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Effect of Drought stress on Medicinal plants and its tolerance mechanism ABSTRACT
Drought stress is especially important in countries where crop agriculture is essentially rain-fed. Drought stress causes an increase in solute concentration in the environment, leading to an osmotic flow of water out of plant cells. This in turn causes the solute concentration inside plant cells to increase, thus lowering water potential and disrupting membranes along with essential processes like photosynthesis.

These drought-stressed plants consequently exhibit poor growth and yield. In worst case scenarios, the plants completely die. Certain plants have devised mechanisms to survive under low water conditions. These mechanisms have been classified as tolerance, avoidance or escape. Medicinal plants have been an integral part of our daily life for thousands of years. Drought is the most important abiotic factor limiting growth, adversely affect growth and crop production. Stress resulting in the non-normal physiological processes that influence one or a combination of biological and environmental factors.

Production is limited by environmental stresses, according to different solar's estimates, only 10 percent of the world's arable land is free from Stress, in general, a major factor in the difference between yield and potential performance, environmental stresses. Drought stress is the most common environmental stresses that almost 25 percent of agricultural lands for agricultural farm products in the world are limited. INTRODUCTION
Medicinal plants in any country form a very heterogeneous group in growth habit, distribution, reproduction, phenology and their ecological requirements. Many of them grow in open starting from wetlands to dry, arid conditions.

They also extend from sea level to higher altitudes. The medicinal value of such plants

also might vary; some important ones are mountainous forms, others bordering the desert or semi-desert areas. The quality and quantity of products they produce also vary depending on the habitat. Interest in the exploitation of medicinal plants as pharmaceuticals, herbal remedies, flavourings, perfumes and cosmetics, and other natural products has greatly increased in the recent years (Anon 1994; Ayensu 1996; Salleh et al. 1997; Kumar et al. 2000).

In India alone, less than 10% of the medicinal plants traded in the country are cultivated, about 90% are collected from the wild, very often in a destructive and unsustainable manner (Natesh 2000). The medicinal plants have been used by humans from the pre-historical times. Some examples of medicinal plant from the Asia-Pacific region are of species such as Rauvolfia, Hyoscyamus, Cassia, Atropa, Podophyllum, Psoralea, Catharanthus, and Papaver. Though much information exists on the species diversity in medicinal plants in the Asia-Pacific region, relatively very little is known about the distribution, abundance, ecology and genetic diversity of the great majority of medicinal and aromatic plants, although some efforts have started in recent years (Chadha and Gupta 1995; Chandel et al. 1996; Kumar et al. 2000; Paisooksantivatana et al. 2001), including the use of molecular markers (Sharma et al 2000; Natesh 2000).

Out of the 350 000 plant species identified so far, about 35 000 (some estimate up to 70 000) are used worldwide for medicinal purposes and less than about 0.5% of these have been chemically investigated. The global market for the medicinal plants and herbal medicine is estimated to be worth US\$800 billion a year (Rajasekharan and Ganeshan 2002). More than 8000 plant species are known for their medicinal properties in the Asia-Pacific and about 10% of them are used regularly, mostly collected from wild.

For example, it has been estimated that not less than 7500 species of medicinal plants exist in the Indonesian archipelago, of which only about 187 species are used as basic materials in traditional medicines industries (Hamid 1990). In China, over 4000 species of medicinal plants have been reported (Ayensu 1996). In India, about 2500 species are used for medicinal purposes, and about 90% of the medicinal plants provide raw materials for the herbal pharmaceuticals, which are collected from the wild habitats (Rajasekharan and Ganeshan 2002).

About 2000 medicinal plants species are reported from Malaysia (Latif 1997), while in another account 1200 species have been reported to have potential pharmaceutical value, some of which are being used as herbal medicines (Kadir 1997). For the Indian Himalayan Region, a total of 1748 species of medicinal plants – 1020 herbs, 338 shrubs, 339 trees, apart from 51 pteridophytes – have been listed (Samant et al. 1998). These include several of the endangered medicinal plant species, using current IUCN, Red Data

criteria under the Biodiversity Conservation Prioritization Project (BCPP), by Conservation Assessment and Management Plan (CAMP) workshop organized by WWF at Lucknow from 21-25 January 1997 (Samant et al. 1998). Some examples of the endangered Himalayan medicinal plant species include: *Aconitum balfourii*, *A.*

deinorrhizum, *Acorus calamus*, *Angelica glauca*, *Atropa belladonna*, *Berberis kashmiriana*, *Coptis teeta*, *Dioscorea deltoidea*, *Gentiana kurroo*, *Nardostachys grandiflora*, *Picrorhiza kurroo*, *Podophyllum hexandrum*, *Saussurea costus*, *Sweria chirayita* and *Taxus baccata* subsp. *wallichiana*; and the sub-tropical/sub temperate species *Aquilaria malaccensis*. Drought stress is one of the most important environmental stress affecting agricultural productivity around the world and may result in considerable yield reductions (Boyer, 1982; Ludlow and Muchow, 1990).

Drought resistance refers to a plant's growth and development, and its ability to slowly modify its structure and function so that it can better tolerate drought (Turner, 1986). A strategy for improving medicinal and aromatic plants yields is to identify the production compounds and practices that are relatively drought resistant and that will result in superior yields under dry land conditions (Popp et al., 2002). Faced with scarcity of water resources, drought is the single most critical threat to world food security.

It was the catalyst of the great famines of the 19th century. Because food supply is limiting, future food demand for rapidly increasing population pressures is likely to further aggravate the effects of drought (Somerville and Briscoe, 2001). Three main mechanisms reduce crop yield by soil water deficit: (i) reduced canopy absorption of photosynthetically active radiation, (ii) decreased radiation-use efficiency and (iii) reduced harvest index (Earl and Davis, 2003). Although plant responses to drought are relatively well known, plant performance under a more complex environment where multiple stresses co-occur is fragmentary. That is why the plants have to respond simultaneously to multiple stresses, e.g.

drought, excessive light and heat, which may coincide in the field. These kinds of investigations are usually not predictable from single factor studies (Zhou et al., 2007). Effects of drought stress on plant activities: The potentials of -10 to -15 more physiological phenomena such as leaf growth, stomatal conductance, photosynthetic rate and nitrogen metabolism decreases (Heidaiy and Moaveni, 2009). In the study of physiological phenomena of drought stress in plants, reported that the plant water status, often by measuring the water potential of tissues, specified by decreasing water potential decreases cell growth and protein synthesis.

The flow of carbon dioxide and leaf transpiration decreases, but the accumulation of

proline and abscisic acid stress increases (Heidaiy and Moaveni, 2009). Drought stress, photosynthesis by stomatal closure and transfer of carbon dioxide in chloroplasts and cell water potential decreased, affected. Drought stress, root and shoot growth is affected and may reduce the level of plants. Drought stress, crop yield reduces largely the following methods: 1- The reduction of photosynthetic active radiation absorbed by vegetation 2- reduce the efficiency of radiation 3- The reduction in harvest index.

Corn dry matter, the reduction in water consumption will decline (Sajedi, 2008).

Medicinal plants under drought conditions: The effect of drought stress on medicinal plants growth and development has been studied lowly. The results were indicated that water deficit during the vegetative period (before flowering stage) can result in shorter plants and smaller leaf areas of mint (Abbaszadeh et al., 2008), yarrow (Sharifi Ashoorabadi et al., 2005) and chicory (Taheri et al., 2008), reduced water use due to the reduction in plant size of calendula (Rahmani et al., 2008), decreased vegetative dry matter of balm (Aliabadi et al., 2009).

Drought stress reduces yield of medicinal plants by three main mechanisms: First, whole canopy absorption of incident photosynthetically active radiation may be reduced, either by drought-induced limitation of leaf area expansion, by temporary leaf wilting or rolling during periods of severe stress, or by early leaf senescence. Second, drought stress decreased the efficiency with which absorbed photosynthetically active radiation is used by the crop to produce new dry matter (the radiation use efficiency). This can be detected as a decrease in the amount of crop dry matter accumulated per unit of photosynthetically active radiation absorbed over a given period of time, or as a reduction in the instantaneous whole-canopy net CO₂ exchange rate per unit absorbed photosynthetically active radiation. Third, drought stress may limit grain yield of medicinal plants by reducing the harvest index (HI).

This can occur even in the absence of a strong reduction in total medicinal plants dry matter accumulation, if a brief period of stress coincides with the critical developmental stage around flowering (Earl and Davis, 2003). Water deficit during the reproductive period can decrease the interval from seed formation to pollen shed and shorten the grain filling period. There also is a large amount of literature on the effect of water deficit on different medicinal plants yields components (Barnabas et al., 2007).

The numerous studies were indicated that grain yield can be drastically reduced as a result of water deficit during the reproductive period of coriander (Aliabadi et al., 2008), Mexican marigold (Mohamed et al., 2002) and grapevine (Scalabrelli et al., 2007). This grain yield reduction has been attributed to reduced grain number, grain weight, or both. Sinclair et al. (1990) attributed the greater sensitivity of grain yield to water deficit

at anthesis to this stage also being the period of maximum biomass accumulation and water use.

Consequently, drought stress reduced vegetative growth period and plant move to flowering stage. Therefore, quantity characteristics of medicinal plants decreased under drought conditions sorely. Essential oil content of medicinal plants under drought stress conditions. An essential oil is a concentrated, hydrophobic liquid containing volatile aroma compounds from some plants. Essential oils do not as a group needs to have any specific chemical properties in common, beyond conveying characteristic fragrances. They are not to be confused with essential fatty acids. Essential oils are generally extracted by distillation.

Other processes include expression or solvent extraction. They are used in perfumes, cosmetics and bath products, for flavoring food and drink, and for scenting incense and household cleaning products (Sellar, 2001). Drought stress increases the essential oil percentage of medicinal plants. because in case of stress, more metabolites are produce in the plants and substances prevent from oxidization in the cells, but essential oil content reduce under drought stress, because the interaction between the amount of the essential oil percentage and shoot yield is consider important as two components of the essential oil content and by exerting stress, increases the essential oil percentage but shoot yield decreases by the drought stress, therefore essential oil content reduces (Aliabadi et al.,

2009). The effect of water stress on essential oil was studied in excised leafs of palmarosa (*Cymbopogon martinii* var. *motia*) and citronella java (*C. winterianus*). Essential oil percentage was increased under water stress and essential oil content was decreased under this condition (Fatima et al., 2006). An experiment was carried out to study the influence of water deficit stress on essential oil of balm. The results of this experiment showed that essential oil yield was reduced under water deficit stress but essential oil percentage was increased under stress (Aliabadi et al., 2009).

Also, Khalid (2006) evaluated the influence of water stress on essential oil of two species. For both species under water stress, essential oil percentage and the main constituents of essential oil increased. Seventy five percent of field water capacity resulted in the highest yield of herb and essential oil for both species of an herb plant that is *Ocimum basilicum* L. (sweet basil) and *Ocimum americanum* L. (American basil). Singh- Sangwan et al. (2006) indicated that the level of essential oils was maintained or enhanced under drought condition. The major oil constituents, geraniol and citral increased substantially in two lemon grasses (*Cymbopogon nardus* and *Cymbopogon pendulus*).

Water stress had significant effect on flowering shoot yield, essential oil yield of flowering shoot and essential oil percentage of flowering shoot of coriander and highest upon characteristics were achieved under without stress conditions and highest oil percentage of flowering shoot was achieved under water stress conditions (Aliabadi et al., 2008). Consequently, drought stress reduces essential oil content of medicinal plants and increases essential oil percentage under drought conditions. Water use efficiency of medicinal plants under drought conditions Limited soil water availability reduces medicinal and aromatic plants growth more than all other environmental factors combined.

In arid and semi-arid regions where water resources for irrigation are being depleted, methods for more efficient irrigation scheduling are needed for commercial growers. The best option for medicinal plants production, yield improvement, and yield stability under soil moisture deficient conditions is to develop drought tolerant medicinal plants varieties. The potential soil moisture deficit produces two meaningful numbers: a critical deficit beyond which yield is reduced, and a reduction in yield per unit of potential deficit when the critical deficit is exceeded (Martin et al.,

2001) medicinal plants sorely, but increased the water use efficiency because, plants use available water in soil optimally. Also, plants decrease evapotranspiration by blocked or half-blocked of stomata and reductions in leaf areas, plant height and lateral stem number. Therefore, water use efficiency of medicinal plants increases under drought conditions. Proline accumulation rate in medicinal plants under drought conditions: Drought stress results in an increase of proline biosynthesis rate.

Proline accumulation may in part involve induction and/or activation of enzymes of proline biosynthesis, possibly coupled with a relaxation of proline feedback inhibition control of the pathway, decreased proline oxidation to glutamate mediated at least in part by down regulation of proline dehydrogenase, decreased utilization of proline in protein synthesis and enhanced protein turnover. Water deficits induce dramatic increases in the proline concentration of phloem sap in medicinal plants, suggesting that increased deposition of proline at the root apex in water stressed plants could in part occur via phloem transport of proline.

A proline transporter gene, ProT2, is strongly induced by water and salt stress in *Arabidopsis thaliana* (Rentsch et al., 1996), Ketchum et al. (1991) suggest that translation but not transcription is necessary for production of proline in stressed cells. Stress-hypersensitive mutants of higher medicinal plants which exhibit disturbed proline metabolism can contribute significantly to the elucidation of the signals to which proline accumulation may respond. *Petunias* (*Petunia hybrida* cv. ') cumulfrproli (Pro) under

drought-stress conditions (Yamanda et al., 2005). A study was conducted to examine the response of date palm (*Phoenix dactylifera* L., cvs. Barhee and Hillali) calli to water stress. After 2 weeks, proline accumulation was assessed.

Increasing PEG concentration was also associated with a progressive reduction in water content and increased content of endogenous free proline (Al-Khayri and Al-Bahrany, 2004). *Rehmannia glutinosa* seedlings were pretreated with choline chloride (CC) in concentrations of 0, 0.7, 2.1 and 3.5 mM, and then subjected to drought and dewatering treatment to study the effect of CC on the proline accumulation. CC pretreatment accelerated accumulation of proline during drought stress and retarded the drop in proline concentration after dewatering. Consequently, 2.1 mM of CC is suitable for promoting proline accumulation of R.

glutinosa seedlings under drought stress (Zhao et al., 2007). Seedlings of two *C. arabica* genotypes (Catuai and BA10C1110-10) with different drought tolerance levels were subject to controlled water stress. Proline content of secondary, tertiary and quaternary leaf pairs, from the apex, were evaluated. In both genotypes, the secondary leaf pair had higher proline content. Although proline levels increased with increased water deficit, it was not possible to distinguish between the two coffee seedlings in using this parameter.

Proline accumulation seemed to be related to injury imposed by water stress (Mazzafera and Teixeira, 2006). Baher et al. (2002) indicated proline accumulation of *S. hortensis* L. was increased under drought stress. Therefore, proline accumulation rate increases under drought conditions in medicinal plants sorely. Oxidative damage Exposure of plants to certain environmental stresses quite often leads to the generation of reactive superoxanion (O_2^-), hydroxyl radicals (OH \cdot), hydrogen peroxide (H_2O_2), alkoxy radicals (RO \cdot) and singlet oxygen (O_1) (Munne-Bosch and Penuelas, 2003). Reactive oxygen species may react with proteins, lipids and deoxyribonucleic acid, causing oxidative damage and impairing the normal functions of cells (Foyer and Fletcher, 2001).

Many cell compartments produce reactive oxygen species; of these, chloroplasts are a potentially important source because excited pigments in thylakoid membranes may interact with O_2 to form strong oxidants such as O_2^- or O_1 (Niyogi, 1999; Reddy et al., 2004). Further downstream reactions produce other reactive oxygen species such as H_2O_2 and \cdot . The interaction of O_2 with reduced components of the electron transport chain in mitochondria can lead to reactive oxygen species formation (Moller, 2001), and peroxisomes produce H_2O_2 when glycolate is oxidized into glyoxylic acid during photorespiration (Fazeli et al., 2007). Accumulation materials such as carbohydrates and amino acids in plant cells that are called compatible solutes are known to play a role

(Ourcut and Nilsson, 2000).

Compatible soluble, low molecular weight compounds that interfere with cellular biochemical reactions normally do during osmotic stress, act as guards. In addition to the primary role in osmoregulation of these compounds may have an important role as protecting enzymes and membrane structure and eliminate active oxygen free radicals (Ourcut and Nilsson, 2000). Moisture reduction reactions such as protein degradation and accumulation of free amino acids in order to adjust the osmotic pressure of the cell followed (Bajji et al., 2001).

In situations where moderate or severe stress, increases the concentration of proline, proline as a nitrogen storage tank or soluble cytoplasmic osmotic potential decrease in acts of plant stress tolerance assists (Ghodsi et al, 1998). Chlorophyll is one of the major chloroplast components for photosynthesis (Rahdari et al, 2012). The decrease in chlorophyll content under drought stress has been considered a typical symptom of pigment photo oxidation and chlorophyll degradation (Anjum et al, 2011).

A decrease of total chlorophyll content with drought stress implies a lowered capacity for light harvesting. Since the production of reactive oxygen species is mainly driven by excess energy absorption in the photosynthetic apparatus, this might be avoided by degrading the absorbing pigments (Mafakheri et al, 2010). In relation to drought effect on chlorophyll a and b in leaf, we can express that drought is due to chloroplastic proteins hydrolysis, decreasing of leaf pigments and chlorophyll destruction as a primary stage in degradation of proteins (Synerri et al.,

1993). Drought stress tolerance mechanisms Drought Resistance in fact, the ability of species or cultivars for growth and production in drought conditions. By a long dry period on the physiological and morphological effects on yield and ultimate effect on yield depends on many factors. This not only depends on the time of drought on the life cycle of plants and water holding capacity of the soil in the root zone. It also depends on plant characteristics (Mohsenzadeh et al, 2006).

To prevent water losses, plants should close the stomatal, reducing absorption or decreased sweating, or a combination of all three levels will reduce the amount of transpiration (Shekari, 2000). With increasing water shortages, plants species can clog your pores. This reduces transpiration and especially when the stomatal are completely blocked and cuticular resistance is much truer. Active and inactive motion and increased leaf wax cracking or effective in reducing the absorption of radiation.

Active motion parallel to the incoming radiation leaves on the response to water

shortages for several plants has been observed (Rahmani, 2006). Drought stress causes to mentose or waxy leaves of some plants are both of these characteristics are reflected by the increasing amount of leaves to reduce water loss (Leila, 2007). One of drought tolerance in crop plants through water conservation and sustaining water absorption. The important feature is that this requires one to have deep roots and branches and a low resistance to flow of water inside the plant (Zareian, 2004).

Maintaining inflammation in the leaves while they are growing shortage of water can maintain the physiological activity. Maintaining inflammation in conditions of reduced leaf water potential can be fully or partially by setting the osmotic conditions, increase or decrease the size of the cell elasticity acquired (Shekari, 2000). Mechanisms to generate reactive oxygen species (ROS) Mechanisms for the generation of reactive oxygen species in biological systems are represented by both non-enzymatic and enzymatic reactions.

The partition between these two pathways under oxygen deprivation stress can be regulated by the oxygen concentration in the system. In non-enzymatic reactions, electron O₂ reduction can occur at higher oxygen concentrations (Apel and Hirt, 2004). At very low O₂ concentrations, plant terminal oxidases and the formation of reactive oxygen species via the mitochondrial electron transport chain still remain functional. Among enzymatic sources of reactive oxygen species, xanthine oxidase, an enzyme responsible for the initial activation of O₂, should be mentioned.

The electron donor xanthine oxidase can use xanthine, hypoxanthine or acetaldehyde, while the latter has been shown to accumulate under oxygen deprivation (Pfister-Sieber and Braendle, 1994; Apel and Hirt, 2004). The next enzymatic step is the dismutation of the superoxide anion by superoxide dismutase to yield H₂O₂ (Lamb and Dixon, 1997). Peroxidases and catalases also play an important role in the fine regulation of reactive oxygen species in the cell through activation and deactivation of H₂O₂ (Sairam et al., 2005).

Several apoplastic enzymes may also generate reactive oxygen species under normal and stressful conditions. Other oxidases, responsible for the two-electron transfer to dioxygen (amino acid oxidases and glucose oxidase) can contribute to H₂O₂ accumulation (Apel and Hirt, 2004). Reactive oxygen species are formed as by-products in the electron transport chains of chloroplasts (Apel and Hirt, 2004), mitochondria and the plasma membrane (Sairam et al., 2005).

The plant mitochondrial electron transport chain, with its redox-active electron carriers, is considered as the most probable candidate for intracellular reactive oxygen species

formation. Mitochondria can produce reactive oxygen species due to the electron leakage at the ubiquinone site – the ubiquinone: cytochrome b region (Gille and Nohl, 2001) – and at the matrix side of complex I (NADH dehydrogenase) (Moller, 2001). Superoxide radical and its reduction product H₂O₂ are potentially toxic compounds, and can also combine by the Haber-Weiss reaction to form the highly toxic OH⁻ (Sairam et al., 1998).

Many reports show the deleterious effects of reactive oxygen species, whose production is stimulated under water, stress (Blokhina et al., 2003). Reactive oxygen species cause lipid peroxidation, and consequently membrane injuries, protein degradation and enzyme inactivation (Sairam et al., 2005). Oxidative stress may also cause protein oxidation, with a loss of enzyme activity and the formation of protease resistant cross-linked aggregates (Berlett and Stadtman, 1997).

Overall, the production of reactive oxygen species is linear with the severity of drought stress, which leads to enhanced peroxidation of membrane lipids and degradation of nucleic acids, and both structural and functional proteins. Various organelles including chloroplasts, mitochondria and peroxisomes are the seats as well as first target of reactive oxygen species produced under drought stress. Drought resistance mechanisms Plants respond and adapt to survive under drought stress by the induction of various morphological, biochemical and physiological responses.

Drought tolerance is defined as the ability to grow, flower and display economic yield under suboptimal water supply. Drought stress affects the water relations of plants at cellular, tissue and organ levels, causing specific as well as unspecific reactions, damage and adaptation reactions (Beck et al., 2007). To cope with the drought, tolerant plants initiate defense mechanisms against water deficit (Chaves and Oliveira, 2004), which need to be investigated in further detail (Zhou et al., 2007).

Morphological mechanisms Plant drought tolerance involves changes at whole-plant, tissue, physiological and molecular levels. Manifestation of a single or a combination of inherent changes determines the ability of the plant to sustain itself under limited moisture supply. An account of various morphological mechanisms operative under drought conditions is given below. **Escape** Escape from drought is attained through a shortened life cycle or growing season, allowing plants to reproduce before the environment becomes dry.

Flowering time is an important trait related to drought adaptation, where a short life cycle can lead to drought escape (Araus et al., 2002). Crop duration is interactively determined by genotype and the environment and determines the ability of the crop to

escape from climatic stresses including drought (Dingkuhn and Asch, Dingkuhn). Matching growth duration of plants to soil moisture availability is critical to realize high seed yield (Siddique et al., 2003).

Drought escape occurs when phenological development is successfully matched with periods of soil moisture availability, where the growing season is shorter and terminal drought stress predominates (Araus et al., 2002). In field-grown clones of robusta coffee, leaf shedding in response to drought stress occurred sequentially from older to younger leaves, suggesting that the more drought-sensitive the clone, the greater the extent of leaf shedding (DaMatta, 2004). Time of flowering is a major trait of a crop adaptation to the environment, particularly when the growing season is restricted by terminal drought and high temperatures.

Developing short-duration varieties has been an effective strategy for minimizing yield loss from terminal drought, as early maturity helps the crop to avoid the period of stress (Kumar and Abbo, 2001). However, yield is generally correlated with the length of crop duration under favorable growing conditions, and any decline in crop duration below the optimum would tax yield (Turner et al., 2001). Avoidance Drought avoidance consists of mechanisms that reduce water loss from plants, due to stomatal control of transpiration, and also maintain water uptake through an extensive and prolific root system (Turner et al., 2001; Kavar et al., 2007).

The root characters such as biomass, length, density and depth are the main drought avoidance traits that contribute to final yield under terminal drought environments (Subbarao et al., 1995; Turner et al., 2001). A deep and thick root system is helpful for extracting water from considerable depths (Kavar et al., 2007). Glauconsness or waxy bloom on leaves helps with maintenance of high tissue water potential, and is therefore considered as a desirable trait for drought tolerance (Richards et al., 1986; Ludlow and Muchow, 1990).

Varying degrees of glauconsness in wheat led to increased water-use efficiency, but did not affect total water use or harvest index. Determination of leaf temperature indicated that, compared with non-glaucons leaves, glaucons leaves were 0.7 °C cooler and had a lower rate of leaf senescence (Richards et al., 1986). Phenotypic flexibility Plant growth is greatly affected by water deficit. At a morphological level, the shoot and root are the most affected and both are the key components of plant adaptation to drought.

Plants generally limit the number and area of leaves in response to drought stress just to cut down the water budget at the cost of yield loss (Schuppler et al., 1998). Since roots are the only source to acquire water from soil, the root growth, its density,

proliferation and size are key responses of plants to drought stress (Kavar et al., 2007). It has long been established that plants bearing small leaves are typical of xeric environments. Such plants withstand drought very well, albeit their growth rate and biomass are relatively low (Ball et al., 1994).

Leaf pubescence is a xeromorphic trait that helps protect the leaves from excessive heat load. Hairy leaves have reduced leaf temperatures and transpiration (Sandquist and Ehleringer, 2003) whilst inter- and intra-specific variation exists for the presence of this trait. Under high temperature and radiation stress, hairiness increases the light reflectance and minimizes water loss by increasing the boundary layer resistance to water vapor movement away from the leaf surface.

Although drought stress also induces the production of trichomes on both sides of wheat leaves, they had no significant influence on boundary layer resistance. The water content in drought-treated mature stems declined by 4% and water potential by -0.25 MPa. It is shown that active phloem supply of assimilates and associated water reserves from mature stems was the mechanism that allowed developing stems of *Hylocereus undatus* to maintain growth under drought conditions (Nerd and Neumann, 2004). Moreover, girdling the phloem of growing stems rapidly inhibited stem elongation, but secretion of sucrose-containing nectar was maintained during drought.

The water potential gradient was in the wrong direction for xylem transport from mature to young growing stems and axial hydraulic conductivity was low to negligible (Nerd and Neumann, 2004). Roots are the key plant organ for adaptation to drought. If tolerance is defined as the ability to maintain leaf area and growth under prolonged vegetative stage stress, the main basis of variation appears to be constitutive root system architecture that allows the maintenance of more favorable plant water status (Nguyen et al., 1997). The possession of a deep and thick root system allowed access to water deep in the soil, which was considered important in determining drought resistance in upland rice (Kavar et al., 2007).

To summarize, plants may escape drought stress by cutting short their growth duration, and avoid the stress with the maintenance of high tissue water potential either by reducing water loss from plants or improved water uptake, or both. Some plants may reduce their surface area either by leaf shedding or production of smaller leaves. Physiological mechanisms Osmotic adjustment, osmoprotection, antioxidation and a scavenging defense system have been the most important bases responsible for drought tolerance.

The physiological basis of genetic variation in drought response is not clear; in part,

because more intricate mechanisms have been suggested. Water conservation through Cell and tissue Under drought stress, sensitive pea genotypes were more affected by a decline in relative water content than tolerant ones (Upreti et al., 2000). In faba bean, determination of leaf water potential was useful for describing the drought effect, but was not suitable for discriminating tolerant from sensitive genotypes.

This suggested that water potential was not the defining feature of the tolerance (Riccardi et al., 2001). Nevertheless, other studies opined that determination of leaf water status in the morning and water content in leaves in the afternoon were potentially useful for screening drought tolerance in chickpea (Pannu et al., 1993). Osmotic adjustment allows the cell to decrease osmotic potential and, as a consequence, increases the gradient for water influx and maintenance of turgor.

Improved tissue water status may be achieved through osmotic adjustment and/or changes in cell wall elasticity. This is essential for maintaining physiological activity for extended periods of drought (Kramer and Boyer, 1995). Wild melon plant survived drought by maintaining its water content without wilting of leaves even under severe drought. Drought stress in combination with strong light led to an accumulation of high concentrations of citrulline, glutamate and arginine in leaves of wild watermelon.

The accumulation of citrulline and arginine may be related to the induction of dopamine receptor interacting protein gene 1, a homologue of the acetylornithine deacetylase gene in *Escherichia coli*, where it functions to incorporate the carbon skeleton of glutamate into the urea cycle (Yokota et al., 2002). It has been identified that among various mechanisms, osmotic adjustment, abscisic acid and induction of dehydrins may confer tolerance against drought injuries by maintaining high tissue water potential (Turner et al., 2001).

With the accumulation of solutes, the osmotic potential of the cell is lowered, which attracts water into the cell and helps with turgor maintenance. The maintenance of turgor despite a decrease in leaf water volume is consistent with other studies of species with elastic cell walls. Osmotic adjustment helps to maintain the cell water balance with the active accumulation of solutes in the cytoplasm, thereby minimizing the harmful effects of drought (Morgan, 1990).

Osmotic adjustment is an important trait in delaying dehydrative damage in water-limited environments by continued maintenance of cell turgor and physiological processes (Taiz and Zeiger, 2006). The osmotic adjustment also facilitates a better translocation of pre-anthesis carbohydrate partitioning during grain filling (Subbarao et al., 2000), while high turgor maintenance leads to higher photosynthetic rate and

growth (Ludlow and Muchow, 1990; Subbarao et al., 2000).

Antioxidant defense mechanism The antioxidant defense system in the plant cell constitutes both enzymatic and non-enzymatic components. Enzymatic components include superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase and glutathione reductase. Non-enzymatic components contain cysteine, reduced glutathione and ascorbic acid (Gong et al., 2005). In environmental stress tolerance, such as drought, high activities of antioxidant enzymes and high contents of non-enzymatic constituents are important. The reactive oxygen species in plants are removed by a variety of antioxidant enzymes and/or lipid-soluble and water soluble scavenging molecules (Hasegawa et al.,

2000); the antioxidant enzymes being the most efficient mechanisms against oxidative stress (Farooq et al., 2008). Apart from catalase, various peroxidases and peroxiredoxins, four enzymes are involved in the ascorbate-glutathione cycle, a pathway that allows the scavenging of superoxide radicals and H_2O_2 . These include ascorbate peroxidase, dehydroascorbate reductase, monodehydroascorbate reductase and glutathione reductase (Fazeli et al., 2007).

Most of the ascorbate glutathione cycle enzymes are located in the cytosol, stroma of chloroplasts, mitochondria and peroxisomes (Jimenez et al., 1998). Ascorbate peroxidase is a key antioxidant enzyme in plants (Orvar and Ellis, 1997) whilst glutathione reductase has a central role in maintaining the reduced glutathione pool during stress (Pastori et al., 2000). Two glutathione reductase complementary deoxyribonucleic acids have been isolated; one type encoding the cytosolic isoforms (Stevens et al.,

2000) and the other encoding glutathione reductase proteins dual-targeted to both chloroplasts and mitochondria in different plants (Chew et al., 2003). Among enzymatic mechanisms, superoxide dismutase plays an important role, and catalyzes the dismutation of two molecules of superoxide into O_2 and H_2O_2 ; the first step in reactive oxygen species scavenging systems. Lima et al. (2002), from a study utilizing two rapidly drought-stressed clones of *Coffea canephora*, proposed that drought tolerance might, or at least in part, be associated with enhanced activity of antioxidant enzymes. In contrast, Pinheiro et al.

(2004) did not find a link between protection against oxidative stress and drought tolerance when four clones of *C. canephora* were subjected to long-term drought. Carotenoids and other compounds, such as abietane diterpenes, have received little attention despite their capacity to scavenge singlet oxygen and lipid peroxy-radicals, as well as to inhibit lipid peroxidation and superoxide generation under dehydrative forces

(Deltoro et al., 1998).

The transcript of some of the antioxidant genes such as glutathione reductase or ascorbate peroxidase was higher during recovery from a water deficit period and appeared to play a role in the protection of cellular machinery against damage by reactive oxygen species (Ratnayaka et al., 2003). A superoxide radical has a half-life of less than 1 sec and is rapidly dismutated by superoxide dismutase into H_2O_2 , a product that is relatively stable and can be detoxified by catalase and peroxidase (Apel and Hirt, 2004).

These metalloenzymes constitute an important primary line of defense of cells against superoxide free radicals generated under stress conditions. Therefore, increased superoxide dismutase activity is known to confer oxidative stress tolerance (Pan et al., 2006). Oxidative damage in the plant tissue is alleviated by a concerted action of both enzymatic and non-enzymatic antioxidant sThese de -carotenes, ascorbic acid, a -tocopherol, reduced glutathione and enzymes including superoxide dismutase, peroxidase, ascorbate peroxidase, catalase, polyphenol oxidase and glutathione reductase (Hasegawa et al., 2000; Prochazkova et al., 2001).

Carotenes form a key part of the plant antioxidant defense system (Havaux, 1998; Wahid, 2007), but they are very susceptible to oxidative destruction. The - carotene present in the chloroplasts of all green plants is exclusively bound to the core complexes of photosystem I and photosystem II. Protection against damaging effects of reactive oxygen species at this site is essential foast functi He -carotene, in addition to functioning as an accessory pigment, acts as an effective antioxidant and plays a unique role in protecting photochemical processes and sustaining them (Havaux, 1998). A major protective role of -carotene in photosynthetic tissue may be through direct quenching of triplet chlorophyll, which prevents the generation of singlet oxygen and protects from oxidative damage.

Stability of Cell membrane Biological membranes are the first target of many abiotic stresses. It is generally accepted that the maintenance of integrity and stability of membranes under water stress is a major component of drought tolerance in plants (Bajji et al., 2002). Cell membrane stability, reciprocal to cell membrane injury, is a physiological index widely used for the evaluation of drought tolerance (Premachandra et al., 1991).

Moreover, it is a genetically related phenomenon since quantitative trait loci for this have been mapped in drought-stressed rice at different growth stages (Tripathy et al., 2000). Dhanda et al. (2004) showed that membrane stability of the leaf segment was the

most important trait to screen the germplasm for drought tolerance. Cell membrane stability declined rapidly in Kentucky bluegrass exposed to drought and heat stress simultaneously (Wang and Huang, 2004).

In a study on maize, K nutrition improved the drought tolerance, mainly due to improved cell membrane stability (Gnanasiri et al., 1991). Tolerance to drought evaluated as increase in cell membrane stability under water deficit conditions was differentiated between cultivars and correlated well with a reduction in relative growth rate under stress (Premachandra et al., 1991). In holm oak (*Quercus ilex*) seedlings, hardening increased drought tolerance primarily by reducing osmotic potential and stomatal regulation, improved new root growth capacity and enhanced cell membrane stability.

Among treated seedlings, the greatest response occurred in seedlings subjected to moderate hardening. Variation in cell membrane stability, stomatal regulation and root growth capacity was negatively related to osmotic adjustment (Villar-Salvador et al., 2004). The causes of membrane disruption are unknown; notwithstanding, a decrease in cellular volume causes crowding and increases the viscosity of cytoplasmic components. This increases the chances of molecular interactions that can cause protein denaturation and membrane fusion. For model membrane and protein systems, a broad range of compounds have been identified that can prevent such adverse molecular interactions.

Some of these are proline, glutamate, glycinebetaine, carnitine, mannitol, sorbitol, fructans, polyols, trehalose, sucrose and oligosaccharides (Folkert et al., 2001). Another possibility of ion leakage from the cell may be due to thermal induced inhibition of membrane-bound enzymes responsible for maintaining chemical gradients in the cell (Reynolds et al., 2001). Arabidopsis leaf membranes appeared to be very resistant to water deficit, as shown by their capacity to maintain polar lipid contents and the stability of their composition under severe drought (Gigon et al., 2004).

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

Osmotic adjustment is a mechanism to maintain water relations under osmotic stress. It involves the accumulation of a range of osmotically active molecules/ions including

soluble sugars, sugar alcohols, proline, glycinebetaine, organic acids, calcium, potassium, chloride ions, etc. Under water deficit and as a result of solute accumulation, the osmotic potential of the cell is lowered, which attracts water into the cell and helps with the maintenance of turgor.

By means of osmotic adjustment, the organelles and cytoplasmic activities take place at about a normal pace and help plants to perform better in terms of growth, photosynthesis and assimilate partitioning to grain filling (Ludlow and Muchow, 1990; Subbarao et al., 2000). As a mechanism, osmotic adjustment has been suggested as an important trait in postponing the dehydration stress in water scarce environments (Morgan, 1990). Variation in osmotic adjustment among chickpea cultivars in response to soil drought has been observed, and seed yield of chickpea was correlated with the degree of osmotic adjustment when grown under a line-source irrigation system in the field (Moinuddin and Khannu-Chopra, 2004). Osmotic adjustment is accomplished with the accumulation of compatible solutes.

Of these, proline is one amongst the most important cytosolutes and its free accumulation is a widespread response of higher plants, algae, animals and bacteria to low water potential (Zhu, 2002; Wahid and Close, 2007). Its synthesis in leaves at low water potential is caused by a combination of increased biosynthesis and slow oxidation in mitochondria. Despite some controversy, many physiological roles have been assigned to free proline including stabilization of macromolecules, a sink for excess reductant and a store of carbon and nitrogen for use after relief of water deficit (Zhu, 2002).

Proline contents were increased under drought stress in pea cultivars (Alexieva et al., 2001). Drought-tolerant petunia (*Petunia hybrida*) varieties were reported to accumulate free proline under drought that acted as an osmoprotectant and induced drought tolerance (Yamada et al., 2005). Glycinebetaine (N, N, N-trimethyl glycine) is one of the most extensively studied quaternary ammonium compounds and compatible solutes in plants, animals and bacteria (Wahid et al., 2007).

Many studies demonstrate that glycinebetaine plays an important role in enhancing plant tolerance under a range of abiotic stresses including drought (Quan et al., 2004). The introduction of genes synthesizing glycinebetaine into non-accumulators of glycinebetaine proved to be effective in increasing tolerance to various abiotic stresses (Sakamoto and Murata, 2002). Naidu et al. (1998) reported that cotton cultivars adapted to water stress conditions accumulated higher glycine betaine than the non-adapted ones under drought.

In addition to direct protective roles of glycinebetaine either through positive effects on enzyme and membrane integrity or as an osmoprotectant, glycinebetaine may also protect cells from environmental stresses indirectly by participating in signal transduction pathways (Subbarao et al., 2000). Citrulline, named after Citrullus; a Latin name of watermelon, from which it was isolated, is an amino acid. Although not built into proteins during their synthesis, and not encoded by a nuclear gene, several proteins are known to contain citrulline (Kawasaki et al., 2000).

Wild watermelon (*Citrullus lanatus*) has the ability to adapt to severe drought stress despite carrying out normal C₃-type photosynthesis, which seem to be correlated with citrulline accumulation (Akashi et al., 2001). Wild watermelon primarily accumulated citrulline followed by glutamate and arginine, in place of proline and glycinebetaine (Kawasaki et al., 2000). Yokota et al. (2002) reported a higher citrulline accumulation in the wild watermelon leaves assuming that citrulline is located only in the cytosol and constitutes 5% of the total volume of the mesophyll cells.

Citrulline is a novel and the most effective OH⁻ scavenger among compatible solutes examined so far. Moreover, it can effectively protect DNA and enzymes from oxidative injuries (Akashi et al., 2001; Bektasoglu et al., 2006). Rapid accumulation of the non-proteinogenic γ -aminobutyric acid was identified in plants upon exposure stress and γ -aminobutyric acid acts as a zwitterion, exists in free form, and has a flexible molecule that can assume several conformations in solution, including cyclic and linear. γ -aminobutyric acid is highly water-soluble (Shelp et al.,

1999), and may function as a signaling molecule in higher plants under stress (Serraj et al., 1998). The physiological roles of γ -aminobutyric acid in drought tolerance entail osmotic regulation (Shelp et al., 1999), detoxication of reactive oxygen radicals, conversion of putrescine into proline and intracellular signal transduction (Kinnersley and Turano, 2000). Drought stress initiates a signal transduction pathway, in which increased cytosolic Ca²⁺ activates Ca²⁺/calmodulin-dependent protein kinase, leading to γ -aminobutyric acid synthesis (Shelp et al., 1999).

Elevated H⁺ and substrate levels can also stimulate glutamate decarboxase leading to γ -aminobutyric acid accumulation. Experimental evidence the involvement of γ -aminobutyric acid in pH regulation, nitrogen storage, plant development and defense, as well as a compatible osmolyte and an alternative pathway for glutamate utilization (Shelp et al., 1999; Wahid et al., 2007). After drought stress the content of proline was more than 50% and at the same time the γ -aminobutyric acid content reached 27% (Simon-Sarkadi et al., 2006).

Trehalose is a non-reducing disaccharide of glucose that functions as a compatible solute in the stabilization of biological structures under abiotic stress (Goddijn et al., 1997). In nature, trehalose is biosynthesized as a stress response by a variety of organisms including bacteria, fungi, algae, insects, invertebrates and lower plants (Wingler, 2002). Capacity to produce trehalose, earlier thought to be absent from higher plants, has now been reported to accumulate in high amounts in some drought-tolerant ferns, the resurrection plant *Selaginella lepidophylla* (Penna, 2003) and desiccation-tolerant angiosperm *Myrothamnus flabellifolia* (Drennan et al., 1993). The presence of low amounts of trehalose was demonstrated even in tobacco (Goddijn et al., 1997) and many higher plants (Kosmas et al., 2006).

Its metabolism may be channelized to enhance drought tolerance in plants (Pilon-Smits et al., 1998; Penna, 2003). Physiological roles of trehalose include efficient stabilization of dehydrated enzymes, proteins and lipid membranes, as well as protection of biological structures under desiccation stress (Wingler, 2002) rather than regulating water potential (Lee et al., 2004). Karim et al. (2007) reported that enhanced drought tolerance by trehalose depends on improved water status and expression of heterologous trehalose biosynthesis genes during *Arabidopsis* root development.

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

In fact, plants can withstand drought stress by conserving cell and tissue water principally by osmotic adjustment, maintenance of the antioxidant defense system for the scavenging of reactive oxygen species, and keeping the cell membranes stabilized. Plant growth regulators and polyamines, γ -aminobutyric acid, free amino acids and sugars also play a vital role in drought tolerance by scavenging the reactive oxygen species, stomatal regulation and protection of vital macromolecules, and maintenance of the cell water balance. Use of osmoprotectants Osmoprotectants are involved in signaling and regulating plant responses to multiple stresses, including reduced growth that they adapt.

In plants, the common osmoprotectants are proline, trehalose, fructan, mannitol,

glycinebetaine and others (Zhu, 2002). They play adaptive roles in mediating osmotic adjustment and protecting subcellular structures in stressed plants. However, not all plants accumulate these compounds in sufficient amounts to avert adverse effects of drought stress (Penna, 2003). Ashraf and Foolad (2007) outlined three approaches to increase the concentrations of these compounds in plants grown under stress conditions to increase their stress tolerance: (1) use of traditional protocols of plant genetics and breeding to develop cultivars with natural abilities to produce high levels of these compounds under stress conditions, (2) engineering genetically modified plants capable of producing sufficient amounts of these compounds in response to environmental stresses and (3) as a short-cut method, exogenous use of these osmolytes on plants to enhance their stress tolerance ability. Exogenously applied glycinebetaine improves the growth and production of some plants under stress (Naidu et al., 1998; Chen et al.,

2000; Hussain et al., 2008). In many crop plants the natural accumulation of glycinebetaine is lower than sufficient to ameliorate the adverse effects of dehydration caused by various environmental stresses (Subbarao et al., 2000). Exogenous application of glycinebetaine has been reported to improve drought tolerance in this regard (Hussain et al., 2008). Foliar-applied glycinebetaine improved the growth of plants subjected to water deficit by the maintenance of leaf water status due to improved osmotic adjustment and enhanced photosynthesis, primarily due to a greater stomatal conductance and carboxylation efficiency of Rubisco (Sakamoto and Murata, 2002). Exogenous application of glycinebetaine effectively diminished the drought effects in terms of greater number of achenes per capitulum in sunflower (Azam et al., 2005).

However, pre-soaking of seeds with glycinebetaine was not effective in preventing the adverse effects of water stress on yield components. Glycinebetaine application at the vegetative stage was more effective in ameliorating the adverse effects of drought (Azam et al., 2005). Glycinebetaine also increased anti-oxidative enzyme activities under water deficit (Ma et al., 2007). Exogenously applied proline enhanced the endogenous accumulation of free proline and improved the drought tolerance in petunia (Yamada et al., 2005).

Inhibitors of polyamine biosynthetic enzymes limit stress tolerance of wheat but the concomitant exogenous application of polyamines restores it (Liu et al., 2004). Exogenous spermidine application before the drought stress significantly improved the stress tolerance in barley (Kubiś, 2003). In a recent review, Liu et al. (2007) concluded that though there was variation in effects between polyamines and plant species, exogenous polyamine application to stressed cells or tissues could lead to injury alleviation and growth promotion. Yang et al.

(2007) suggested that for rice, to perform well under drought stress, it should have higher levels of free spermidine/free spermine and insoluble-conjugate putrescine. Conclusion Frequent drought is the major consequence of global climate change. Physiological, biochemical, molecular changes occur in plant during stress condition. Low water availability reduces metabolic process such as water and mineral absorption, rate of photosynthesis, dry matter production and yield. Oxidative damage of cellular organization occurs during drought stress by the production of reactive oxygen species. Plant has specific innate anti-oxidant mechanism to mitigate the effect of water stress.

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