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Plant Water-Stress Response Mechanisms

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1. Introduction

Drought (water stress) is one the major abiotic stress factors that affect all organisms lives including human in terms of health and food. Water absence from the soil solutions affect the natural evaporative cycle between earth and atmosphere that contribute amount of rainfall. Drought occurs when soil moisture level and relative humidity in air is low while temperature is also high. UN reports (2006) [1] estimate that one third of world population has been living in areas where the water sources are poor. Water stress resulting from the withholding of water, also changes the physical environment for plant growth as well as crop physiology [2]. Almost every plant process is affected directly or indirectly by water supply [3]. Plants, as one of basic food sources, either in nature or cultivations, in their growing period, require water or at least moisture for germination. Certainly, most land plants are exposed to short or long term water stress at some times in their life cycle and have tended to develop some adaptive mechanisms for adapting to changing environmental conditions. Some plants may adapt to changing environment more easily than others giving them an advantage over competitors. Water stress may range from moderate, and of short duration, to extremely severe and prolonged summer drought that has strongly influenced evolution and plant life. [4-6]. Crop yields are restricted by water shortages in many parts of the world [7]. The physiological responses of plants to water stress and their relative importance for crop productivity vary with species, soil type, nutrients and climate. On a global basis, about one-third of potential arable land suffers from inadequate water supply, and the yields of much of the remainder are periodically reduced by drought [2]. It is estimated that 10 billion people in the world will be hungry and malnourished by the end of this century [8]. One of the aims of the researches is to gain an understanding of survival mechanisms which may be used for improving drought tolerant cultivars for areas where proper irrigation sources are scarce or drought conditions are common.

In research aimed at improvements of crop productivity, the development of high-yielding genotypes, which can survive unexpected environmental changes, particularly in regions dominated by water deficits, has become an important subject.

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2. As a major plant growth inhibitor: Drought

2.1 Water and whole plant responses

The amount of water available to plants is important, since water accounts for 80-90% of the fresh weight of most herbaceous plant structures and over 50% of the fresh weight of woody plants [9]. Water supply is restricted in many parts of the world and productivity in these environments can only be increased by the development of crops that are well adapted to dry conditions [10].

Data of Raheja (1966, cited in Hurd, 1976) [11] show that 36% of world's land area is under semi-arid conditions, receiving only 5 to 30 in. of rainfall annually and the remaining (64%) is exposed to temporary drought during the crop season. On a global basis, about one-third of potential arable land suffers from inadequate water supply, and the yields of much of the remainder are periodically reduced by drought [2]. Moreover, water deficits may occur during a plant's life cycle outside of arid and semi-arid regions [12,13] even in tropical rainforests [14]. Water is progressively lost from a fully "**saturated soil**", firstly by draining freely, under the influence of gravity, and the rate of loss gradually slows down until no further water drains away, when the soil is said to be at "**field capacity**". Further loss of water by evaporation or by absorption by plant roots reduces the moisture content still further, until no further loss from these causes can occur, a stage known as the "**wilting point**" at which plants can no longer obtain the water necessary to meet their needs and they therefore wilt and die from moisture starvation.

Initially, stress conditions occur transiently as "cyclic water stress" even under adequate soil moisture conditions and may prevail certain time in the daytime and normalized after reduction of transpiration rate by the night [15].

Crop yields are restricted by water shortages in many parts of the world and the total losses due to this cannot be estimated with confidence [2,7]. According to Rambal and Debussche (1995) [16], changes in plant conductance under water stress are attributable to effects on the roots and xylem. As the soil dries, decreased permeability, due to root suberization and/or increased loss of fine roots, can reduce the balance between water extraction capacity and transpiring leaf area. Roots of unwatered plants often grow deeper into the soil than roots of plants that are watered regularly.

Plants exposed to stress due to decreasing supply of water or other resources, or because of climatic changes, show different responses according to species and the nature and severity of the stress. By altering the chemical and physical composition of tissues, water deficits also modify various aspects of plant quality, such as the taste of fruits and the density of wood [17]. Water shortage significantly affects extension growth and the root-shoot ratio at the whole plant level [18,19]. Although plant growth rates are generally reduced when soil water supply is limited, shoot growth is often more inhibited than root growth and, in some cases; the absolute root biomass of plants in drying soil may increase water use efficiency relative to that of well-watered controls [15,20,21]. Almost every plant process is affected directly or indirectly by water supply. When soil dries, the reduction in water content is accompanied by other changes such as increase in salt concentration and increasing mechanical impedance. The growth of plants is controlled by rates of cell division and enlargement, as well as by the supply of organic and inorganic compounds required for the synthesis of new protoplasm and cell walls.

It is well known that water stress not only affects morphological appearance but also changes bio-mass ratio. Bradford and Hsiao (1982) [22] and Sharp and Davies, (1979) [20]

reported that water stress drastically decreases root elongation and leaf area expansion but that these two processes are not equally affected. Leaf growth is usually decreased to a greater extent than root growth, and photosynthate partitioning is altered to increase root/shoot ratio [23,24]. Timpa *et al*., (1986) [25]; Akıncı and Lösel (2009,2010) [26,27] reported that the water stress caused major reductions in height, leaf number, leaf area index, fresh and dry weight of cotton plants and some *Cucurbitaceae* members.

2.2 Classification attempts of the survival mechanisms of plants response to water stress

Physiological and ecological strategies that plants evolved to cope with water shortages by either avoidance or tolerance to stress. On the nature, since plants are subjected to unavailability of water varying in length from hours to days from the water sources, therefore stress is determined by the extent and duration of the deprivation from water. Plant responses roughly may be classified as; i) short term changes related to mainly physiological responses (linked to stomatal regulation); ii) acclimation to availability of certain level of water (solute accumulation resulted with adjustment of osmotic potential and morphological changes); iii) adaptation to water stress conditions (sophisticated physiological mechanisms and specifically modifications in anatomy) [28-30]. Many processes affect the "fitness" of a plant in water-limited situations but those, such as survival, that may be appropriate in natural ecosystems are often of less interest in some agricultural crops, where productivity is usually of the greatest importance. It is not easy to define "*drought tolerance*", as stability of yield may be the biggest consideration in some situations. However, Jones (1993) [31] has pointed that out drought-tolerant genotypes of most crop plants are those giving some yield in a particular water-limited environment. Kramer (1980) [2] classified as "*drought avoidance*", the adaptations by which plants survive in regions subject to drought, in addition to drought tolerance, since this name fitted the actual situation more accurately than Levitt's term "*drought escape*".

Plants showing improved growth with limited water are considered to tolerate drought, regardless of how the improvement occurs. Kramer and Boyer (1995) [9] have reviewed strategies of drought tolerance, including (1) rapid maturation before onset of drought, or reproduction only after rain, (2) postponement of dehydration by having deep roots, (3) protection against transpiration or storing water in fleshy tissues, (4) allowing dehydration of the tissues and simply tolerating water stress by continuing to grow when dehydrated or surviving severe dehydration. These effects are generally distinct from the factors controlling water use efficiency. *Drought avoiders* often reproduce rapidly after only brief minimal accumulation of dry weight, ensuring that they are represented in the next generation. *Dehydration postponers,* with deep roots, may have a water use efficiency identical to that of other species but will accumulate more dry weight because they can reach a larger amount of water than shallow rooted types, although their water use efficiency may be similar to other spp. *Dehydration tolerators* may have the same water use efficiency as dehydration sensitive species when water is available, but can also grow at lower tissue hydration levels than the other species [9].

The physiology of crop plant responses to drought stress has been classified by Blum (1989) [32] into two domains: (1) a positive carbon balance is maintained by the plant under moderate stress, so that resistant genotypes achieve a greater net gain of carbon than

susceptible ones, and have a correspondingly better yield, (2) a net loss of carbon takes place under severe stress, so that growth stops and plants are merely surviving stress. Resistant genotypes generally survive and recover better upon rehydration than susceptible ones, depending upon the degree of stress.

2.3 Plant strategies under water depletion

Major efforts of plant physiologists and breeders during the past 30 years, have concentrated on improving the drought tolerance of many agricultural and horticultural crops. It is clear that, with the increasing world requirement for food, there is an urgent need for research to improve the stress tolerance of crop plants and to develop better management techniques to keep food production at levels near to demand, in spite of limited availability of land and water [33]. According to Borlaug and Dowswell (2005) [34] crop production will have to be doubled achieved by expanding land area for cultivation or increase crop productivity from per hectare. As pointed out earlier by Kozlowski (1968) [17] there is a need to increase crop production, in the face of mounting food shortages, and water conservation is an important factor in overcoming food deficiencies.

Land plants adapted to a moderate water supply are termed **mesophytes** while those adapted to arid zones are **xerophytes**. There are, of course, all gradations between these groups and it is, therefore, not always easy to place a plant in one or other group. It is even possible for a plant to fit into more than one group (Levitt, 1972) [35]. Plants under severe drought conditions tend to develop xeromorphic characteristics including those listed by Walter (1949, cited in Parker, 1968) [36], namely increases in proportion of leaf vein tissue compared to leaf surface, increased stomatal number per unit leaf area, smaller sizes of stomata, epidermal and mesophyll cells, greater density of leaf hairs but smaller hairs, thicker outer epidermal walls and cuticle.

Fresnillo Fedorenko *et al.*, (1995) [37] found similar trends for live and total leaf production, total length per plant of the central leaflet in leaves, and branch and root segment production, all of which decreased proportionally with increasing water stress in *Medicago minima*. Schulze (1986) [38] also reported that water shortage significantly affects extension growth and the root-shoot ratio at the whole-plant level.

Leaf adaptations are among the main factors favouring the success of a species in a water-stressed environment [39]. Morgan (1980) [40] pointed out that, in some species, reduction in leaf area by rolling may also be important in controlling water loss and reflects changes in leaf turgor. Fitter and Hay (1987) [41] pointed out that any reduction in cell size of mesophytes or xerophytes, due to loss of turgor during expansion, will lead to a higher stomatal frequency than in unstressed leaves, since the number of potential guard cells is unchanged.

A few reports discuss changing (reducing) of stomatal index by water stress [42,43]. It may also relate to reduction in leaf growth and production of smaller cells [42,44,45]. Decreasing water content is accompanied by loss of turgor and wilting, cessation of cell enlargement, closure of stomata, reduction in photosynthesis, and interference with many other basic metabolic processes [9].

Larcher (1995) [46] also stated that leaves growing under conditions of water deficiency develop smaller, but more densely distributed, stomata, enabling the leaf to reduce transpiration by a quicker onset of stomatal regulation. In addition, leaves of genotypically adapted plants tend to have more densely cutinized epidermal surfaces, covered with thicker layers of wax.

Water deficit increases wax deposition on the leaf surface, and results in a thicker cuticle that reduces water loss at the epidermis. This reduces CO_2 uptake, but without affecting leaf photosynthesis, because the epidermal cells underneath the cuticle are nonphotosynthetic [47].

3. Physiological and morphological responses to water stress

3.1 Drought effect on photosynthesis

Water stress reduces photosynthesis by decreasing both leaf area and photosynthetic rate per unit leaf area [48]. Photosynthesis by crops is severely inhibited and may cease altogether as water deficits increase. The decrease in leaf growth, or increasing senescence of leaves under drought conditions, may also inhibit photosynthesis in existing leaves [49]. Decreasing water content is accompanied by loss of turgor and wilting, cessation of cell enlargement, closure of stomata, reduction in photosynthesis, and interference with many other basic metabolic processes [9]. Photosynthesis by crops is severely inhibited and may cease altogether as water deficits increase. The decrease in leaf growth, or increasing senescence of leaves under drought conditions, may also inhibit photosynthesis in existing leaves [49]. Ehleringer (1980) [50] pointed out that leaf pubescence, which increases under water stress, can decrease the photosynthesis by reflecting quanta that might have been used in photosynthesis.

In the field, plants are normally not deprived of water rapidly. During slowly increasing water stress photosynthesis and transpiration usually decrease at similar rates [51]. The two main factors causing stomatal closure are usually an increase in the concentration of gaseous carbon within leaves and a decrease in water potential of leaf cells [52,53].

The simplest explanation for the inhibition of photosynthesis during water stress would be that the stomata close and the internal CO_2 concentration decreases [54,55], since stomatal limitation is more severe when a plant is stressed than when it is not [54]. Therefore, it is rather surprising that photosynthesis often decreases in parallel with, or more than, stomatal conductance [56-59]. The photosynthetic rate in higher plants decreases more rapidly than respiration rate with increased water stress, since an early effect of water reduction in leaves is usually a partial or complete stomatal closure, markedly decreasing the movement of carbon dioxide into the assimilating leaves and reducing the photosynthetic rate up to ten times, according to the amount of water removal and the sensitivity of the plant [35]. In terms of the relationship between photosynthesis and leaf water status, Quick et al. (1992) [60] reported that, in field conditions, photosynthesis in ambient CO_2 reached a maximum value in the morning and declined later in the day when water potential decreased and leaf-to-air water vapour pressure deficits increased. In non-watered plants the decline was larger, and occurred earlier. In most cases stomatal conductance followed a diurnal pattern similar to that of photosynthesis.

3.2 Osmotic adjustment mechanisms under water stress

Water is essential in the maintenance of the turgor which is essential for cell enlargement and growth and for maintaining the form of herbaceous plants. Turgor is also important in the opening of stomata and the movements of leaves, flower petals, and various specialised plant structures [9]. Although turgor measurements on segments the non-growing lamina have often appeared to show declining rates of leaf growth with decreasing turgor, turgor measurement in regions of leaves and stems, where cell enlargement usually occurs, often show little or no decrease, even when cell enlargement is largely inhibited due to soil drying [9,61-63]. This is believed to be due to osmotic adjustment, the process in which solutes

accumulate in growing cells as their water potential falls [64,65] of osmotic potential arising from the net accumulation of solutes in response to by maintaining turgor in tissues, osmotic adjustment may allow growth to continue at low water potential. Turner and Jones (1980) [64] have defined osmotic adjustment as "the lowering water deficits or salinity".

Osmotic adjustment usually depends mainly on photosynthesis to supply compatible solute. As dehydration becomes more severe, photosynthesis is inhibited, resulting in a smaller solute supply for osmotic adjustment. With continued water limitation, osmotic adjustment delays, but cannot completely prevent, dehydration [9]. In leaves and stems at least, solute accumulation does not fully compensate for the effects of limited water supply on cell enlargement. Turner and Jones (1980) [64] stated that the rate of development of stress has a major effect on the degree of osmotic adjustment. Oosterhuis and Wullschleger (1987) [66] pointed out that increasing the number of stress cycles increased the amount of osmotic adjustment in cotton. Turner (1986) [67] noted that leaf expansion can decrease without change in leaf turgor pressure.

Osmotic adjustment has been found in many species [64,65], and has been implicated in the maintenance of stomatal conductance, photosynthesis, leaf water volume and growth [64,65,67].

Wheat and other cereals show other additional strategies: turgor loss and stomatal closure may occur at different relative water contents, while osmotic adjustment leads to rapid responses decreasing the effect of water stress [68].When soil dries, the reduction in water content is accompanied by other changes such as increase in salt concentration and increasing mechanical impedance [69]. The growth of plants is controlled by rates of cell division and enlargement, as well as by the supply of organic and inorganic compounds required for the synthesis of new protoplasm and cell walls [9].

Wheat and other cereals show other additional strategies: turgor loss and stomatal closure may occur at different relative water contents, while osmotic adjustment leads to rapid responses decreasing the effect of water stress [68]. Russel (1976) [70] pointed out that water stress increases the osmotic pressure of the cell sap, increasing the percentage of sugar in sugar-cane and often in sugar beet, although the yield per acre may be reduced.

Solutes known to accumulate with water stress and to contribute to osmotic adjustment in non-halophytes, include inorganic cations, organic acids, carbohydrates and free amino acids. In some plants potassium is the primary inorganic cation accumulating during water stress and it is often the most abundant solute in a leaf [71,72]. Osmotic adjustment is usually not permanent and plants often respond rapidly to increased availability of water. Loss of osmotic adjustment can occur in less than 2d in durum wheat [73], and both osmotic potentials and concentrations of some individual solutes have been shown to return to pre-stress levels within 10d after watering [64,74].

Studies by Blum and co-workers (reviewed by Blum, 1989) [34] and Kameli (1990) [75] have suggested that drought-resistant wheat varieties, with long-term yield stability under drought stress, were characterised by a greater capacity for osmoregulation than less resistant varieties. Landraces of sorghum and millet from dry regions in India and Africa were found to be more drought resistant (in terms of plant growth and delayed leaf senescence) than those from humid regions [32]. Munns et al., 1979 [76] found that the change in osmotic potential in the apex and enclosed developing leaves of wheat seedlings under rapidly developing water stress, was due mainly to the accumulation of soluble sugars, amino acids (particularly asparagine and proline) and K+ ions.

Morgan and Condon (1986) [77] showed that such increase in solute concentration gives tissues a temporary advantage, enabling turgor to be maintained at low water potentials by decreasing their osmotic potentials. Westgate and Boyer (1985) [78] pointed out that, when dehydration occurs in the absence of high external salinities, there can also be rapid increases in solute content of cells. The growing tissues throughout the plant may show osmotic adjustment when the soil loses water.

In less severe stress, the elongating regions of wheat leaves were found to adjust osmotically by the accumulation of sugars, principally glucose [73,79]. Osmoregulation was very active in races from dry regions. Osmoregulation and turgor maintenance permit continued root growth and efficient uptake of soil moisture [20]. However, despite the accumulation of ions and organic solutes, allowing osmotic adjustment in the meristematic and expanding regions, growth of the shoot may still be inhibited by stress, either because osmotic adjustment may not be sufficiently rapid to compensate for growth or due to a stress-induced fall in turgor.

4. Plant metabolic response to water scarcity

One of the gains an understanding of survival mechanisms which may be used for improving drought tolerant cultivars for areas where proper irrigation sources are scarce or drought conditions are common. Plants adaptations to dry environments can be expressed at four levels: phenological or developmental, morphological, physiological, and metabolic the least known and understood of which are the metabolic or biochemical adaptations involved [80]. Physiological and biochemical changes including carbohydrates, proteins and lipids observed in many plant species under various water stress levels, which may help in better understanding survival mechanisms in drought.

4.1 Carbohydrates changes under water stress

The available reports (listed in Table 1) stated that the content of soluble sugars and other carbohydrates in the leaves of various water stressed plants are altered and may act as a metabolic signal in the response to drought [26,27,81-83] however, accumulation or decrease of sugars depending on stress intensity and role of sugar signalling in these processes is not totally clear yet [84].

Among the major effects are those involving carbohydrate metabolism, with the accumulation of sugars and a number of other organic solutes [75]. Munns *et al.*, (1979) [76] and Quick *et al.*, (1992) [60] showed that sugars are major contributors to osmotic adjustment in expanding wheat leaves. Moreover, short-term water stress inhibited starch synthesis more strongly than sucrose synthesis, in both ambient CO_2 and in saturating CO_2. Short-term water stress was earlier also reported to stimulate the conversion of starch to sucrose in bean leaves [85,86]. The increase of sugar in various plant tissues response to water stress are supported the idea of contribution of solutes while the plants exposed to different stress levels. The studies have shown that soluble sugars accumulate in leaves during water stress [60,71,79,87-90], and have suggested that these sugars might contribute to osmoregulation [65], at least under moderate stress.

Quick *et al.*, (1992) [60] compared the effect of water stress on the rate of photosynthesis and the partitioning of photosynthate in four different species, including two annuals (*Lupinus albus* L. and *Helianthus annuus* L.), and two woody perennials (*Vitis vinifera* cv. Rosaki and

Eucalyptus globulus Labill.) and concluded that, when water stress develops under field conditions, there is an alteration in the balance between sucrose synthesis and translocation, which allows many species to maintain or increase the pool of soluble sugars in their leaves. In *Eucalyptus* soluble sugars were low compared to starch and non-watered plants contained higher levels of soluble sugars in their leaves than watered plants, but much less starch. Similarly, leaves of non-watered sunflower plants contained almost twice as much soluble sugar those of watered plants. Hodges and Lorio (1969, cited in Levitt, 1972) [35] detected a marked increase in reducing sugars, nonreducing sugars, and total carbohydrates, with an approximately equivalent decrease in starch.

Carbohydrates changes	References
Increasing total carbohydrates	cotton (Timpa *et al.*, 1986)
Total soluble sugars increasing	durum wheat (Kameli and Lösel, 1996) Nodulated alfalfa (Irigoyen *et al.*, 1992)
Increasing soluble sugars	South African grasses (Westgate *et al.*, 1989)
Increasing sucrose	lupins and *Eucalyptus* (Quick *et al.*, 1992), Alfalfa (Al-Suhaibani, 1996), embryos from Soybean (Westgate *et al.*, 1989), wheat (Drossopoulos *et al.*, 1987), wilted bean (Steward, 1971), durum wheat (Kameli and Lösel, 1993), -in leaves under severe stress-*Cucumis sativus* L., *C. melo* L. (snake cucumber), *Cucurbita pepo* L., *Ecballium elaterium* (L.) A. Rich. (Akıncı and Lösel, 2009).
Fructose, glucose accumulation	durum wheat (Kameli and Lösel, 1993)
Starch accumulation	cotton (Ackerson and Hebert, 1981)
Fructans enhancing resistance	tobacco (Pilon-Smiths *et al.*, 1995)
Carbohydrate unchanged	*Artemisia tridentata* (Evans *et al.*, 1992)
Sucrose content decreasing	soybean cotyledon (Westgate *et al.*, 1989)
Sucrose and starch decreasing	grapevine (Rodriguez *et al.*, 1993)
Raffinose utilisation prevented by water stress	*Citrullus lanatus* seeds (Botha and Small, 1985)
Starch depletion	*Lupinus*, *Helianthus*, *Vitis*, *Eucalyptus* (Quick *et al.*, 1992), wilted bean leaves (Steward, 1971), South African grasses (Schwab and Gaff, 1986), cucumber (Akıncı and Lösel, 2010)

Table 1. Changes in plant metabolics (Carbohydrates)

Drossopoulos *et al.*, (1987) [91] concluded that, in two wheat cultivars, sucrose generally formed the major portion of the ethanol soluble carbohydrates. High concentrations of glucose and fructose were observed in the stems of the water-stressed plants towards maturation as well as in the ears, immediately after heading. The major differences between cultivars were in the sucrose levels of leaves and roots before heading. There have been many reports that water stress leads to a general depletion of soluble sugars and starch in

leaves. Hanson and Hitz (1982) [80] and Huber *et al.*, (1984) [57] have concluded that water stress has a larger effect on carbon assimilation than on translocation and use of photosynthate.

Barlow (1986) [92] showed that much of the sugar accumulation, which began with the first indication of suppression in leaf elongation under water stress in wheat, was due to glucose, fructose and sucrose. The inhibition of germination of *Citrullus lanatus* seeds by water stress was investigated by Botha and Small (1985) [93], who observed a marked effect on carbohydrate metabolism. Smaller changes in glucose content and in the reducing substance content of the control seeds occurred during germination, coinciding with a decrease in sucrose. However, this decrease did not entirely account for the observed increase in glucose content. Fructose decreased in control seeds, over the first 30 h of incubation, and then increased again, whereas the glucose content of stressed seeds tended to increase throughout the 48 h incubation period, with fructose remaining fairly constant. On the other hand, Pattanagul and Madore, (1999) [94] also reported various sugars depletion in variegated coleus (*Coleus blumei* Benth.). In the green leaf tissues the diurnal - light period levels of the raffinose family oligosaccaharides stachyose and raffinose and non – structural carbohydrates (galactinol, sucrose, hexoses and starch) decreased whereas drought had little effect on soluble carbohydrate content in the other part of non – photosynthetic white leaf tissues. There was no difference in glucose and fructose levels between the wilted (incubated) and turgid bean leaves as well as depletion of starch concentrations was observed in plants of bean exposed to drought stress [60,85].

4.2 Plant proteins: Responses to drought

Many specified protein synthesized under water scarcity have been isolated and characterized by researches [95-98]. The water stress-specific proteins (stress induced) have been described by different groups such as dehydrins (polypeptide), LEAs (late embryogenesis abundant), RABs (responsive to ABA), storage proteins (in vegetative tissues) [99]. LEAs proteins are also subdivided into several groups and expect to be located in cytosol and with hydrophylic and soluble on boiling featured [100].

Under water stress conditions plants synthesize alcohols, sugars, proline, glycine, betaine and putrescine and accumulate that of those molecular weights are low [101,102]. Dehydrins have been the most observed group among the accumulated proteins in response to loss of water and increased in barley, maize, pea, and *Arabidopsis* and under water stress LEA proteins plays important role as protection of plants. Osmotin is also accumulated protein under water stress in several plant species such as tobacco, triplex, tomato and maize [103].

Changes of amino acids and protein have been mentioned in many reports which have stated that water stress caused different responses depending on the level of stress and plant type and listed in Table 2. For instance, in *Avena* coleoptiles water stress clearly caused a significant reduction in rate of protein synthesis [104]. Water stress has a profound effect upon plant metabolism, and results in a reduction in protein synthesis. Several proteins were reduced by stress in maize mesocotyls [105,106]. Dasgupta and Bewley (1984) [107] pointed out water stress reduced protein synthesis in all regions of barley leaf. Vartanian *et al.*, (1987) [108] mentioned the presence of drought specific proteins in tap root in *Brassica*. Dasgupta and Bewley (1984) [107] pointed out water stress reduced protein synthesis in all regions of barley leaf.

Protein changes	References
Inhibited protein synthesis	*Avena* coleoptiles (Dhindsa and Cleland, 1975)
Increased protein levels	*Cicer arietinum* (Rai *et al.*, 1983)
Increased protein content	*Zea mays* (Rai *et al.*, 1983)
Water stress induced spefisic proteins (Dehydrins, LEAs, RABs, vegetative storage proteins)	cotton (Artlip and Funkhouser, 1995), rice (Xu *et al.*, 1996)
Proline, glycine accumulation, betain, putrescine	tobacco (Chopra *et al.*, 1998), (Galston and Sawhney, 1990)
Dehydrin, LEA group 1 (D19)	cotton, barley, carrot (Ramagopal, 1993)
Dehydrin-like transcripts accumulate	*Lathyrus sativus* (Sinha *et al.*, 1996)
LEA (D7, D29)	desiccating mature cotton embryos, *Craterostigma plantagineum* chloroplast, *Citrus* seedlings exposed to drought (Bray, 1995; Naot *et al.*, 1995)
Osmotin	tobacco, triplex, tomato and maize (Ramagopal, 1993)
87kDa and 85kDa proteins (stress-associated –SAPs-) accumulation	rice varieties (Pareek *et al.*,1997)
Boiling-staple protein (BspA) accumulation	*Populus popularis* (Pelah *et al.*, 1997)
RAB18 protein accumulation	*Arabidopsis thaliana* (Mantyla *et al.*, 1995)
Chloroplastic proteins (CDSP 32 and CDSP 34)	*Solanum tuberosum* (Pruvot, *et al.*, 1996)
Total proteins decrease	sugar beet (Shah and Loomis, 1965)
Soluble protein decrease	Bermuda grass (Barnett and Naylor, 1966)
12.6- k.Da protein (cell wall) synthesis decrease	*Lycopersicon chilense* (Yu *et al.*, 1996)
Soluble protein level decline	*Pisum sativum* L. nodules (Gogorcena *et al.*, 1995)
Total and soluble protein content	*Populus popularis* (Pelah *et al.*, 1997)

Table 2. Changes in plant metabolics (Proteins)

A stress episode which inhibits cell division and expansion, and consequently leaf expansion, will also halt protein synthesis, which is also inhibited by osmotic stress imposed on excised plant parts. The direct significance of the inhibition of protein synthesis by stress to growth and leaf expansion is difficult to assess. Hsiao (1970) [109] concluded that inhibition of cell expansion precedes the decline in polysome content and that changes in polysome profile might be caused by cell growth rather than the reverse. Although water stress may inhibit protein synthesis [104,110] some specific types of proteins and mRNA increase in water stressed plants. For instance, free proline accumulation in response to drought in many plant species tissues is well documented [111-115]. Vartanian *et al.*, (1987) [108] mentioned the presence of drought specific proteins in tap root of *Brassica*.

The functions of many of these proteins have not been established [116]. However, water stress may inhibit the synthesis of different proteins equally whilst inducing the synthesis of a specific stress protein [107]. Changes of amino acids and protein have been mentioned in many reports which have stated that water stress caused different responses depending on the level of stress and plant type. For instance, in *Avena* coleoptiles water stress clearly caused a significant reduction in rate of protein synthesis [104]. Treshow (1970) [117] concluded that water stress inhibited amino acid utilisation and protein synthesis. While amino acid synthesis was not impaired, the cellular protein levels decreased and since utilisation of amino acids was blocked, amino acids accumulated, giving a 10- to 100-fold accumulation of free asparagine. Valine levels increased, and glutamic acid and alanine levels decreased. Barnett and Naylor (1966) [118] found no significant differences in the amino acid and protein metabolism of 2 varieties of Bermuda grass during water stress and reported that amino acids were continually synthesised during the water stress treatments, but protein synthesis was inhibited and protein content decreased. Similarly, water stress did not change protein content uniformly in the different cultivars of Cucumber and *Cucurbita pepo* L., *Cucumis melo* L. (snake cucumber) and *Ecballium elaterium* (L.) A. Rich. (Squirting cucumber) which show differing responses to moderate and severe stress treatment and during recovery [3]. Tully and Hanson (1979) [119] found that water stress slightly increased the amino acid to sugar ratio of the exudate, but did not change the amino acid composition very markedly. Several proteins were reduced by stress in maize mesocotyls [105,106].

4.3 Plant lipids – water stress interactions

The effect of water stress lipid composition on the higher plants have been the subject of considerable research. Phospholipids and glycolipids serve as the primary nonprotein components of plant membranes, while triglycerides (fats and oils) are an efficient storage form of reduced carbon, at various developmental stages and particularly in seeds [47]. The functions of membrane proteins are influenced by the lipid bilayer, in which they are either embedded or bound at the surface. For this reason, a knowledge of the lipid composition of membranes in plant cells is important.

Ideas about the adaptive value of lipid changes induced by environmental conditions are often based upon physical properties of the lipids involved in membrane structure, such as phase separation temperatures and fluidity, which may affect the permeability of bio membranes [120]. About 70% of the total protein and 80% of the total lipid of leaf tissue are present in chloroplasts. Any changes in chloroplast membranes, therefore, will usually be reflected by corresponding alterations to leaf total lipids [121].

Lipids, being one of the major components of the membrane, are likely to be affected by water stress. In plant cell, polar acyl lipids are the main lipids associated with membraneous structures [122,123]. Glycolipids (GL) are found in chloroplasts membranes (more than 60%) and phospholipids (PL) are thought to be the most important mitochondrial and plasma membrane lipids [124]. Many workers have investigated the effect of different levels of water stress on lipid content and composition in different parts of plants [75,90,125-132] and their changes listed in Table 3. However, researches concerning on plant lipids affected by water stress have often contradictory since absence of enough information about the plant water status i.e. description of stress effects [133].

Lipid changes	References
PL and GL decline	cotton (Wilson *et al.*, 1987)
GL decrease	cotton (Ferrari Ilou *et al.*, 1984),wheat, barley (Chetal *et al.*, 1981)
Total lipids and PL, GL and diacylglycerols decrease	sunflower (Navari-Izzo *et al.*, 1993)
PL decrease	sunflower (Quartacci and Navari-Izzo, 1992), maize (Navari-Izzo *et al.*, 1989) cotton (Wilson *et al.*, 1987), cotton (El-Hafid *et al.*, 1989), oat (Liljenberg and Kates, 1982)
Diacylglycerol, free fatty acid and polar lipid decrease	maize (Navari-Izzo *et al.*, 1989)
Total lipid content decrease	cucumber Cvs., squash, squirting cucumber (Akıncı, 1997)
Trans-hexadecenoic acid decrease	cotton (Pham Thi *et al.*, 1982)
Linoleic and linolenic acid biosynthesis, galactolipid decrease	cotton (Pham Thi *et al.*, 1985)
Diacylglycerol, triacylglycerol and glycolipid increase	soybean (Navari-Izzo *et al.*, 1990)
Saturation of the fatty acids increase	cotton (Pham Thi *et al.* 1982)
Phospholipid (phosphatidylcholin) increase	wheat (Kameli, 1990)
Total lipid content increase	alfalfa (Al-Suhaibani, 1996)
Triglyceride ands streryl ester levels increase	maize (Douglas and Paleg,1981)
Free fatty acids (FFA) increase	wheat (Quartacci *et al.*, 1994)

Table 3. Changes in plant metabolics (Lipids)

Navari-Izzo *et al.*, (1993) [131] pointed out that, since the plasma membrane has a key position in cell biology, understanding membrane function is a major challenge. The selectivity of membranes and their functioning vary with the types and proportions of lipid and protein components.

Investigations on various crop species record a general decrease in phospholipid, glycolipid and linoleic acid contents and an increase in the triacylglycerol of leaf tissues exposed to long periods of water deficits, although the intensity of the stress applied is not always specified. [126,127,134]. The physical state and composition of the lipid bilayer, in which enzymic proteins are embedded, influence both structural and functional properties of membranes. Enzyme activity and transport capacity are affected by the composition and phase properties of the membrane lipids [120,135,136]. Wilson *et al.*, (1987) [137] observed that water deficit caused a significant decline in the relative degree of acylunsaturation (i.e. FA -unsaturation) in phospholipids and glycolipids in two different drought tolerant cotton plants. Pham Thi *et al.*, (1987) [130] pointed out that changes in oleic and linoleic acid during water stress resulted in desaturation changes in one drought sensitive and another more resistant cotton variety and showed that water stress markedly inhibited the incorporation of the precursors into the leaf lipids.

Navari-Izzo *et al.*, (1993) [131] found that, in plasma membranes isolated from sunflower seedlings grown under water stress, there was a reduction of about 24% and 31% in total lipids and phospholipids, respectively, and also significant decreases in glycolipids and diacylglycerols. There was no change in free fatty acids, but triacylglycerols and free sterols increased. However, diacylglycerol, triacylglycerol and glycolipid content increased in soybean seedling shoots under water stress [129]. On the other hand, total lipid content of leaves tended to decrease in two cucumber cultivars as well as *C. pepo* and *Ecballium* in severe stress [3]. The researches indicated that PL in plant tissues under long time drought have been decreased in various crop species [127,129,137,138].

Navari-Izzo *et al.*, (1989) [127] studying responses of maize seedling to field water deficits, found that the diacylglycerol, free fatty acid and polar lipid contents decrease significantly with stress. In the latter class the dryland conditions induced a decrease of more than 50% in phospholipid levels, whereas they did not cause any change in glycolipid levels; and triacylglycerols increased by about 30% over the control.

Pham Thi *et al.*, (1982) [125] investigated the effect of water stress on the lipid composition of cotton leaves. The most striking effects were a decrease of total fatty-acids, due especially to a decrease of trans-hexadecenoic acid. The fatty acid composition of all acyl lipids changed during stress in the direction of increased saturation of the fatty acids. This increased saturation remained even after 10 days of recovery growth under non-stressed conditions.

Pham Thi *et al.*, (1985) [126] pointed out that water deficits inhibit fatty acid desaturation, resulting in a sharp decrease of linoleic and linolenic acid biosynthesis. The decrease in unsaturated fatty acid biosynthesis occurs in all lipid classes, but is greatest in the galactolipid fractions. Wilson *et al.*, (1987) [137] similarly observed that water deficit caused a significant decline in the relative degree of acylunsaturation (i.e. FA -unsaturation) in phospholipids and glycolipids in two different drought tolerant cotton plants. Navari-Izzo *et al.*, (1993) [131] found that, in plasma membranes isolated from sunflower seedlings grown under water stress, there was a reduction of about 24% and 31% in total lipids and phospholipids, respectively, and also significant decreases in glycolipids and diacylglycerols. There was no change in free fatty acids, but triacylglycerols and free sterols increased. Douglas and Paleg (1981) [128] noted that the fatty acids of triglycerides, of maize seedling were quite responsive to stress and in half of the comparisons were found to differ significantly. Stem triglycerides, in general, responded, whereas the major triglyceride change in the leaf was an increase in linolenic, which is essentially absent from this fraction in stems and roots. Kameli (1990) [75] observed that total leaf phospholipids content and, especially, phosphatidylcholine increased, rose in stressed plants of a relatively water stress resistant cultivar of wheat but did not change significantly in another, less tolerant cultivar.

5. Drought and nutrient uptake

Reduction in photosynthetic activity and increases in leaf senescence are symptomatic of water stress and adversely affect crop growth. Other effects of water stress include a reduction in nutrient uptake, reduced cell growth and enlargement, leaf expansion, assimilation, translocation and transpiration. Water and nutrient availability is one of suboptimal phenomenons like most of the natural environments occur continuously, with respect to one or more environmental parameters. Soils are very important natural source for plant growth where the plants anchored however millions of hectares of land becoming unproductive and affecting plant growth every year. The nutrient uptake of crop plants

greatly influenced by including overuse of the land in agricultural activities, climate change, precipitation regimes, root morphology, soil properties, quantity and quality of fertilizers, amount of irrigation [139-141]. The root structures such as root extension rate and length, the means of root radius and root hair density affect the quantity of nutrient uptake by a plant. Nutrient elements availability plays vital role for plant growth, nevertheless these physiological factors in nutrient, in soil, in plant or at the root absorpsion sites may in interact as well as antagonistically and synergistically of the plants [141-143].

Many nutrient elements are actively taken up by plants, however the capacity of plant roots to absorb water and nutrients generally decreases in water stressed plants, presumably because of a decline in the nutrient element demand [141]. It is well documented that essential plant nutrients are known to regulate plant metabolism even the plants exposed to drought by acting as cofactor or enzymes activators [144].

It is rather difficult to identify the effects of water stress on mineral uptake and accumulation in plant organs. Many workers have reported different effects of water stress on nutrient concentrations of different plant species and genotypes, and most studies have reported that mineral uptake can decrease when water stress intensity is increased [145-150]. For instance, nitrogen uptake decreased in soybean plants under water stress conditions [145] and nitrogen deficiency causes cotton plants to be sensitive to stress with a higher water stress [151] and decrease of nutrient presumably because of a decline in the nutrient element demand since the reduced root-absorbing power or capacity absorb water and nutrients generally declines accompanied to decrease in transpiration rates and impaired active transport and membrane permeability of crop plants [152].

Water stress generally favoured increases in nitrogen, K^+, Ca^{2+}, Mg^{2+}, Na^+, and Cl^- but decreases in phosphorus and iron [147]. Although the many report stated that water stress mostly causes reduction in uptake of nutrients [152], for instance phosphorus, K^+, Mg^{2+}, Ca^{2+} in some crops [153-155], Ca^{2+}, Fe^{3+}, Mg^{2+}, nitrogen and phosphorus and potassium in *Spartina alterniflora* [156]; Fe^{3+}, Zn^{2+} and Cu^{2+} in sweet corn [157]; Fe^{3+}, K^+ and Cu^{2+} in *Dalbergia sissoo* leaves [150], Gerakis *et al.*, (1975) [158] and Kidambi *et al.*, (1990) [159] stated that nutrient elements increased in forage plant species and alfalfa and soinfoin (*Onobrychis viciifolia* Scop.) respectively. An increase in some specific elements such as K^+ and Ca^{2+} were reported in maize [145], and K^+ in drought tolerant wheat varieties [160], and in leaves of *Dalbergia sissoo* nitrogen, phosphorus, Ca^{2+}, Mg^{2+}, Zn^{2+} and Mn^{2+} increased with increasing water stress [149].

Under water stress, the uptake of K^+ and Ca^{2+} by maize plants increased [145]. The relative amounts of K^+, Ca^{2+}, and Mg^{2+} increased considerably more in barley than in rye when water stresses were imposed [150]. Potassium contributes to osmotic adjustment as one of the primary osmotic substances in many plant species [161,162] and under water stress conditions, K^+ application is beneficial for plant survival with improved plant growth [163,164]. There are a few reports indicating that water stress favored increases in K^+ [147] in plants such as maize [145], drought-tolerant wheat varieties [160], creeping bentgrass [165] and *Ammopiptanthus mongolicus* (evergreen xerophyte shrub) [166]. Contrary to reports stating that water stress generally favored increases in Ca^{2+} [145,147,167,168]. Kırnak *et al.*, (2003) [148] who stated that water stress can cause Ca^{2+} reduction in bell pepper, and suggested antagonistic affects of Zn^{2+} and Mn^{2+} on Ca^{2+} uptake. In moderate and severe stressed leaves of bean (*Phaseolus vulgaris* L.) Ca^{2+} content was lower than the amount of potassium with a Ca/K ratio of 0.12, 0.15 and 0.16 in the control, and in both stress levels

[168]. The reason for total Ca^{2+} content being lower than K^+ was considered to be directly related to antagonistic effects of Ca^{2+} on K^+[169]. According to Kuchenbuch *et al.*, (1986) [170], a reduction in leaf area of onion plants can be explained by declining amount of K^+ caused by decreasing water content in the soil.

Unlike previous reports which have stated that water stress causes a reduction in nutrients uptake [152-155] as well as Mn^{2+} [150], Mn^{2+} content in bean leaves tended to increase with increased in water stress levels [168]. Nambiar (1977) [150] pointed out that drying the upper layer of a siliceous soil profile strongly reduced the absorption of Mn^{2+} by rye grass, but Cu^{2+} and Zn^{2+} uptake were not relatively affected. For several grassland plants, total nutrients generally decreased with increasing water stress [158].

It is generally accepted that the uptake of phosphorus by crop plants is reduced in dry soil conditions [171,172]. The studies carried out before the mid 1950s, 12 of the 21 papers reported that P concentration decreased, and 9 papers stated that P status was not changed in plants [158]. Although Fawcett and Quirk (1962) [173] reported that only severe water stress reduced plant phosphorus absorption, Nuttall (1976), [174] stated that increased soil moisture resulted in increased phosphorus but decreased sulphur in alfalfa. It is believed that, P uptake by plants increased with increased P levels in the soil ignoring water stress. Olsen (1961) [175] highlighted that the correlations among the soil P levels and monovalent phosphate uptake by plant and magnitude of water stress. In alfalfa (*Medicago sativa* L.) P and that of Ca^{2+}, Mg^{2+}, and Zn^{2+} in alfalfa and soinfoin (*Onobrychis viciifolia* Scop.) increased with decreased soil moisture supply [159]. On the other hand, there was no effect on moisture stress on the concentrations of P, N, K [176].

Magnesium has an inverse relationship with calcium, phosphorus, iron, manganese and potassium with Ca^{2+} and Mg^{2+} having antagonistic effects on Mn^{2+} of a complex nature [47,177] Although some studies have found that Mg^{2+} absorption is increased by water stress in many crops [147,158], in bean leaves Mg^{2+} content decreased by 18% and 45% respectively in two increased water stress levels [168].

In particularly, the presence of Ca^{2+} is of great importance since zinc absorption is closely related with nutrient concentrations, with Zn^{2+} solubility and availability negatively correlated with Ca^{2+} saturation in soils [177]. The increase in Zn^{2+}, particularly in severely stressed plants, seemed to show a competing relationship between Zn^{2+} and Ca^{2+}, with Ca^{2+} appearing at a lower level in the S2 treatment. Dogan and Akıncı (2011) [168] stated that Zn^{2+} supply is expected to decrease the uptake of most nutrients, K^+ and Mg^{2+} suppressed, while Ca^{2+}, Fe^{3+} only slightly decreased in bean leaves.

According to Singh and Singh (2004) [149], availability of soil nutrients decreases with increasing soil drying, with K^+, Ca^{2+}, Mg^{2+}, Zn^{2+}, Fe^{3+} and Mn^{2+} decreasing by 24%, 6%, 12%, 15%, 25% and 18%, respectively. Nambiar (1977) [150] pointed out that drying the upper layer of a siliceous soil profile strongly reduced the absorption of Mn^{2+} by rye grass, but Cu^{2+} and Zn^{2+} uptake were not relatively affected. In herbage plants, the uptake and solubility of nutrient elements depressed but Ca/K and Ca/P ratios increased under water stress conditions. In dried soil, older roots lost their ability to function and nutrients are absorbed by the more active root tips. Most of the studies revealed that water stress restricted uptake of nutrient elements by crops, active transport systems were impaired or destroyed by severe water stress while the presence of various ions responded differently in growth conditions.

6. Conclusion

Wherever they grow, plants are subject to stresses, which tend to restrict their development and survival. Moisture limitation can affect almost every plant process, from membrane conformation, chloroplast organisation and enzyme activity, at a cellular level, to growth and yield reduction in the whole plant and increased susceptibility to other stresses [178]. Reduction in photosynthetic activity and increases in leaf senescence are symptomatic of water stress and adversely affect crop growth. Other effects of water stress include a reduction in nutrient uptake, reduced cell growth and enlargement, leaf expansion, assimilation, translocation and transpiration. In research aimed at improvements of crop productivity, the development of high-yielding genotypes, which can survive unexpected environmental changes, particularly in regions dominated by water deficits, has become an important subject. As pointed out earlier by Kozlowski (1968) [17] there is a need to increase crop production, in the face of mounting food shortages, and water conservation is an important factor in overcoming food deficiencies. From the above survey, it is clear that a wide range of morphological, physiological and biochemical responses have been correlated with differences in drought tolerance in various crop plants.

7. References

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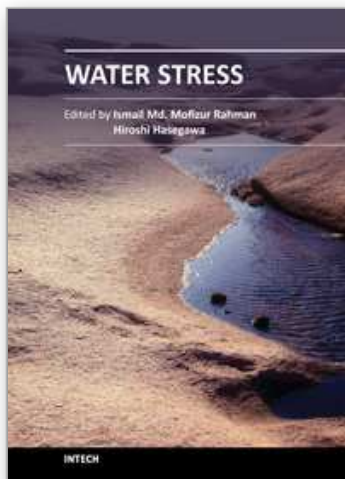
Water Stress

Edited by Prof. Ismail Md. Mofizur Rahman

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

How to reference

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