol Distrib Funct Ecol Plants. 2010; 205:144-151.

34. Hetherington AM, Woodward FI. The role of stomata in sensing and driving environmental change. Nature. 2003; 424:901-908.

35. Hosy E, Vavasseur A, Mouline K, Dreyer I, Garmard F, Poree F *et al.* The Arabidopisis outward k+ channel GORK is involved in regulation of stomatal movements and plant transpiration. Proc Natl Acad Sci USA. 2003; 100:5549-5554.

36. Li L, Kim BG, Cheong YA, Pandey GK, Luan S. A Ca^{2+} signaling pathway regulates a K+ channel for low-K response in *Arobidopsis*. Proc Nati Acad Sci USA. 2006; 103:12625-12630.

37. Cousson A, Vavasseur A. Putative in cyclic-GMP-mediated induction of stomatal opening by auxin in *Commelina communis* L. Planta. 1998; 206:308-314.

38. Wang H, Wang X, Zhang S, Lou C. Muscarinic acetylcholine receptor is involved in acetylcholine regulating stomatal movement. Chin Sci Bull. 2000; 45:250-252.

39. Shimazaki KI, Doi M, Assmann SM, Kinoshita T. Light regulation of stomatal movement. Annu Rev Plant Biol. 2007; 58:219-247.

40. Yamazaki D, Yoshida S, Asami T, Kuchitsu K. Visualization of abscisic acid-perception sites on the plasma membrane of stomatal guard cells. Plant J. 2003; 35:129-139.

41. Schroeder JI, Kwat JM, Allen GJ. Guard cell abscisic acid signaling and engineering drought hardiness in plants Nature. 2001; 410:327-330.

42. Zhang J, Jia W, Yang J, Ismail AM. Role of ABA in integrating plant responses to drought and salt stresses. Field Crop Res. 2006; 97:111-119.

43. Ball RA, Oosterhuis DM, Mauromoustakor A, Growth dynamics of the cotton plant during water-deficit stress, Agron J. 1994; 86:788-795.

44. Sandquist DR. Ehleringer JR. Population-and family-level variation of brittlebush (*Encelia farinose,* Asteraceae) pubescence: its relation to drought and implications for selection in variable environments, Am. J Bot. 2003; 90:1481-1486.

45. Nilsen ET, Orcutte DM. Phytohormones and plant response to stress, In: Nilsen E.T., Orcutte D.M. (Eds.). Physiology of Plant under Suress: Abiotic Factors, John Wiley and Sons, New York, 1996, 183-198.

46. Ludwig-Muller J. Indole-3-butyric acid synthesis in ecotypes and mutants of *Arabidopsis thaliana* under different growth conditions, J Plant Physiol. 2007; 164:47-59.

47. Sadiqov ST, Akbulut M, Ehmedov V. Role of Ca^{2+} in drought stress signaling in wheat seedings, Biochemistry-Moscow. 2002; 67:491-497.

48. Vartanian N, Marcotte L, Ciraudat J. Drought Rhizogenesis in *Arabidopsis thaliana*: differential responses of hormonal mutants. Plant Physiol. 1994; 104.761-767.

49. Morgan PW. Effects of abiotic stresses on plant hormone systems, in: Stress Responses in plants adaptation and acclimation mechanisms, Wiley-Liss, Inc, 1990, 113-146.

50. Taylor IB. Genetics of ABA synthesis, in: Davies W.J., H.G., Jones (Eds.), Abscisic acid: Physiology and Biochemisrtry, Bios Scientific Publishers Ltd. UK, 1991, 23-38.

51. Sharp RE, Wu Y, Voetberg GS, Soab IN, Le Noble ME. Confirmation that abscisic acid accumulation is required for maize primary root elongation at low water potentials. J Exp. Bot. 1994, 45:1743-1751.

52. Turner NC, Wright GC, Siddique KHM. Adaptation of grain legumes (pulses) to water-limited environments, Adv. Agron. 2001; 71:123-231.

53. Zhang X, Zhang Z, Chen J, Chen Q, Wang X, Huang R. Expressing TERFI in tobacco enhances drought tolerance and abscisic acid sensitivity during seeding development. Plants. 2005; 222:494-501.

54. Bray EA. Plant responses to water deficit, Trends Plant Sci. 1997; 2:48-54.

55. Crowe JH, Crowe LM, Chapman D. preservation of membranes in anhydrohiotic organisms: The role of trehalose Science. 1984; 223:701-703.

56. Wang S, Wan C, Wang Y. Chen H, Zhou Z, Fu H *et al.* The Characteristics of Na^+, K^+ and free proline distribution in several drought-resistant plants of the Alxa Desert, China, J Arid Environ. 2004; 56:525-539.

57. Young TE, Meeley RB, Galllie DR. ACC synthase expression regulates leaf performance and drought tolerance in maize. Plant J. 2004; 40:813-825.

58. Pierik R, Sasidharan R, Voesenek LACJ. Growth control by ethylene: adjusting phenotypes to the environment J Plant Growth Regul. 2007; 26:188-200.

59. Borsani O, Valpuesta V, Botella MA. Evidence for a role of salicylic acid in the oxidative damage generated by NaCI and osmotic stress in *Arabidopsis* seedihings, Plant Physiol. 2001; 126:1024-1030.

60. Boucherau A, Aziz A, Larher F, Tanguy M. Polyamines and environmental challenges: Rec. Develop. Plant SCi. 1999; 140:103-125.

61. Kasukabe Y, He L, Nada K, Misawa S, Ihara I, Tachibana S. Overexpression of spermidine synthase enhance tolerance to multiple environmental stresses and up-regulates the expression of various stress-regulated genes in transgenic *Arabidopsis thaliana*, Plant Cell Physiol. 2004; 45:712-722.

62. Wen XP, Pang XM, Matsuda N, Kita M, Inoue H, Hao YJ *et al*. Over-expression of the apple spermidine synthase gene in pear confers multiple abiotic stress tolerance by altering polyamine titers, Transgenic Res. 2007; 17:251-263.

63. Yang J, Zhang J, Liu K, Wang Z, Liu L. involvement of polyamines in the drought resistance of rice. J Exp. Bot. 2007; 58:1545-1555.

64. Reddy AR, Chaitanya KV, Vivekanandan M. Drought – induced responses of photosynthesis and antioxidant metabolism in higher plants. J Plant Physiol. 2004; 161:1189-1202.

65. Pagter M, Bragato C, Brix H. Tolerance and physiological responses of *Phragmites australis* to water deficit. Aquat Bot. 2005; 81:285-299.

66. Basu P, Sharma A, Garg I, Sukumaran N. Tuber sink modifies photosynthetic response in potato under water stress. Environ Exp Bot. 1999; 42:25-39.

67. Ashraf M, Harris P. Photosynthesis under stress environments: An overview. Photoynthetica. 2013; 51:163-190.

68. Chaves MM, Maroco JP, Pereira JS. Understanding plant responses to drought-from genes to the whole plant. Funct Plant Biol. 2003; 30:239-264.

69. Cushman JC. Crassulacean acid metabolism. A plastic photosynthetic adaptation to arid environments. Plant Physiol. 2001; 127:1439-1448.

70. Lin Z, Peng C, Lin G. Photooxidation in leaves of facultative CAM plant Sedum spectabile at C3 and CAM mode Acta Bot Sin. 2008; 45:301-306.

71. Kerbauy GB, Takahashi CA, Lopez AM, Matsumura AT, Hamachi L, Felix LM *et al.* Crassulacean acid metabolism in epiphytic orchids: current knowledge, future perspectives, Appl Photosyn, 2012, 81-104.

72. Sanchez R, Flores A, Cejudo FJ. Arabidopsis phosphor-enolpyruvate carboxylase genes encode immunologically unrelated polypeptides and are differentially expressed in response to drought and salt stress. Planta. 2006; 223:901-909.

73. Shao HB, Liang ZS, Shao MA. LEA proteins in higher plants: structure, function, gene expression and regulation Colloid Surf B. 2005; 45:131-135.

74. Close TJ. Dehydrins: emergence of a biochemical role of a family of plant dehydration proteins. Physiol Plantarum. 1996; 97:795-803.

75. Vinocur B *et al.,* Recent advancements in engineering plant tolerance against drought stress. Achievements and limitations. Curr Opin Biotecerol. 2006:16:123:132.

76. Munns R *et al.*, Comparative physiology of salt and water stress. Plant cell Environ. 2012l; 25:239-250.

77. Zhang JY *et al.*, Overexpression of WXPI a putative medicageo tranculate AP2 domain containing transcription factors gene increases wax accumulation and enhances drought tolerance, Plant Journal. 2005; 42:689-707.

78. Zinu J *et al.*, OSML/SYP61 a syntaxin protein in Arabidopsis, Plant Cell. 2004; 16:2001:2019.

79. Sunkar R *et al*. Novel and stress related miRNAs from Arabidopsis. Plant cell. 2004; 16:2001-2019.

80. Yancey PH *et al*. Organic osmolytes as compatible, metabolic and counteracting cytoprotectants in high osmolarity and other stresses. J Exp Biol. 2005; 208:2819-2830.

81. Ali M *et al*. Differential responses of anti-oxidants enzymes, lipoxygenase activity, ascorbate content and the production of saponins in tissue cultured root of mountain Panax ginseng CA Mayer and *Panax quinquefolius* L. in bioreactor subjected to methyl jasmonate stress. Plant science. 2005; 169:83-92.

82. Anderson JV *et al.*, An improved whole-seed assay for screening wheat germplasam for polyphenol oxidase activity. Crop Science. 2001; 41:1697-1705.

83. Yamaguchi-Shinozaki K *et al.* Transcripational regulatory networks in celluar responses and tolearance to dehydration and cold stresses. Annu Rev Plant Biol. 2006; 57:781-803.

84. Rajaram S *et al.*, Role of conventional plant breeding and biotechnology in future wheat production. Turk J Agric Forest. 2005; 29:105-11.

85. Bartels D *et al.*, Curretn status and implications of engineering drought tolerance in plants using transgenic approaches. CAB Rev. 2008; 3:20.