Chapter 3

WATER-DEFICIT STRESS IN COTTON

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INTRODUCTION

Water deficit is the major abiotic factor limiting plant growth and crop productivity around the world (Kramer, 1983). Approximately one third of the cultivated area of the world suffers from chronically inadequate supplies of water (Massacci et al., 2008). In all agricultural regions, yields of rain-fed crops are periodically reduced by drought (Kramer, 1983), and the severity of the problem may increase due to changing world climatic trends (Le Houerou, 1996). Advances in irrigation technology have helped reduce the gap between potential and actual yield, but irrigation costs and limited water supplies constrain irrigation throughout the world.

Water availability and quality affect the growth and physiological processes of all plants since water is the primary component of actively growing plants ranging from 70-90% of plant fresh mass (Gardner et al., 1984). Due to its predominant role in plant nutrient transport, chemical and enzymatic reactions, cell expansion, and transpiration, water stresses result in anatomical and morphological alterations as well as changes in physiological and biochemical processes affecting functions of the plants (Hsiao, 1973; Kramer, 1980).

Plant water deficits depend both on the supply of water to the soil and the evaporative demand of the atmosphere. In general, plant water stress is defined as the condition where a plant’s water potential and turgor are decreased enough to inhibit normal plant function (Hsiao et al., 1973). The effects of water stress depend on the severity and duration of the stress, the growth stage at which stress is imposed, and the genotype of the plant (Kramer, 1983).

This review discusses the effects of water-deficit stress on several facets of growth and development in domestic cotton (Gossypium hirsutum L.).

EFFECTS OF WATER-DEFICIT STRESS ON MORPHOLOGICAL CHARACTERISTICS

Water-deficit stress adversely affects plant performance and yield development throughout the world (Boyer, 1982). Water-deficit stress reduces cell and leaf expansion, stem elongation, and leaf area index (Jordan et al., 1970; McMichael and Hesketh, 1982; Turner et al., 1986; Ball et al., 1994; Gerik et al., 1996). Leaf, stem and root growth rate are very sensitive to water stress because they are dependent on cell expansion (Hsiao, 1976; Hearn, 1994).
Krieg and Sung (1986) reported that water stress caused a reduction in the whole plant leaf area by decreasing the initiation of new leaves, with no significant changes in leaf size of leaf abscission. Both the main stem and sympodial branches developed significantly less leaves; however, the effect was less severe on the main-stem leaves. Pettigrew (2004) reported that water-deficit stress resulted in a decrease in leaf size, but noted that this decrease was accompanied by an increase in the specific leaf weight (SLW), a phenomenon also observed by Wilson et al. (1987). Significantly fewer nodes and lower dry weights of stems and leaves of water-stressed plants compared to those of the control were reported by Pace et al. (1999) (Table 1), while McMichael and Quisenberry (1991) observed decreased shoot-to-root ratios of plants grown under conditions of severe water stress. Malik et al. (1979) reported that root growth appears to be less affected by drought than shoot growth. Several researchers (Creelman et al., 1990; McMichael and Quisenberry, 1991; Ball et al., 1994; Pace et al., 1999) observed that seedlings of water-stressed cotton showed increased root elongation, accompanied by a reduction in root diameter.

**Table 1.** Plant height, stem and leaf dry weight, leaf area, and node number in drought-stressed and well-watered control plants of Stonevelle 506 and Tamcot HQ95 at the end of the drought, 49 days after planting. The drought treatment was imposed by withholding water for 13 d. (From Pace et al., 1999).

<table>
<thead>
<tr>
<th>Plant Part</th>
<th>Treatment</th>
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<tbody>
<tr>
<td></td>
<td>Drought</td>
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<tr>
<td>Plant height (cm)</td>
<td>20.0*</td>
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<tr>
<td>Stem dry weight (g)</td>
<td>1.13*</td>
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<tr>
<td>Leaf dry weight (g)</td>
<td>1.41*</td>
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<tr>
<td>Leaf area (cm²)</td>
<td>56*</td>
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<tr>
<td>Node number</td>
<td>7.8*</td>
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* Means in a row are significantly different at the 0.05 probability level.

A correlation between leaf abscission and low plant water potentials has been commonly reported (Addicott and Lynch, 1955; Bruce et al., 1965), and McMichael et al. (1972) identified a linear relationship between the rates of leaf abscission and the levels of the imposed water-deficit stress; however, leaf abscission occurred after the stress was relieved and not during the period of stress. Addicott and Lynch (1955) speculated that formation of the abscission layers requires sufficient plant turgor. In addition, McMichael et al. (1973) observed that younger leaves were not as prone to abscission as older ones.

Water-deficit stress has also been shown to alter cell ultrastructure. Ackerson et al. (1981) observed that leaves of adapted plants contained large starch granules in the chloroplast wherein the structure of the thylakoid membranes appeared to be damaged. In addition, Berlin et al. (1982) indicated that water stress caused significant changes in the grana and stroma lamellae, palisade cell walls, number and size of chloroplasts, and the structure of mitochondria. In support of that observation, Bondada and Oosterhuis (2002) reported loss of chloroplast membrane integrity accompanied by an increase in leaf wax production (Bondada and Oosterhuis, 2002;
Oosterhuis et al., 1991; Meek and Oosterhuis, 2010). Changes in the chemical composition of epicuticular wax and lipid content were also observed. The wax from water-stressed leaves contained more long-chain alkanes compared to the control (Oosterhuis et al., 1991; Bondada et al., 1996). Conversely, water-deficit stress decreased glycolipids and, to a lesser effect, phospholipids, while the triacylglycerols increased (Pham Thi et al., 1985; Wilson et al., 1987).

**EFFECTS OF WATER-DEFICIT STRESS ON PHYSIOLOGICAL CHARACTERISTICS**

The effects of water deficit on different plant physiological processes are complex and interrelated. Cellular water content largely controls stomatal aperture, and stomatal conductance directly affects CO₂ diffusion and photosynthetic carbon fixation, which in turn affects metabolic functions such as respiration. However, for ease of discussing these physiological functions, we have addressed each function separately.

**Photosynthesis**

Photosynthesis plays a major role in determining crop productivity in all species and is directly affected by water stress. Photosynthetic rates of the leaves decrease as the relative water content and leaf water potential decrease (Lawlor and Cornic, 2002) (Fig. 1). The effects of water stress on photosynthesis are complex, and may include a combination of stomatal closure (Sharkey, 1990; Chaves, 1991; Cornic, 1994) and the inhibition of metabolic processes, including ribulose bisphosphate synthesis and adenosine triphosphate synthesis.

![Figure 1. Relationship between photosynthesis and leaf water potential of vegetative and reproductive cotton leaves. (Redrawn from Ackerson et al., 1977a).](image-url)
In cotton, several reports have indicated that water stress causes a reduction in photosynthesis rates due to a combination of stomatal and non-stomatal limitations (Pallas et al., 1967; McMichael and Hesketh, 1982; Turner et al., 1986; Sung and Krieg, 1986; Genty et al., 1987; Ephrath et al., 1990; Faver et al., 1996; Lacape et al., 1998; Leidi et al., 1999). However, there has been some controversy concerning the relative importance of these two processes responsible for photosynthetic impairment under water deficit (Flexas and Medrano, 2002; Lawlor and Cornic, 2002; Chaves et al., 2002, Lawlor, 2002).

The relative contributions of stomatal opening and metabolic processes to the decrease of photosynthesis in drought-stressed plants are still being studied and debated. According to Chaves and Oliveira (2004) and Flexas et al. (2004a), decreased CO$_2$ diffusion from outside the plant to the site of carboxylation is the main cause for reduced photosynthetic rates under most water-stress conditions. Reduced CO$_2$ diffusion has been attributed to stomatal closure, reduced mesophyll conductance, or a combination of these factors (Flexas et al., 2002; Warren et al., 2004). Additionally, other factors, such as time of day, ambient CO$_2$ concentrations, nutrient levels, leaf type, growth stage, genotypic differences and abscisic acid (ABA) concentrations may affect photosynthetic rate in drought-stressed plants.

**Stomatal Factors**

Stomatal closure decreases water loss, but also decreases the movement of CO$_2$ into the plant. Significant correlations between leaf water potential and stomatal conductance under conditions of water-deficit stress have been reported (Socias et al., 1997), but diverse reports exist for cotton. Experiments with potted plants have shown stomatal closure due to water stress in cotton to be similar to other crops. Kanemasu and Tanner (1969) and Boyer (1970) quantified stomatal resistance on a variety of crops, including cotton, and found that stomatal resistance due to stomatal closure increased dramatically at between -0.8 and -1.2 MPa. Harris (1973) and Bielorai et al. (1975) also reported that in potted experiments stomatal conductance was significantly decreased under conditions of water-deficit stress.

However, field experiments have shown cotton stomatal conductance to be adaptable to water stress. Ackerson et al. (1977) reported that leaf stomatal conductance of field-grown cotton was slightly affected and leaf stomata did not completely close even under very low water potentials, and they speculated that light intensity is probably more of a controlling factor than leaf water status. Jordan and Ritchie (1971) observed that cotton plants that had been adapted to low water conditions were capable of stomatal conductance and photosynthesis at very negative leaf water potentials. Complete stomatal closure did not occur even at leaf water potentials approaching -3.0 MPa and it was suggested that stomatal closure in field-grown plants is prevented in order for the plants to maintain water flux.

Ackerson (1981) and Ackerson and Herbert (1981) expanded on this discovery, finding that water stress adapted plants had similar leaf conductance under wet conditions, but maintained turgor at more negative leaf potentials than non-adapted plants. Wullschleger and Oosterhuis (1990) reported that while both moderate and severe water stress significantly decreased leaf stomatal conductance, bract stomatal conductance remained unaffected.
Non-Stomatal Factors

Changes in the photosynthetic apparatus under drought through metabolic impairment are far more complicated than those resulting from inhibition of stomatal function, and they are predicted to occur under conditions of severe drought stress. Gimenez et al. (1992) reported that capacity of ribulose 1,5-bisphosphate (RuBP) regeneration could be a metabolic process that could be a limiting step in photosynthesis under water-deficit stress, while Medrano et al. (1997) speculated over the activity of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco). Additionally, adenosine 5-triphosphate (ATP) synthesis or ATP-synthase activity could be severely inhibited resulting in a decrease in photosynthetic rates (Younis et al., 1979; Tezara et al., 1999). Leaf photochemistry (Cornic and Massacci, 1996) and permanent photoinhibition (Bjorkman and Powles, 1984) have also been suggested to be affected under limiting water conditions.

Pettigrew (2004) speculated that the higher photosynthetic rates and increased PSII quantum efficiency ($\Phi_{\text{PSII}}$) with rehydrated plants could be attributed to the higher chlorophyll content per unit leaf area that was observed. Similar results were reported from Massacci et al. (2008) who observed that photosynthetic electron transport was enhanced under conditions of water stress due to an increased efficiency in the open PSII reaction centers. They also observed that photorespiration increased at the onset of water stress in order to prevent an inhibition of the photosynthetic apparatus and over-production of damaging reactive oxygen species. Massacci et al. (2008) attributed this to an increase in photorespiration rates in order to prevent an inhibition of the photosynthetic apparatus and over-production of damaging reactive oxygen species. Genty et al. (1989) also reported that $\Phi_{\text{PSII}}$ is positively correlated with the quantum efficiency of CO$_2$ fixation. They also noted that photon receptors were not impaired under conditions of water stress. Similarly photon distribution and PSII photochemistry was not affected, however electron transport through PSI was inhibited. In contrast, Enahli and Earl (2005), Inamullah and Isoda (2005), and Kitao et al. (2007) observed that quantum efficiency of PSII decreases under conditions of water stress. Additionally, Enahli and Earl (2005) observed in their study, where water stress levels varied from moderate to severe, that even though photosynthetic rates remained unaffected under moderate stress rates, significant decreases were observed in the velocity of carboxylation of Rubisco and at the CO$_2$ concentration at the site of carboxylation. Those responses became more prominent under severe water-deficit stress where both photosynthetic rates as well as concentration of CO$_2$ at the site of carboxylation decreased. Upon relief from the water stress, CO$_2$ concentrations returned to control levels however, photosynthetic rates remained low indicating metabolic and non-stomatal inhibition, which is in contrast with Pettigrew (2004). The explanation for these contrasting results has been suggested to lie in the heterogeneity of the photosynthetic apparatus across the cotton leaf (Wise et al., 1992). However, Massacci et al. (2008) indicated that leaf patchiness is significantly decreased under conditions of water deficit.

Other Factors Affecting Photosynthesis in Drought-Stressed Plants

In addition to stomatal closure and changes in metabolic rates and leaf photochemistry, several other factors have been linked to decreases in photosynthesis in drought-stressed cotton plants. Ackerson et al. (1977) observed differences between photosynthesis rates at different
times of the day (morning vs. afternoon) as well as between leaves of different age, which agreed with previous reports (Jordan and Ritchie, 1971; Jordan et al., 1975).

Furthermore, Ackerson (1981) and Ackerson and Herbert (1981) observed that the older leaves in plants adapted through successive drought cycles, contained up to five times more starch than corresponding leaves in non-adapted plants. In addition, photosynthetic rates of the adapted older leaves were lower under wet conditions compared to non-adapted plants while no effect was observed on the photosynthetic rates of the young leaves by the adaptation. The reduction in photosynthetic rates was attributed to feedback inhibition of photosynthesis due to carbohydrate accumulation and not to stomatal restriction.

Other factors such as abscisic acid (ABA) concentration, ambient CO$_2$ concentrations and nutrient deficiencies have been shown to have an effect on leaf stomatal conductance under limited water conditions. Radin and Ackerson (1981) in potted experiments with different CO$_2$ concentrations and nitrogen rates indicated that water-deficit stress significantly decreased both stomatal and mesophyll conductance compared to the control. They also reported that nitrogen deficiency significantly increased stomatal sensitivity to the intercellular CO$_2$ concentrations at low water potentials, a result which was similar to the effect of ABA application. They concluded that behavior of stomata is closely controlled by ABA concentrations under conditions of water deficit. Similar responses of stomatal conductance were reported for phosphorus-deficient cotton plants (Radin, 1984).

In experiments with different cotton genotypes, Pettigrew (1993) found that okra and super okra leaf type plants had lower stomatal conductance values than normal leaf type isolines at high water potentials and this was attributed to the lower abaxial stomatal density of okra leaf types (Wells et al., 1986). Similar findings were reported by Karami et al. (1980) and Nepomuceno et al. (1998) who also noticed that super okra was able to maintain higher leaf and turgor potentials at lower osmotic potentials compared to the normal leaf plants under water deficit. In addition, okra and super okra leaf type plants exhibited higher photosynthetic rates at similar low water potentials compared to the normal leaf type plants in greenhouse and field experiments (Karami et al., 1980; Nepomuceno et al., 1998; Pettigrew, 2004).

Marani et al. (1985) reported reduced canopy photosynthetic rates under conditions of water stress which they attributed to decreased leaf expansion and hence, leaf area as well as to the leaf age of the canopy and the increased senescence rates due to reduced supply of water. However, Constable and Hearn (1981) observed in field experiments that net assimilation rate was not affected by irrigation treatments, whereas Pettigrew (2004) reported that leaf photosynthetic rates increased in the morning for water-stressed field-grown cotton plants in the Mississippi Delta before decreasing in the afternoon. Those different responses however, could be attributed to the different stages of growth that water-deficit stress was imposed, the different genotypes, the different leaf ages and position of leaves in the canopy.

As Karami et al. (1980) reported, photosynthesis during the reproductive stage was less sensitive to water stress compared to the vegetative stage while young leaves had higher photosynthetic rates compared to older ones at the same leaf water potentials. Pettigrew (2004) also speculated that the higher photosynthetic rates could be attributed to the hydraulic conductivity of the soils that allowed the plants to rehydrate during the night, hence enabling their photosynthetic apparatus to operate more efficiently during the morning.
Photosynthetic responses under conditions of water-deficit stress appear to be affected by several factors. Even though recently, Flexas et al. (2006) observed that photosynthetic rates are mostly limited by decreased stomatal conductance as well as reduced mesophyll conductance that ultimately result in a general metabolic impairment due to lower carbon substrate concentration, a conclusion over which photosynthetic metabolic process or factor is most sensitive under water-deficit stress has yet to be made.

**WATER-DEFICIT STRESS EFFECTS ON RESPIRATION, ATP, AND CARBOHYDRATES**

Respiration is the process by which a plant obtains energy by reacting oxygen with sugars (glucose) to produce water, carbon dioxide and adenosine 5-triphosphate (ATP). Dark respiration (in contrast to photorespiration and photosynthesis) occurs during the day and night, and its rates during the day vary between 25 and 100% of the respiratory activity during the night (Krömer, 1995). Of the CO$_2$ fixed each day by net photosynthesis, about 30-70% is released back to the atmosphere through dark respiration (Atkin et al., 1996) with 50-70% of whole plant respiration occurring in leaves (Atkin et al., 2007). However, Flexas et al. (2005, 2006) pointed out that the percentage of daily fixed carbon that is respired is expected to be higher in water-stressed plants, mainly because of the inhibitory effect of water deficit has on photosynthesis.

According to Atkin et al. (2009) the responses of respiration rates to water deficit vary by plant genotype, the type and the age of tissue (mature or still actively growing), the duration and severity of stress, changes in activity of respiratory enzymes, substrate availability, and ATP demand. De Vries et al. (1979) conducted studies in maize (Zea mays L.) and wheat (Triticum aestivum L.) and observed that while respiration rates remained unaffected at low or moderate water stress, they decreased at severe water stress. A similar pattern was also observed by McCree et al. (1984) in sorghum (Sorghum bicolor L.), and Boyer (1970) and Ribas-Carbo et al. (2005) in soybean (Glycine max L.). However, Boyer (1970, 1971) in studies with sunflower (Helianthus annuus L.), found a decrease in respiration rates when drought stress was imposed, while Ghashgaie et al. (2001) noticed an increase, and Lawlor and Fock (1977) reported no change.

Limited data exists concerning water-deficit stress effects on respiration of cotton. Pallas et al. (1967) reported that respiration initially decreased with increasing severity of the water stress and eventually increased at more severe stress. Loka and Oosterhuis (unpublished data) observed that respiration rates of water-stressed plants decreased compared to unstressed plants in controlled environment experiments. Wullschleger and Oosterhuis (1990) reported that boll respiration remained unaffected under moderate water stress and significantly decreased once the stress became more severe.

**ATP Content**

Adenosine 5-triphosphate (ATP) constitutes the molecular currency of intracellular energy transfer for plant metabolism. Photosynthesis and respiration are the main plant processes through which ATP is produced, and specifically through the pathways of (a) photophosphorylation (cyclic and non-cyclic) in the chloroplasts, (b) glycolysis in the cytosol, and the most important pathway, and (c) oxidative phosphorylation in the mitochondria (Raymond and Pradet, 1983).
Measurements of ATP in water-stressed tissues show considerable variation. Flexas and Medrano (2002) reported a decrease in ATP content of leaves with a relatively small decrease in relative water content; however, Tezara et al. (1999) observed that ATP content was not depleted completely even at very low relative water content and when photosynthesis had stopped. Sharkey and Seeman (1989) found no differences in the ATP content of mildly-stressed bean (*Phaseolus vulgaris* L.) leaves, while Meyer et al. (1992) indicated that ATP content progressively decreased as the relative water contents decreased.

Recently, Lawlor and Tezara (2009) speculated that drought stress might also result in an increased ATP content through the respiratory pathway in order to compensate for reduced rates of chloroplast ATP synthesis. Pandey et al. (2002) conducted studies to determine the effect of water-deficit stress on the photosynthetic metabolites on cotton during the reproductive stage. They reported that water-stress resulted in a decrease in leaf ATP content while, nicotinamide adenine dinucleotide phosphate (NADP) content was increased. Leaf 3-phosphoglyceric acid (3-PGA) and pyruvate content remained unaffected by the water stress treatments.

**Carbohydrate Metabolism and Translocation**

As mentioned above, photosynthesis has been shown to be adversely affected by water stress. Photosynthesis is the fundamental function through which plants fix carbon and produce carbohydrates, so it is expected that water stress would also affect carbohydrate metabolism.

An early study by Eaton and Ergle (1948) showed that water stress significantly reduced starch concentrations and increased hexose sugars in cotton leaves, with variable effects on sucrose accumulation. Parida et al. (2007) found that total leaf soluble carbohydrate and leaf hexose concentrations increased, while leaf starch contents decreased in both drought-tolerant and drought-sensitive cultivars. Increase in hexose and depletion of leaf starch concentration have also been reported in soybean (*Glycine max* L. Merr.) (Huber et al., 1984; Liu et al., 2004) and pigeonpea (*Cajanus cajan* L.) (Keller and Ludlow, 1993).

In contrast, Ackerson (1980) observed that higher quantities of starch were accumulated in water-stressed cotton leaves compared to those of the control. Additionally, acclimated young cotton leaves had the ability to export sucrose, whereas non-acclimated plants did not at the same low leaf water potential. He speculated that translocation of photosynthates was greatly inhibited under conditions of water stress. In support of this observation, Timpa et al. (1986) reported that drought stress caused no change in leaf sucrose concentrations of non-flowering cotton strains, while glucose levels were significantly higher in the drought-stressed leaves compared to the control, indicating that the source sink-relationships are affected by drought.

Impairment of the photoassimilate translocation mechanism under conditions of water-deficit stress has been reported for other crops as well, such as sugarcane (*Beta vulgaris* L.) (Hartt, 1967), maize (*Zea mays* L.) (Boyer and McPherson, 1977), and wheat (*Triticum aestivum* L.) (Johnson and Moss, 1976). Liu et al. (2004) made a similar observation for soybean source-sink relationships and reported that sucrose and leaf starch concentrations decreased significantly under water stress resulting in a decrease in the rate of sucrose export from the leaves.
Sung and Krieg (1979) conducted experiments with different leaf-type cotton genotypes and water stress at different stages of development to study the effect of water stress on the rate of assimilate export from the leaf by measuring the disappearance of labeled $^{14}$C from the leaf. They reported that translocation of assimilates was reduced under much lower water potential values compared to photosynthesis, concluding that photosynthesis is more sensitive to water-deficit stress than translocation (Fig. 2), which is in accordance with Wardlaw (1967), who also concluded that main consequence of water stress on translocation is on the availability of photosynthate. Sung and Krieg (1979) however, observed that water-deficit stress altered the assimilate export pattern of the upper canopy leaves allocating more photosynthate to vegetative growth and fruits while the water stress had no effect on the export pattern of the lower canopy leaves.

Figure 2. Response of photosynthesis and translocation rates to increasing water stress in cotton as a function of leaf type and growth stage (○, △: flower bud development; ●, Δ: boll-filling period). (From Sung and Krieg, 1979).
Guinn (1976) however, did not notice any difference in carbohydrate accumulation in 4-day-old bolls in cotton plants that had been subjected to water stress compared to those that had been properly watered. Additionally, Heitholt et al. (1994) reported that carbohydrate concentrations of the receptacle and ovary had no relationship with subsequent retention of 5-day-old floral buds or two-day-old bolls in cotton, however, the plants were not subjected to water stress. Similarly, Liu et al. (2004) failed to correlate pod abortion of water-stressed soybeans with pod carbohydrate concentrations. Zinselmeier et al. (1995, 1999) observed that accumulation of sucrose in young water-stressed maize ovaries paralleled the cessation of ovary growth and an additional decrease in hexose concentration. They speculated that the ratio of hexose to sucrose could play an important role in ovary development. An inhibition of invertase activity due to drought stress could also result in an increase in ovary sucrose content (Schussler and Westgate, 1991; Liu et al., 2004). This was also noted by Weber et al. (1998) for legume seed development. Further explanation of carbohydrate metabolism in cotton flowers and developing bolls during drought stress is needed.

PLANT MECHANISMS UNDERLYING RESILIENCE TO WATER-DEFICIT STRESS

Antioxidants

Drought stress has been reported to induce an oxidative stress due to inhibition of photosynthesis (Smirnoff, 1993) resulting from the production and accumulation of toxic oxygen species such as peroxide radicals, hydrogen peroxide and hydroxyl radicals (Foyer et al., 1997). The accumulation of reactive oxygen species (ROS) originates mainly from the decline in CO₂ fixation which leads to higher leakage of electrons to O₂ (Foyer et al., 1997), while other factors triggering formation of free radicals involve fatty acid β-oxidation (del Rio et al., 1998), membrane associated oxidases (Desikan et al., 1996) and photorespiration (Faria et al., 1999).

These reactive oxygen species produced during water-deficit stress can damage many cellular components including lipids, proteins, carbohydrates and nucleic acids (Monk et al., 1987). Membrane lipid peroxidation and protein oxidation constitute the simplest criteria of assessing the extent of oxidative damage in the tissue (Noctor and Foyer, 1998; Mittler 2002). Efficient antioxidant systems in the plant can minimize the level of oxidative stress and protect the tissues. Such antioxidant systems can be enzymatic or non-enzymatic. The major antioxidant species in the plants are superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (AP), and glutathione reductase (GR), along with carotenoids and α-tocopherol (Gaspar et al., 2002). Additionally, polyamines and flavonoids have been shown to provide some protection from free radical injury (Bouchereau et al., 1999), while the photosynthetic system through the xanthophyll-zeaxanthin cycle can also contribute in the relief of oxidative stress. The levels of these antioxidant systems, however, have shown increases, decreases or no effect, depending on the species, duration of drought stress and the specific antioxidants investigated (Reddy et al., 2004).
Mahan and Wanjura (2005) performed field studies to identify changes in antioxidant metabolism in cotton. They observed that even though the glutathione amount and form changed during the season, the changes were not in response to the water-stresses, and they concluded that cotton has a limited ability to alter glutathione metabolism in response of drought stress. In contrast, ascorbate peroxidase activity was increased in water-stressed plants compared to the well-watered plants, while no significant change was reported in the levels of malondialdehyde (MDA), an indicator of cell-membrane damage, leading them to speculate that the oxidative stress was alleviated before membrane damage could occur. However, Kawakami et al. (2010) also reported that glutathione reductase of potted grown plants was not affected by water-deficit stress, whereas superoxide dismutase of water-stressed plants was significantly decreased compared to the control.

Proteins

Plants have been shown to accumulate specific stress-associated proteins in order to survive adverse environmental conditions (Vierling, 1991; Ingram and Bartels, 1996). Heat shock proteins (HSPs) and late embryogenesis abundant (LEA)-type proteins are two major types of stress-induced proteins that are produced upon the induction of drought stress and are considered to play a role in cellular protection during the stress (Ingram and Bartels, 1996; Zhu et al., 1997).

Heat shock proteins have been observed to be produced at any stage of crop development and under different environmental factors such as water-deficit stress (Bray, 1993), UV-radiation (Dohler et al., 1995), or heavy metal accumulation (Neumann et al., 1994). Their molecular weights and proportions differ among species, and they are considered as molecular chaperones essential for the maintenance of protein homeostasis and prevention of denaturation (Vierling, 1991), even though the mechanism by which they contribute to drought tolerance is still not certain. One hypothesis is that they are involved in energy dependent protein unfolding or assembly/disassembly reactions, and they prevent protein degradation under adverse conditions (Pelham, 1986). Another hypothesis is that they are related to the protection and stabilization of particular organelles such as chloroplasts, ribosomes and mitochondria. Additionally, some members of the HSPs have been shown to aid in the maintenance and restoration of enzymes (Sun et al., 2001).

In arid and semi-arid regions, dryland crops may synthesize and accumulate substantial levels of HSPs in response to elevated leaf temperatures due to decreased rates of transpiration. Burke et al., (1985) conducted experiments with field-grown cotton, where soil water deficits resulted in canopy temperatures of 40°C or greater for two to three weeks. At least eight new polypeptides accumulated in about half of the water-stressed leaves while no polypeptides were accumulated in the irrigated cotton leaves. In another study, Kuznetsov et al. (1999) imposed a short-term heat shock treatment to cotton plants at flowering, prior to water-deficit stress imposition, and they observed that heat-treated plants accumulated greater quantities of two HSPs (70 and 80kDa) as well as amino acids (asparagine, proline and arginine especially). Additionally, larger osmotic adjustment values were observed, and the authors speculated that HSPs have a protective role in cotton under condition of water-deficit stress. However, in a similar experiment with field-grown soybean (Glycine max (L.) Merr.), several HSPs were observed in both irrigated and water-deficit stress plants (Kimpel and Key, 1985).
Late embryogenesis abundant proteins, the second major type of stress-induced proteins, have been found in a wide range of plant species in response to desiccation or drought stress (Ingram and Bartels, 1996). Even though they were first identified in cotton seeds during their maturation and desiccation phases (Baker et al., 1988), it has since been recognized that they also accumulate in vegetative tissues under conditions of water stress (Bray, 1993). According to Bray et al. (2000) most LEA proteins exist as random coiled α-helices. They are characterized by their high hydrophilicity index and glycine content (Garay-Arroyo et al., 2000). They are considered to act as water-binding molecules, participate in ion sequestration, and contribute in membrane stabilization (Ingram and Bartels, 1996).

**Osmotic Adjustment and Compatible Osmolytes**

Plants experiencing stressful conditions, such as drought, tend to actively accumulate highly soluble organic compounds of low molecular weight, called compatible solutes, as well as inorganic ions, i.e. K, in order to prevent water loss, maintain water potential gradients and re-establish cell turgor (Hsiao, 1973). This process is called osmotic adjustment and according to Boyer (1982) enables plants to: (1) continue normal leaf elongation but at a reduced rate, (2) adjust their stomatal and photosynthetic functions, (3) maintain the development of their roots and subsequently continue soil moisture extraction, (4) postpone leaf senescence, and (5) achieve better dry matter accumulation and yield production under adverse conditions. Osmotic adjustment has been reported in the leaves of a number of crops such as wheat (*Triticum aestivum* L.) (Morgan, 1977), maize (*Zea mays* L.) (Acevedo et al., 1979), sorghum (*Sorghum bicolor* L.) (Jones et al., 1978; Turner et al., 1978), rice (*Oryza sativa* L.) (Cutler et al., 1980), barley (*Hordeum vulgare* L.) (Matsuda et al., 1981), pearl millet (*Pennisetum americanum* L.) (Henson et al., 1982), sunflower (*Helianthus annuus* L.) (Turner et al., 1978), as well as cotton (*Gossypium hirsutum* L.) (Acevedo et al., 1979, Oosterhuis and Wullschleger, 1987). Interestingly, cotton appears to have a greater ability to osmotically adjust to water stress compared to other major crops (Ackerson et al. 1977; Oosterhuis and Wullschleger, 1988). Additionally, Oosterhuis et al. (1987) observed that primitive landraces and wild types of cotton exhibited higher osmotic adjustment compared to commercial cultivars. They investigated the osmotic adjustment of cotton roots under water deficit and demonstrated that cotton roots show a considerably larger percentage adjustment than the leaves (Fig. 3), reinforcing the ability of the plant to maintain a positive turgor and hence continue normal growth under water stress. A similar pattern was observed in cotton flowers (Trolinder et al., 1993) and bolls (Van Iersel and Oosterhuis, 1996) wherein both flowers and fruits were found to be less affected by the water stress imposed than the subtending leaves. These authors concluded that cotton flowers and bolls are largely independent on the xylem connections for their water supply and that the phloem is the most important factor in water transport to the flowers and developing bolls. Ackerson and Hebert (1980) observed that cotton plants that had been subjected to consecutive water-stress cycles exhibited increased osmoregulation compared to plants that had not been subjected to stress previously. They reported that photosynthetic rates were higher due to higher stomatal conductance at low water potentials, but the opposite was observed under high water potentials.
Osmolytes are organic compounds that exist in a stable form inside the cells and are not easily metabolized. In general, they do not have an effect on cell functions, even when they have accumulated in high concentrations, i.e. more than 200mM (Hare et al., 1998; Sakamoto and Murata, 2002). Compatible solutes include sugars and sugar alcohols (polyols) (Yancey et al., 1982), amino acids such as proline (Aspinall and Paleg, 1981; Bonhert et al., 1995) and its analogues (Naidu et al., 1987), quaternary ammonium compounds (betaines) and tertiary sulfonium compounds (Rhodes and Hanson, 1993). Production of osmolytes is a general method in plants to maintain osmotic potential and cell turgor, as stated above; however, they also have secondary roles such as stabilization of membranes and maintenance of proper protein conformation at low leaf water potentials (Papageorgiou and Morata, 1995), protection of cells by scavenging for ROS (Pinhero et al., 2001), as well as regulation and integration in the metabolism of stressed photosynthetic tissues (Lawlor and Cornic, 2002). Their synthesis and accumulation varies among plant species, as well as among cultivars of the same species. They are most often confined to the chloroplasts and cytoplasmic compartments and according to Ain-Lhout et al. (2001) occupy less than 20% of the total volume of mature cells.

Figure 3. Effect of number of water stress cycles of osmotic adjustment in cotton leaves and roots. The percentage osmotic adjustment was calculated as the percentage decrease in treatment osmotic adjustment compared to the unstressed control. (From Oosterhuis and Wulfscheleger, 1987).
EFFECT OF WATER-DEFICIT STRESS ON YIELD

Water deficit significantly compromises plant development and productivity around the world (Boyer, 1982). In many crops, reproductive development is most sensitive period to drought stress following seed germination and seedling establishment (Saini, 1997). In cotton, however, there is still debate about the most sensitive period to water-stress during development in relation to yield, even though water sensitivity during flowering and boll development has been well established (Constable and Hearn, 1981; Cull et al., 1981a,b; Turner et al., 1986).

According to Reddell et al. (1987) the early flowering period is the most sensitive to water stress, whereas Orgaz et al. (1992) concluded that water stress during peak flowering had the most detrimental effects on cotton yield. On the other hand, a number of reports (Radin et al., 1992; Plaut et al., 1992; de Cock et al., 1993) state that boll development, particularly well after the end of effective flowering, is the most water-deficit-sensitive period for cotton. Additionally, in an earlier experiment, Harris and Hawkins (1942) reported that delaying irrigation at fruiting could increase yield by inhibiting excessive vegetative growth, a result reinforced by Singh (1972), who reported increased number of flowers and bolls per plant as well as increased yield when cotton plants were stressed during the pre-flowering season. Conversely, Stockton et al. (1961) and Lashing et al. (1970) observed that increased irrigation resulted in increased flowering. Guinn et al. (1981) concluded that a moderate water-deficit stress early in the season could be beneficial to the plants by slowing vegetative growth, but that the risk of negative results meant that these practices should be approached with caution. Other crops such as wheat, rice, barley and maize vary in drought sensitivity by growth stage (Saini and Westgate, 2000). However, this variable sensitivity of growth stages in cotton, together with the perennial nature and indeterminate growth pattern, which makes distinct growth stages indistinguishable, may explain the poor understanding of the effects of water deficit on cotton seed set and development.

According to Grimes et al. (1969) there is a positive correlation between the yield and the number of bolls produced. However, the biochemical or metabolic functions affecting boll retention have not been adequately investigated. Both irrigation rate and application type have both been shown to affect boll production and retention (Ritchie et al., 2009; Whitaker et al., 2008; Dumka et al., 2004) but the physiological explanations are not clear. The majority of studies have focused on the consequences of water stress on dry matter, boll number and weight, as well as lint yield and their correlations to leaf photosynthesis and plant water relations, without any emphasis on the biochemical and metabolic processes of the reproductive units themselves. Guinn et al. (1976, 1981, 1984, 1988, and 1990) focused mainly on the hormonal aspects of water-stressed cotton fruiting forms and specifically on the responses of abscisic acid (ABA), indole-3-acetic acid (IAA) and ethylene. They observed that water stress increased ethylene evolution from young bolls as well as their ABA content while it decreased the concentrations of free IAA. However, they were unable to conclude as to which hormone was solely responsible for causing boll abscission and ultimately yield reduction. Research in other crops however, has indicated that ABA caused pollen sterility in barley, wheat and rice (Saini and Westgate, 2000). McMichael et al. (1973) also reported a strong, linear correlation between boll shedding rates and decreasing pre-dawn leaf water potentials. However, they speculated that boll abscission
was also controlled by endogenous factors that were dependent on plant water status such as increased ethylene production (McMichael et al., 1972).

Lint yield is generally reduced under water stress because of reduced boll production primarily due to the production of fewer flowers and bolls (Stocton et al., 1961; Grimes, 1969; Gerik et al., 1996), but also because of increased rates of boll abortion when the stress is extreme during the reproductive growth stage (Grimes and Yamada, 1982; McMichael and Hesketh, 1982; Turner et al., 1986). In addition, Pettigrew (2004) reported that the distribution of the bolls, both vertically and horizontally, was affected by water-deficit stress with the water-stressed plants retaining more bolls at the first fruiting position and producing less bolls above main-stem node 11 compared to the control. He speculated that the reduction observed in lint yield production was due to the loss of these fruiting positions as well as reduced lint per seed (Fig. 4).

Fiber properties have been reported to be insensitive to water-deficit stress (Bennett et al., 1967; Marani and Amara, 1971, Hearn, 1976, 1995), unless the water-deficit stress is extremely severe. Leaf water potentials of -2.8 MPa have been shown to reduce fiber length (Bennett et al., 1967). Water-deficit stress has also been reported to cause a significant reduction in micronaire (Eaton and Ergle, 1952; Marani and Amirav, 1971). Timing of water-deficit stress is also a significant factor since Marani and Amirav (1971) showed that stress early in the flowering season had no
effect on fiber quality. However, when the stress occurred shortly after flowering, it significantly decreased fiber length. Since the extension of the cotton fiber is a process primarily dependent on turgor (Dhindsa et al., 1975) and carbohydrate supply, the reductions in plant water status and photosynthesis that occur under conditions of water-deficit stress would result in decreases in fiber growth. This was supported by Cosgrove et al. (1993) who reported that increased volume of growing plant cells depends on the water uptake by the vacuole. However, lint yield is a function not only of fiber qualities but also a function of number of fibers/seed and number of seeds/unit area (Lewis et al., 2000). According to Rabadia et al. (1999) a strong correlation exists between plant water content and accumulation of dry matter in the developing fiber and seed, which implies that rapid water uptake is required for supporting seed growth. Additionally, the number of motes (unfertilized ovules) has also been demonstrated to increase under conditions of water-stress deficit (Saranga et al., 1998) leading to further yield reduction.

**COTTON WATER USE EFFICIENCY**

Water use efficiency (WUE) quantifies plant biomass production based on water consumption. Physiological WUE is calculated as the ratio of carbohydrate fixation to transpiration, while agronomically, it is defined as the ratio between dry matter produced and quantity of water used. Because high WUE results in increased biomass production per unit of water, WUE is attractive as a trait to estimate drought tolerance.

Measurements of WUE are difficult to obtain, particularly when attempting to quantify efficiency and needs throughout the growing season. Crop WUE can be influenced by a number of environmental and management factors including radiation load, temperature, humidity, ambient CO$_2$ concentration, soil type and structure, soil water availability, nutrition, and genetic makeup (Lin and Ehleringer, 1982; Constable and Rawson, 1980; Reich et al., 1985; Zur and Jones 1984; Reddy et al., 1995; Loveys et al., 2004).

Numerous physiological factors need to be considered when dealing with improving WUE, including stomatal regulation of gas exchange, regulation of plant development and functioning, increased photosynthetic capacity of the mesophyll, increased root hydraulic conductivity, and osmotic adjustment (Bacon, 2004). Additionally, WUE depends upon plant morphological characteristics, such as leaf size and position and canopy structure along with management practices, such as row spacing and plant density (Rosenow et al., 1983; Krieg, 2000).

Measurements of WUE are further complicated by the difficulty in measuring whole-plant carbon dry matter accumulation and transpiration in the field, as well as the inaccuracies associated with scaling from occasional leaf photosynthesis measurements to estimates of whole-plant growth and water use. Hence, agronomic whole plant WUE evaluations are mostly based on general measurements of total dry matter production at the end of the season, as well as the combined total of the soil water bank, irrigation, and rainfall over a growing season. Despite the inherent errors and difficulties in measurement, a number of studies have evaluated cotton WUE; with values ranging from 0.1 to 0.3 kg lint/m$^3$ water (Hearn, 1979).

It has been suggested that WUE depends primarily on photosynthesis (Radin, 1992). Because photosynthesis is tied so closely to stomatal opening, it is not surprising that genes involved in
stomatal opening and closing regulate WUE (Chaves et al., 2004). Hence, any discussion of WUE centers around gas exchange via the stomata. According to Bjorkman and Pearcy (1982) photosynthetic WUE in C3 plants could be expected to double with a doubling of the CO2 in the atmosphere, due to decreases in stomatal conductance required to meet CO2 demand in elevated CO2 environments and the increase of intrinsic WUE (Morison, 1993; Drake et al., 1997).

Farquhar and his colleagues pioneered the carbon isotope ratio technique (δ13C), and demonstrated its value by relating a low level of discrimination with enhanced WUE (Farquhar and Richards, 1984; Farquhar et al., 1988; Condon et al., 1987; Hubrick and Farquhar, 1989). Therefore, a possible solution to the difficulty in measuring WUE is to use δ13C discrimination ratio between intercellular and ambient CO2 concentration to estimate WUE (Farquhar et al., 1982b; Ehleringer et al., 1989, 1993), but even this method is influenced by other factors that may change Ci concentration and affect δ13C discrimination. Researchers using carbon isotope analysis have found varying relationships between WUE and drought tolerance in cotton. Positive relationships between isotope measurements of WUE and productivity were found by Gerik et al. (1996b). However, Leidi et al. (1993, 1999) reported inconsistent results across years, and multiple researchers have reported no correlation between carbon isotope measurements of WUE and plant productivity (Yakir et al., 1990; Saranga et al., 1998a). Lu et al. (1996) reported a positive association between carbon isotope discrimination and stomatal conductance. Saranga et al. (2004) observed no correlation between carbon isotope discrimination and yield production under water-deficit stress conditions and concluded that WUE needed to be combined with other physiological parameters for more accurate results. Therefore, the relationship between physiological WUE and cotton productivity is still unsettled.

Water use efficiency has been shown to vary substantially among species, genotypes and within species (Yoo et al., 2009). Roark and Quisenberry (1977) and Quisenberry et al. (1981, 1984) found significant variability among exotic strains of Gossypium hirsutum, indicating possible improvements in growth stress characteristics. Chaves and Oliveira (2004) pointed out that it is important to understand the mechanism of drought tolerance, since different genotypes adapt to water deficit in different ways. Breeding crop varieties for higher WUE is a solution for improving water use in both rainfed and irrigated crop production (Condon et al., 2004).

Water use efficiency also varies between cultivars and growth habits. Eaton and Belden (1929) and Gustein (1969) reported that Acala cultivars had lower water requirements than Pima cultivars. Quisenberry et al. (1976, 1991) reported that primitive cultivars, characterized by indeterminate growth patterns, had much higher WUE’s compared to the modern determinate cultivars. They concluded that WUE was positively correlated with the indeterminate growth habit. According to a review by Gerik et al. (1995), relatively little progress had been made in increasing productivity of cotton or other crops per unit of water, i.e. by enhanced WUE, even though dryland and irrigated yields have increased. These yield increases have been mainly due to improved partitioning of carbohydrate to fruit (Gifford et al., 1984).

Water use efficiency can vary by leaf age, node, and fruiting position, with variations occurring from one leaf to another in a cotton plant (Rawson and Constable, 1980; Wullschleger and Oosterhuis, 1989; Quisenberry et al., 1976; Quisenberry et al., 1991). Leaf shape, surface features, and position in the canopy can influence WUE. Picotte et al. (2007) using isotope discrimination reported that WUE was increased in plants with smaller, narrower leaves that had
higher trichome densities. Loveys et al. (2004) maintained that changes in leaf size may change the CO$_2$ and H$_2$O fluxes in and out of the leaf due to modification in the boundary layer. Differences in leaf thickness could significantly affect WUE, with thinner leaves decreasing WUE (Stanhill, 1980). Rapid leaf development in annuals influences WUE due to more efficient use of soil water through minimizing surface evaporation (Lopez-Castaneda, 1996). Leaves shaded in the canopy may have greater WUE than leaves in the sun, as was shown for *Betula pendula* (Sellin et al., 2011), because of more conservative stomatal behavior and lower hydraulic conductance. There has not been any related work on cotton. Diaphloiotropic leaves, that track the sun, like in cotton can increase carbon gain and WUE while not intensifying photo inhibition (Zhang et al., 2009). These diaphloiotropic leaf movements of cotton may reduce heat stress under dry conditions (Wang et al., 2004), which could improve WUE.

Cultural practices have been shown to have an effect on WUE in some cases. Raven et al. (2004) concluded that restricted availability of soil nutrients decreases, or frequently has no effect, on plant WUE, mainly because decreased growth rate parallel decreased WUE. Ahmed et al. (1990) reported that WUE improved with increasing Zn fertilization through enhanced gas exchange. Blum (2005) said that maximizing soil moisture use is a crucial component of drought resistance and generally expressed in lower WUE. Salinity has also been shown to decrease both photosynthesis and transpiration (Hoffman and Phene, 1971) resulting in lower WUE indicating an effect on stomatal aperture. Additionally, failure to control insect pests in cotton early in the season results in yield losses and lower WUE (Jordan, 1986).

### AMELIORATION OF WATER-STRESS DEFICIT

Alleviation of water-deficit stress through management practices such as early planting and irrigation has been known to farmers for a long time. Recent technological advances have provided scientists with a better understanding of the physiology of crops, thereby enabling them to make predictions and schedule management practices to minimize yield losses due to water stress.

### Plant Growth Regulators

Amelioration of water-stress deficit through the use of plant growth regulating (PGR) substances has been suggested as a potential solution to water-deficit stress. Glycine betaine, a quaternary ammonium compound that is naturally accumulated in higher plants, has been shown to protect functional enzymes and lipids of the plant photosynthetic apparatus and maintain electron flow through thylakoid membranes (Xing and Rajashekar 1999; Allakverdiev et al., 2003). Foliar application of glycine betaine has been reported to enhance drought tolerance and yield in maize (Agboma et al., 1997a), tomato (Makela et al., 1998), tobacco (Agboma et al., 1997b), and wheat (Diaz-Zarita et al., 2001). In cotton however, there are contrasting results depending upon the growing region. For instance, Gorham et al. (2000) found that glycine betaine aids in drought tolerance of cotton grown in Pakistan, while Meek et al. (2003) reported that foliar application of glycine betaine in Arkansas had no significant effect on yield.

Salicylic acid, a plant hormone that has been shown to increase the production of antioxidants, has also been observed to induce drought tolerance and improve yield in wheat (Singh...
PGR-IV is a plant growth regulator that contains gibberellic acid (GA) and indolebutyric acid (IBA) that has been reported to increase root growth, nutrient uptake, boll retention and lint yield of well-watered cotton (Hickey, 1992; Oosterhuis, 1995; Oosterhuis and Zhao, 1994). In a 4-year field study, foliar application of PGR-IV was shown to increase yield under dryland conditions (Livingston et al., 1992). Zhao and Oosterhuis (1997) conducted growth chamber experiments and indicated that application of PGR-IV before the onset of water stress could result in enhanced photosynthesis and dry matter accumulation. The increase in photosynthesis was attributed to either an increase in the nutrient absorption or improved carbohydrate translocation (Oosterhuis, 1995).

1-Methylcyclopentane (1-MCP), an ethylene inhibitor (Binder and Bleecker, 2003) has also been demonstrated to have a positive effect on stomatal resistance of water-stressed cotton leaves but with no significant changes in yield (Kawakami et al., 2010). However, in another experiment, no significant effect of 1-MCP application on leaf stomatal conductance was observed in cotton plants experiencing water stress during flowering (Loka and Oosterhuis, 2011). However, the sucrose concentrations of water-stressed pistils though were lower compared to the control indicating that 1-MCP may improve the activity of sucrose cleaving enzymes resulting in better utilization of pistil carbohydrates.

It would appear that the use of PGRs has the potential to ameliorate water-deficit stress in cotton production. However, there is insufficient information on the use of these chemicals for such a purpose, specifically, how they influence metabolism to offset the adverse effect of drought and help maintain yield potential.

### Selection for Drought Tolerant Genotypes

Drought tolerance is a quantitative trait, which means that it is controlled by more than one gene and has a complex inheritance. Since cotton originates from areas that are often exposed to water-deficit stress, considerable genetic variability in drought tolerance exists (Saranga et al., 1998b; Pettigrew and Meredith, 1994; Quisenberry et al., 1981). Past research focused on physiological traits such as photosynthesis and stomatal conductance (Leidi et al., 1993; Nepomuceno et al., 1998; Jones et al., 1999), transpiration rates (Quisenberry et al., 1982; Leidi et al., 1993), canopy temperature (Hatfield and Quisenberry, 1987; Jackson et al., 1988), specific leaf weight (Morey et al., 1974; Kumar et al., 1987, Lopez et al., 1995), excised leaf water loss (Roark et al., 1975; Quisenberry et al., 1982), leaf turgor maintenance (Quisenberry et al., 1983), leaf carbon isotope discrimination (Yakir et al., 1990; Saranga et al., 1998a, 1999; Leidi et al., 1999), leaf and root osmotic adjustment (Wullschleger and Oosterhuis, 1987; Nepomuceno et al., 1998; Saranga et al., 2001), leaf fluorescence (Burke, 2007; Longenberger et al., 2009), WUE (Quisenberry and McMichael, 1991; Saranga et al., 1998, 1999), biomass accumulation (Quisenberry et al., 1981; Hatfield et al., 1987), root growth and root-to-shoot ratio (Quisenberry et al., 1981; Cook, 1985; McMichael and Quisenberry, 1991), cell membrane stability (Rahman et al., 2008) and fruiting habit (Burke et al., 1985a; Sharp and Davies, 1989; Lopez et al., 1995). However, none of the above physiological traits has so far been consistently correlated positively with drought toler-
Molecular studies have also been conducted for identifying quantitative trait loci (QTLs) responsible for improved cotton production under water limiting conditions (Saranga et al., 2004, 2008) while use of genetic engineering and transgenic plants has been shown to result in helpful correlations (Lv et al., 2007; Parkhi et al., 2009).

**SUMMARY**

Water-deficit stress has a significant effect on cotton’s growth and development, with primary affects on plant structure, leaf morphology and cell ultrastructure. Physiological processes such as stomatal conductance, photosynthesis and respiration are consequently impaired with further implications on the metabolic functions such as carbohydrate and energy production as well as carbohydrate translocation and utilization. Even though cotton possesses mechanisms to anticipate the negative effects of water-deficit stresses (i.e., accumulation of antioxidants, osmolytes and heat shock proteins) their protective capacity depend not only on the extent of the stress, but also on the timing of the stress as well as on the way the stress occurs (sudden or gradual). Yield reductions and fiber quality compromises are inescapable when water-deficit stress conditions override the plant’s protective mechanisms. However, advances are being made at the physiological level entailing identification of exogenous or endogenous substances that can ameliorate the negative effects of drought and at the molecular level identification of genes involved with increased drought tolerance.

**REFERENCES**


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