Chapter 3

WATER-DEFICIT STRESS IN COTTON

Dimitra A. Loka[1], Derrick M. Oosterhuis[1], and Glen L. Ritchie[2]
[1]Department of Crop, Soil, and Environmental Sciences
University of Arkansas, Fayetteville, AR 72704
[2]Department of Plant and Soil Science
Texas Tech University, Lubbock, TX 79409

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 Mc-Michael 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).

Plant Part	Treatment	
	Drought	Control
Plant height (cm)	20.0*	27.9
Stem dry weight (g)	1.13*	1.39
Leaf dry weight (g)	1.41*	2.16
Leaf area (cm^2)	56*	153
Node number	7.8*	9.4

* 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 inter-related. Cellular water content largely controls stomatal aperture, and stomatal conductance directly affects CO_2 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.
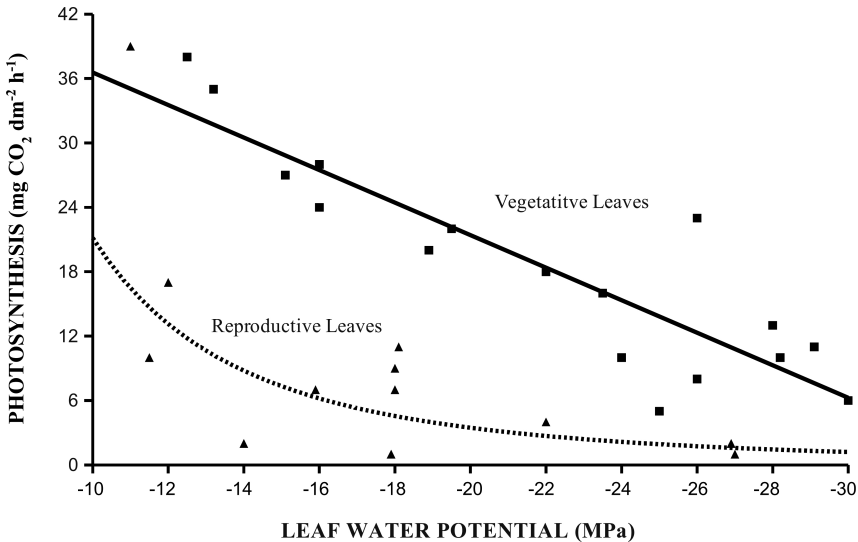

Figure 1. Relationship between photosynthesis and leaf water potential of vegetative and reproductive cotton leaves. (Redrawn from Ackerson *et al*., 1977a).

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/oxidase (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 (ΦPSII) 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 ΦPSII 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 (Krômer, 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 were 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.
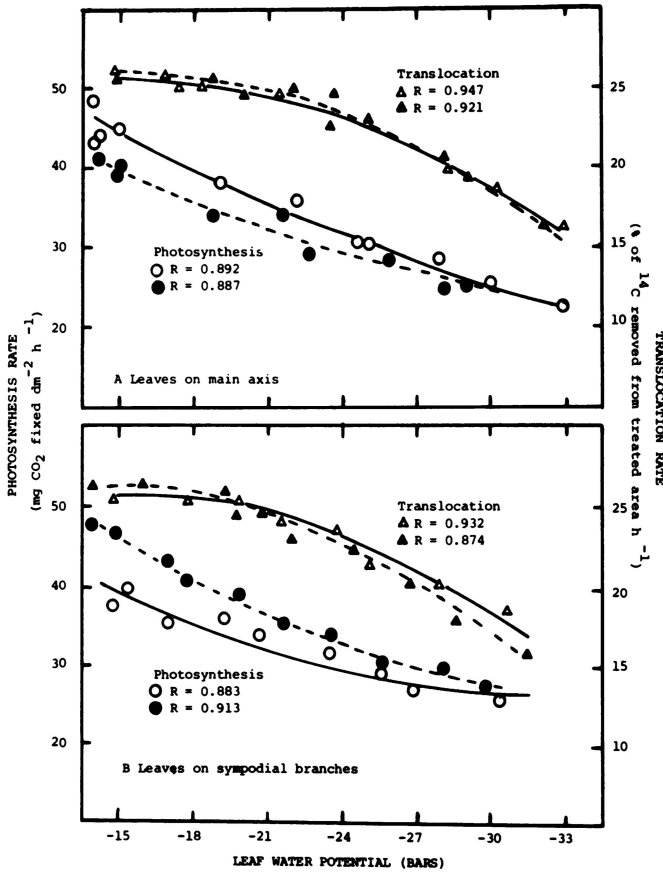

Figure 2. Response of photosynthesis and translocation rates to increasing water stress in cotton as a function of leaf type and growth stage (○, ▲: flower bud development; ●, △: boll-filling period). (From Sung and Krieg, 1979).

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 CO_2 fixation which leads to higher leakage of electrons to O_2 (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 in-organic 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.
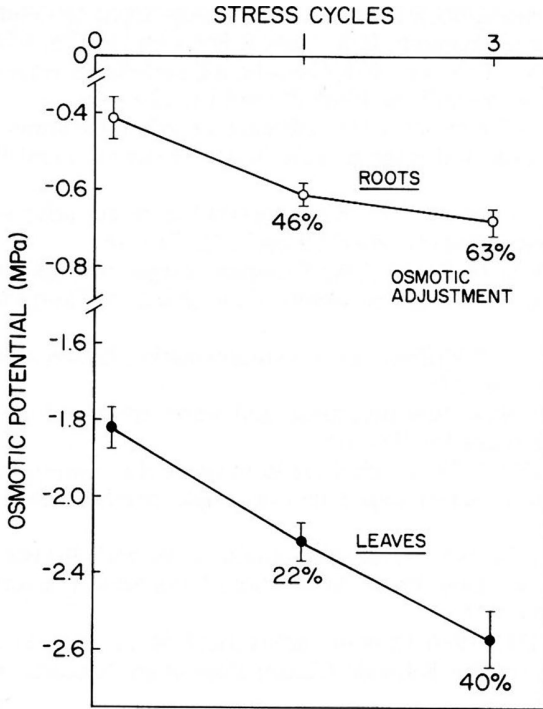
Figure 3. Effect of number of water stress cycles of osmotic adjustment in cotton leaves and roots. The percentage osmotic adjustment was calculated as the percentage decrease in treatment osmotic adjustment compared to the unstressed control. (From Oosterhuis and Wullscheleger, 1987).

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.

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).
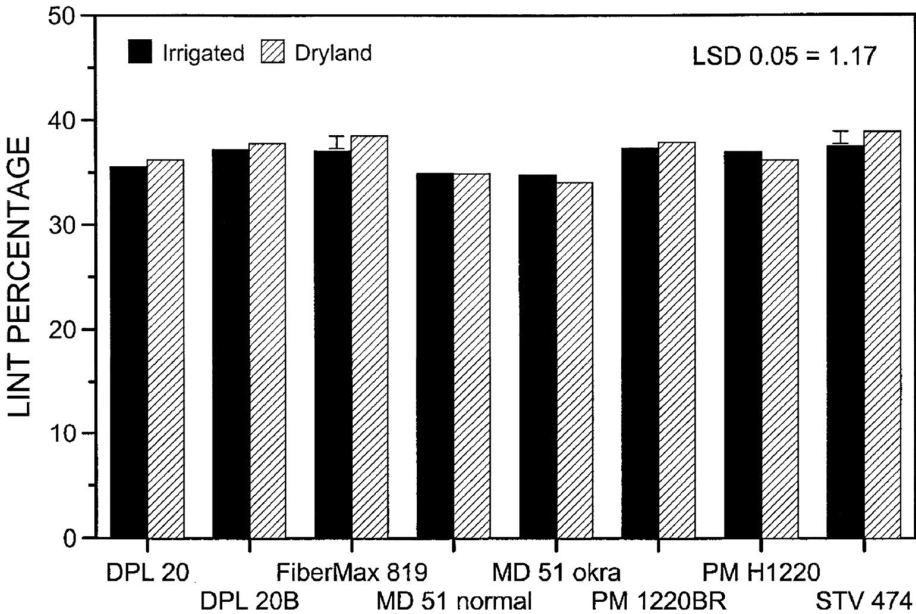

Figure 4. Lint percentage response of eight cotton genotypes when grown under either dryland or irrigated conditions. Genotype means averaged across the years 1998 to 2001. Vertical bars denote LSD values at the 0.05 level and are present only when the differences between soil moisture treatments for the individual genotypes are significant at P=0.05. (From Pettigrew, 2004).

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 CO_2 environments and the increase of intrinsic WUE (Morison, 1993; Drake *et al.*, 1997).

Farquhar and his colleagues pioneered the carbon isotope ratio technique ($\delta^{13}C$), 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 $\delta^{13}C$ discrimination ratio between intercellular and ambient CO_2 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 $\delta^{13}C$ 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_2O 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. Diaheliotropic leaves, that track the sun, like in cotton can increase carbon gain and WUE while not intensifying photoinhibition (Zhang *et al.*, 2009). These diaheliotropic 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

and Usha, 2003; Waseem *et al.*, 2007) and sunflower (Hussain *et al.*, 2008c, 2009). Application of salicylic acid however, has yet to be tested in cotton.

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-Methylcyclopropene (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-

ance. 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

Acevedo, E., T.C. Hsiao, and D.W. Henderson. 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiol. 48:631-636.

Acevedo, E., E. Fereres, T.C. Hsiao, and D.W. Henderson. 1979. Diurnal growth trends, water potential, and osmotic adjustment of maize and sorghum leaves in the field. Plant Physiol. 64:476-480.

Ackerson, R.C., D.R. Krieg, C.L. Haring, and N. Chang. 1977a. Effects of plant water status on stomatal activity, photosynthesis, and nitrate reductase activity of field grown cotton. Crop Sci. 17:81-84.

Ackerson, R.C., D.R. Krieg, T.D. Miller, and R.E. Zartman. 1977b. Water relations of field grown cotton and sorghum: Temporal and diurnal changes in leaf water, osmotic, and turgor potentials. Crop Sci. 17:76.

Ackerson, R.C. 1981. Osmoregulation in cotton in response to water stress. II. Leaf carbohydrate status in relation to osmotic adjustment. Plant Physiol. 67:476-480.

Ackerson, R. C., and R.R. Hebert. 1981. Osmoregulation in cotton in response to water stress. I. Alterations in photosynthesis, leaf conductance, translocation, and ultrastructure. Plant Physiol. 67:484-488.

Addicott, F.T., and R.S. Lynch. 1955. Physiology of abscission. Annu. Rev. Plant Physiol. 6:211-238.

Agboma, P., M.G.K. Jones, P. Peltonen-Sainio, H. Rita, and E. Pehu. 1997a. Exogenous glycine betaine enhances grain yield of maize, sorghum and wheat grown under two watering regimes. J. Agron. Crop Sci. 178:29-37.

Agboma, P., P. Peltonen-Sainio, R. Hikkanen, and E. Pehu. 1997b. Effect of foliar application of glycine betaine on yield components of drought stressed tobacco plants. Exp. Agri. 33:345-352.

Ain-Lhout, F., M. Zunzunegui, M.C.D. Barradas, R. Tirado, A. Clavijo, and F.G. Novo. 2001. Comparison of proline accumulation in two Mediterranean shrubs subjected to natural and experimental water deficit. Plant Soil. 230:175-183.

Allakhverdiev, S.I., H. Hayashi, Y. Nishiyama, A.G. Ivanov, J.A. Aliev, V.V. Klimov, N. Murata, and R. Carpentier. 2003. Glycine betaine protects the D1/D2/Cytb559 complex of PS II against the photo-induced and heat-induced inactivation, J. Plant Physiol. 160:41-49.

Aspinall, D., and L.G. Paleg. 1981. Proline accumulation: physiological aspects. pp. 205-241. In: L.G. Paleg and D. Aspinall (eds.).The Physiology and Biochemistry of Drought Resistance in Plants. Academic Press: Sydney, Australia.

Atkin, O.K., B. Botman, and H. Lambers. 1996. The causes of inherently slow growth in alpine plants; an analysis based on the underlying carbon economies of alpine and lowland Poa species. Funct. Ecol. 10:698-707.

Atkin, O.K., I. Scheurwater, and T.L. Pons. 2007. Respiration as a percentage of daily photosynthesis in whole plants is homeostatic at moderate, but not high growth temperatures. New Phytol. 174:367-380.

Atkin, O.K., and D. Macherel. 2009. The crucial role of plant mitochondria in orchestrating drought tolerance. Ann. Bot. 103:581-597.

Baker, J., C. Steele, and L. Dure. 1988. Sequence and characterization of 6 Lea-proteins and their genes from cotton. Plant Mol. Biol. 11:277-291.

Ball, R.A., D.M. Oosterhuis, and A. Maromoustakos. 1994. Growth dynamics of the cotton plant during water-deficit stress. Agron. J. 86:788-795.

Bennett, O.L., L.J. Erie, A.J. MacKenzie. 1967. Boll, fiber and spinning properties of cotton as affected by management practices. pp. 109. Tech. Bull. No. 1372. USDA. Washington, D.C.

Berlin, J., J.E. Quisenberry, F. Bailey, M. Woodworth, and B.L. McMichael. 1982. Effect of water stress on cotton leaves : I. an electron microscopic stereological study of the palisade cells. Plant Physiol. 70:238-243.

Bielorai, H., and P.A.M. Hopmans. 1975. Recovery of leaf water potential, transpiration, and photosynthesis of cotton during irrigation cycles. Agron. J. 67:629-632.

Binder, B.M., and A.B. Bleecker. 2003. A model for ethylene receptor function and 1-MCP action. Acta Hort. 628, ISHS 2003.

Bjorkman, O., and S.B. Powles. 1984. Inhibition of photosynthetic reactions under water stress: interaction with light level. Planta. 161:490-504.

Blankenship, S.M., and J.M. Dole. 2003. 1-Methylcyclopropene: a review. Postharvest Biol. Technol. 28:1-25.

Bouchereau, A., A. Aziz, F. Larher, and J. Martin-Tanguy. 1999. Polyamines and environmental challenges: recent development. Plant Sci. 140:103-125.

Boyer, J.S. 1970. Leaf enlargement and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. Plant Physiol. 46:233-235.

Boyer, J.S. 1971. Non-stomatal inhibition of photosynthesis in sunflower at low leaf water potentials and high light intensities. Plant Physiol. 48:532-536.

Boyer, J.S. 1982. Plant productivity and environment. Science. 218:443-448.

Boyer, J.S. 1985. Water transport. Annu Rev Plant Physiol. 36:473-516.

Boyer, J.S., and H.G. McPherson. 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27:1-23.

Bondada, B. R.,D. M. Oosterhuis, J. B. Murphy, and K. S. Kim. 1996. Effect of water stress on the epicuticular wax composition and ultrastructure of cotton (*Gossypium hirsutum* L.) leaf, bract, and boll. Environ. Exp. Bot. 36:61-69.

Bondada, B.R., and D.M. Oosterhuis. 2002. Ontogenic changes in epicuticular wax and chloroplast integrity of cotton (*Gossypium hirsutum* L.) leaf. Photosynthetica. 40:431- 436.

Bonhert, H.J., D.E. Nelson, and R.G. Jensen. 1995. Adaptations to environmental stresses. Plant Cell 7:1099-1111.

Bray, E.A. 1993. Molecular responses to water deficit. Plant Physiol. 103: 1035-1040.

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

Bray, E.A., J. Bailey-Serres, and E. Wereltilnyk. 2000. Responses to abiotic stresses. pp: 1158-1249. *In*: W. Gruissem (ed.). Biochemistry and Molecular Biology of Plants. American Society of Plant Physiologists.

Brevedan, E.R., and H.F. Hodges. 1973. Effects of moisture deficits on C14 translocation in corn (Zea mays L.). Plant Physiol. 52:436-439.

Bruce, R. R., and M.J.M. Romkens. 1965. Fruiting and growth characteristics of cotton in relation to soil moisture tension. Agron. J. 57:135-140.

Burke, J.J., P.E. Gamble, J.L. Hatfield, and J.E. Quisenberry. 1985. Plant morphological and biochemical responses to field and water deficits. I. Responses of glutathione reductase activity and paraquat sensitivity. Plant Physiol. 98:1222-1227.

Burke, J.J., J.L. Hatfield, R.R. Klein, and J.E. Mullet. 1985. Accumulation of heat shock proteins in field grown soybean. Plant Physiol. 78:394-398.

Burke, J.J. 2007. Evaluation of source leaf responses to water-deficit stresses in cotton using a novel stress bioassay. Plant Physiol. 143:108-121.

Chaves, M.M., J.S. Pereira, J. Maroco, M.L. Rodriguez, C.P.P. Ricardo, M.L. Osorio, I. Carvalho, T. Faria, and C. Pinheiro. 2002. How plants cope with water stress in the field. Photosynthesis and growth. Ann. Bot. 89:907-916.

Chaves, M.M. and M.M. Oliveira. 2004. Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. J. Exp. Bot. 55:365-384.

Creelman, R.A., H.S. Mason, R.J. Bensen, J.S. Boyer, and J.E. Mullet. 1990. Water deficit and abscisic acid cause differential inhibition of shoot versus root growth in soybean seedlings. Plant Physiol. 92:205-214.

Constable, G.A., and H.M. Rawson. 1980. Effect of leaf position, expansion and age on photosynthesis, transpiration and water use efficiency of cotton. Funct. Plant Biol. 7:89-100.

Constable, G. A., and A.B. Hearn. 1981. Irrigation of crops in a subhumid climate, 6: effects of irrigation and nitrogen fertilizer on growth, yield and quality of cotton. Irrig. Sci. 2:17-28.

Cook, C.G., and K.M. el Zik. 1993. Fruiting of cotton and lint yield of cotton cultivars under irrigated and non-irrigated conditions. Field Crops Res. 33:411-421.

Cornic, G., and A. Massacci. 1996.Leaf photosynthesis under drought stress. pp. 347-366. *In*: N.R. Baker (ed.). Photosynthesis and Environment, Kluwer Academic Publishers.

Cull, P.O., A.B. Hearn, and R.C.G. Smith. 1981a. Irrigation scheduling of cotton in a climate with uncertain rainfall. I. Crop water requirements and response to irrigation. Irrig. Sci. 2:127-140.

Cull, P.O., R.G.C. Smith, and K. McCaffery. 1981b. Irrigation scheduling of cotton in a climate with uncertain rainfall. II. Development and application of a model for irrigation scheduling. Irrig. Sci. 2:141-154.

Cutler, J.M., D.W. Rains, and R.S. Loomis. 1977. Role of changes in solute concentration in maintaining favorable water balance in field grown cotton. Agron. J. 69:773-779.

Cutler, J.M., K.W. Shahan, and P.L. Steponkus. 1980. Dynamics of osmotic adjustment in rice. Crop Sci. 20:310-314.

De Kock, J., L.P. de Bruyn, and J.J. Human. 1993. The relative sensitivity to plant water stress during the reproductive phase of upland cotton. Irrig. Sci. 14:239-244.

De Vries, F.W.T., J.M. Witlage, and D. Kremer. 1979. Rates of respiration and of increase in structural dry matter in young wheat, ryegrass and maize plants in relation to temperature, to water stress and to their sugar content. Ann. Bot. 44: 595-609.

Del Rio, L.A. 1998. The activated oxygen role of peroxisomes in senescence. Plant Physiol. 116:1195-1200.

Desikan, R., J.T. Hancock, M.J. Coffey, and S.J. Neill. 1996. Generation of active oxygen in elicited cells of Arabidopsis thaliana is mediated by an NADPH-oxidase like enzyme. FEBS Lett. 382:213-217.

Dhindsa, R.S., C.A. Beasley, and I.P. Ting. 1975. Osmoregulation in cotton fiber. Accumulation of potassium and malate during growth. Plant Physiol. 56:394-398.

Diaz-Zorita, M., M.V. Fernandez-Canigia, and G.A. Grosso. 2001. Application of foliar fertilizers containing glycine betaine improve wheat yields. J. Agron. and Crop Sci. 186:209-216.

Dohler, G., M. Hoffmann, and U. Stappel. 1995. Pattern of proteins after heat-shock and UV-B radiation of some temperature marine diatoms and the Antarctic odontella. Bot. Acta 108:93-98.

Dumka, D., C.W. Bednarz, and B.W. Maw. 2004. Delayed initiation of fruiting as a mechanism of improved drought avoidance in cotton. Crop Sci. 44:528-544.

Eaton, F.M., and D.R. Ergle. 1948. Carbohydrate accumulation in the cotton plant at low moisture levels. Plant Physiol. 23:169-187.

Eaton, F.M., and D.R. Ergle. 1952. Fiber properties and carbohydrate and nitrogen levels of cotton plants as influenced by moisture supply and fruitfulness. Plant Physiol. 27:542-562.

Eaton, F.M., and G.O. Belden. 1929. Leaf temperatures of cotton and their relation to transpiration, varietal differences, and yields. USDA Tech. Bull.91, p.40.

Ehleringer, J.R. 1989. Carbon isotope ratios and physiological processes in arid land plants. p. 41-54. *In* P.W. Rundel *et al.* (ed.) Stable Isotopes in Ecological Research. Springer-Verlag, New York.

Ehleringer, J.R., A.E. Hall, and G.D. Farquhar (ed.) 1993. Stable Isotopes and Plant Carbon-Water Relations. Academic Press: San Diego, Calif.

Ennahli, S. and H.J. Earl. 2005. Physiological limitations to photosynthetic carbon assimilation in cotton under water stress. Crop Sci. 45:2374-2382.

Ephrath, J. E., A. Marani, and B.A. Bravdo. 1990. Effects of moisture stress on stomatal resistance and photosynthetic rate in cotton (*Gossypium hirsutum* L.) I. Controlled levels of stress. Field Crops Res. 23:117- 131.

Ephrath, J.E., A. Marani, and B.A. Bravdo. 1993. Photosynthetic rate, stomatal resistance and leaf water potential in cotton (*Gossypium hirsutum* L.) as affected by soil moisture and irradiance. Photosynthetica. 29:63-71.

Faria, T., M. Vaz, P. Schwanz, A. Polle, J.S. Pereira, and M.M. Chaves. 1997. Responses of photosynthetic and defense systems to high temperature stress in Quercus suber seedlings grown under elevated CO_2. Plant Biol. 1:365-371.

Farquhar, G.D., M.C. Ball, S. Von Caemmerer, and Z. Roksandic. 1982 . On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol. 9:121-137.

Faver, K.L., T.J. Gerik, P.M. Thaxton, and K.M. El-Zik. 1996. Late season water stress in cotton: II. Leaf gas exchange and assimilation capacity. Crop Sci. 36:922-928.

Flexas, J., and H. Medrano. 2002. Drought-inhibition of photosynthesis in C3 plants: Stomatal and non-stomatal limitations revisited. Ann. Bot. 89:183-189.

Flexas, J., J. Bota, F. Loreto, G. Cornic, T.D. Sharkey. 2004a. Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. Plant. Biol. 6: 269-279.

Flexas, J., J. Bota, J. Galmes, H. Medrano, and M. Ribas-Carbo. 2006. Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. Physiol. Plant. 127:343-352.

Flexas, J., A. Diaz-Espejo, J. Galmes, R. Kaldenhoff, H. Medrano, and M. Ribas-Carbo. 2007. Rapid variations of mesophyll conductance in response to changes in CO_2 concentration around leaves. Plant Cell Environ. 30:1284-1298.

Flexas, J., M. Ribas-Carbo, A. Diaz-Espejo, J. Galmes, and H. Medrano. 2008. Mesophyll conductance to CO2: current knowledge and future prospects. Plant Cell Environ. 31:601-612.

Foyer, C.H., H. Lopez-Delgado, J.F. Dat, and I.M. Scott. 1997. Hydrogen peroxide and glutathione-associated mechanisms of acclamatory stress tolerance and signaling. Annu. Plant Rev. 22:325-346.

Garray-Arroyo, A., J.M. Colmenero, A. Garciarrubio, and A. A. Covarrubias. 2000. Highly hydrophilic proteins in prokaryotes and eukaryotes are common during conditions of water deficit. J. Biol. Chem. 275:5668-5674.

Gardner, W.R., and H.R. Gardner. 1983. Principles of water management under drought conditions. Agric. Water Manage. 7:143-155.

Gaspar, T., T. Franck, B. Bisbis, C. Kevers, L. Jouve, J.F. Hausman, and J. Dommes. 2002. Concepts in plant stress physiology. Application to plant tissue cultures. Plant Growth Regul. 37:263–285.

Genty, B., J.M. Briantais, and J.B. Vieir Da Silva. 1987. Effects of drought on primary photosynthetic processes of cotton leaves. Plant Physiol. 83:360-364.

Gerik, T.J., K.L. Faver, P.M. Thaxton, and K.M. El-Zik. 1996. Late season water stress in cotton: I. Plant growth, water use and yield. Crop Sci. 36:914-921.

Gerik, T.J., J.R. Gannaway, K.M. El-Zik, K.M. Faver, and P.M. Thaxton. 1996. Identifying high yield cotton varieties with carbon isotope analysis. pp. 1297-1300. *In*: Proc. Beltwide Cotton Prod. Res. Conf. Natl. Cotton Counc. Am. Memphis, Tenn.

Ghashgaie, J., M. Duranceau, F.W. Badeck, G. Cornic, M.T. Adeline, and E. Deleens. 2001. $\delta^{13}C$ of CO_2 respired in the dark in relation to $\delta^{13}C$ of leaf metabolites: comparison between Nicotiana sylvestris and Helianthus annuus under drought. Plant Cell Environ. 24:505-515.

Gifford, R.M., J.H. Thorne, W.D. Hitz., and R.T. Giaquinta. 1984. Crop productivity and photoassimilate partitioning. Science. 225:801-808.

Gimenez, C., V.J. Mitchell, and D.W. Lawlor. 1992. Regulation of photosynthetic rate of two sunflower hybrids under water stress. Plant Physiol. 98:516-524.

Gorham, J., J. Jokinen, N.A. Malik, and I.A. Khan. 2000. Glycine betaine treatment improves cotton yields in field trials in Pakistan. pp. 624-627. *In*: Proc. World Cotton Res. Conf. II. Athens, Greece.

Grimes, D.W., W.L. Dickens, and W.D. Anderson. 1969. Functions for cotton (Gossypium hirsutum L.) production from irrigation and nitrogen fertilization variables. II. Yield components and quality characteristics. Agron. J. 61:773-776.

Grimes, D.W., and H. Yamada. 1982. Relation of cotton growth and yield to minimum leaf water potential. Crop Sci. 22:134-139.

Guinn, G. 1976. Water deficit and ethylene evolution by young cotton bolls. Plant Physiol. 57:403-405.

Guinn, G. 1981. Fruit age and changes in abscisic acid content, ethylene production, and abscission rate of cotton fruits. Plant Physiol. 69:349-352.

Guinn, G. and J.R. Mauney. 1984. Moisture effects on cotton. I. Effects of moisture status on flowering. Agron. J. 76:90-94.

Guinn, G. and J.R. Mauney. 1984. Fruiting of cotton. II. Effects of plant moisture status and active boll load on boll retention. Agron. J. 76:94-98.

Guinn, G., J.R. Dunlap, and D.L. Brummett. 1990. Influence of water deficits on the abscisic acid and indole-3-acetic acid contents of cotton flower buds and flowers. Plant Physiol. 93:1117-1120.

Guinn, G., and D.L. Brummett. 1988. Changes in free and conjugated indole-3-acetic acid and abscisic acid in young cotton fruits and their abscission zones in relation to fruit retention during and after moisture stress. Plant Physiol. 86:28-31.

Gutstein, Y. 1969. Relationship between row spacing, depth of root penetration and water use efficiency and the reproductive yield of dryland cotton. Qual. Plant Water. Veg. 17:347-366.

Hare, P.D., W.A. Cress, and J.V. Staden. 1998. Dissecting the roles of osmolyte accumulation during stress. Plant Cell Environ. 21:535-553.

Harris, D.G. 1973. Photosynthesis, diffusion resistance and relative plant water content of cotton as influenced by induced water stress. Crop Sci. 13:570-572.

Harris, K. and R.S. Hawkins. 1942. Irrigation requirements of cotton on clay loam soils in the Salt River Valley. Arizona Agric. Exp. Sta. Bulletin No. 181.

Hartt, C.E. 1967. Effect of moisture supply upon translocation and storage of 14C in sugarcane. Plant Physiol. 42:338-346.

Hatfield, J.L., J.E. Quisenberry, and R.E. Dilbeck. 1987. Use of canopy temperature to identify water conservation in cotton germplasm. Crop Sci. 26:269-273.

Hearn, A.B. 1972. Cotton spacing experiments in Uganda. J. Agric. Sci. 78:13-25.

Hearn, A.B. 1979. Water relationships in cotton. Outlook in Agricutlure. 10:159-166.

Hearn, A.B. 1994. The principles of cotton water relations and their application in management. pp. 66-92. *In*: Constable G.A., and N.W. Forrester (eds.), Challenging the Future. Proc. World Cotton Conf. Brisbane, Australia.

Heitholt, J.J., and J.H. Schmidt. 1994. Receptacle and ovary assimilate concentrations and subsequent boll retention in cotton. Crop Sci. 34:125-131.

Henson, I.E., V. Mahalakshmi, F.R. Bidinger, and G. Alagarswamy. 1982. Osmotic adjustment to water stress in pearl millet under field conditions. Plant Cell Environ 5:147-154.

Hickey, J.A. 1991. Increasing fruit set, relation, and yield in cotton with PGR-IV. pp.78-79. *In* D.J. Herber and D.A. Richter, eds. Proc. of the Beltwide Cotton Prod. Res. Conf. Natl. Cotton Counc. Am., Memphis, Tenn.

Hsiao, T.C. 1973. Plant responses to water stress. Annu. Rev. Plant Physiol. 24: 519-570.

Hsiao, T.C., E. Acevedo, E. Fereres, and D.W. Henderson. 1976. Stress metabolism: Water stress, growth and osmotic adjustment. Phil. Trans. R. Soc. Lond. B. 273:479-500.

Huber, S.C., H.H. Rogers, and F.L. Mowry. 1984. Effects of water stress on photosynthesis and carbon partitioning in soybean (*Glycine max* L.) plants grown in the field at different CO_2 levels. Plant Physiol. 76:244-249.

Hubick, K.T., and G.D. Farquhar. 1989. Carrbon isotope discrimination and the ratio of carbon gain to water loss in barley cultivars. Plant Cell Environ. 12:795-804.

Hussain, M., M.A. Malik, M. Farooq, M.Y. Ashraf, and M.A. Cheema. 2008a. Improving drought tolerance by exogenous application of glycine betaine and salicylic acid in sunflower. J. Agron. Crop Sci. 194:193-199.

Hussain, M., M. Farooq, K. Jabran, H. Rehman, and M. Akram. 2008b. Exogenous glycine betaine application improves yield under water limited conditions in hybrid sunflower. Arch. Agron. Soil Sci. 54:557-567.

Inamullah, and A. Isoda. 2005. Adaptive responses of soybean and cotton to water stress II. CO_2 assimilation rate, chlorophyll fluorescence and photochemical reflectance index. Plant Prod. Sci. 8:131-138.

Ingram, J., and D. Bartels. 1996. The molecular basis of dehydration tolerance in plants. Annu. Rev. Plant Physiol. Plant Mol. Biol. 47:377-403.

Jackson, R.D., S.B. Idso, R.L. Reginato, and P.J. Pinter. 1981.Canopy temperature as a crop water stress indicator. Water Resour. Res. 17:1133-1138.

Johnson, R.R., and D.N. Moss. 1976. Effect of water stress on $^{14}CO_2$ fixation and translocation in wheat during grain filling. Crop Sci. 16:697-701.

Jones, M.M., and N.C. Turner. 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. Plant Physiol. 61:122-126.

Jordan, W.R.1986. Water deficits and reproduction. pp.63-73. *In*: J.R. Mauney and J.M. Stewart (ed.). Cotton Physiology. The Cotton Foundation, Memphis, Tenn.

Jordan, W.R. 1970. Growth of cotton seedlings in relation to maximum daily plant-water potential. Agron. J. 62:699-701.

Jordan W.R., and T.J. Ritchie. 1971. Influence of soil water stress on evaporation, root absorption, and internal water status of cotton. Plant Physiol. 48:783–78.

Jordan, W.R., K.W. Brown, and J.C. Thomas. 1975. Leaf age as a determinant in stomatal control of water loss from cotton during water stress. Plant Physiol. 56:595-599.

Kanemasu, E.T., and C.B. Tanner. 1969. Stomatal diffusion resistance of snap beans. I. Influence of leaf water potential. Plant Physiol. 44:1547-1552.

Karami, E., D.R. Krieg, and J.E. Quisenberry. 1980. Water relations and carbon-14 assimilation of cotton with different leaf morphology. Crop Sci. 20:421-426.

Kawakami, E.M., D.M. Oosterhuis, and J.L. Snider. 2010. Physiological effects of 1-Methylcyclopropene on well-watered and water-stressed cotton plants. J. Plant Growth Regul. 29:280-288.

Keller, F., and M.M. Ludlow. 1993. Carbohydrate metabolism in drought-stressed leaves of pigeonpea (*Cajanus cajan*). J. Exp. Bot. 44:1351-1359.

Kimpel, J.A., and J.L. Key. 1985. Presence of heat shock mRNA's in field grown soybean. Plant Physiol. 79:622-678.

Kitao, M., and T.T. Lei. 2007. Circumvention of over-excitation of PSII by maintaining electron transport rate in leaves of four cotton genotypes developed under long-term drought. Plant Biol. 9:69-76.

Krieg, D.R., and F.J.M. Sung. 1986. Source-sink relationships as affected by water stress. pp. 73-78. *In*: J.R. Mauney and J.M. Stewart (eds.). Cotton Physiology. The Cotton Foundation, Memphis, Tenn.

Krieg, D.R. 2000. Cotton water relations. pp. 7-15. *In*: D.M. Oosterhuis (ed). Proc. 2000 Cotton Research Meeting and Summaries of Cotton Research. Arkansas Agric. Exp. Sta., Special Report 198.

Kramer, P.J. 1980. Drought stress and the origin of adaptation. pp. 7-20. *In*: N.C. Turner, and P.J. Kramer (eds.). Adaptation of plants to water and high temperature stress. John Wiley, New York.

Kramer, P.J. 1983. Water deficits and plant growth. pp: 342-389. *In*: P.J. Kramer (ed.). Water relations of plants. Academic Press, New York.

Krômer, S. 1995. Respiration during photosynthesis. Annu. Rev. Plant Physiol. and Plant. Mol. Biol. 46:45-70.

Kuznetsov, V.V., V. Rakitin, and V.N. Zholkevich. 1999. Effects of preliminary heat-shock treatment on accumulation of osmolytes and drought resistance in cotton plants during water deficiency. Physiol. Plant. 107:399-406.

Lacape, M.J., J. Wery, and D.J.M. Annerose. 1998. Relationships between plant and soil water status in five field-grown cotton cultivars. Field Crops Res. 57:29-43.

Lashin, H., A.Raafat, and M. Elkadi. 1970. Fruiting and shedding of cotton as influenced by irrigation frequency and nitrogen level. Z Acker Pflanzenbau. 131:128-140.

Lawlor, D. W., and H. Fock. 1977. Water stress induced changes in the amounts of some photosynthetic assimilation products and respiratory metabolites of sunflower leaves. J. Exp. Bot. 28:329-337.

Lawlor, M.M., and G. Cornic. 2002. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. Plant Cell Environ. 25:275-294.

Lawlor, D.W. 2002. Limitation to photosynthesis in water stressed leaves: stomata vs. metabolism and the role of ATP. Ann. Bot. 89:871-885.

Lawlor, D.W., and W. Tezara. 2009. Causes of decreased photosynthetic rate and metabolic capacity in water deficient leaf cells: a critical evaluation of mechanisms and integration of processes. Ann. Bot. 103:561-579.

Le Houerou, H.N. 1996. Climate changes, drought and desertification. J. Arid. Environ. 34:133-185.

Leidi, E. O., J.M. Lopez, M. Lopez, and J.C. Gutierrez. 1993. Searching for tolerance to water stress in cotton genotypes: photosynthesis, stomatal conductance and transpiration. Photosynthetica. 28:383-390.

Leidi, E.O., J.M. López, J. Gorham, and J.C. Gutiérrez. 1999. Variation in carbon isotope discrimination and other traits related to drought tolerance in upland cotton cultivars under dryland conditions. Field Crops Res. 61:109-123.

Lewis, H., L. May, and F. Bourland. 2000. Cotton yield components and yield stability. pp. 532-536. *In*: Proc. Beltwide Cotton Conf., San Antonio, TX. 4-8 Jan. 2000. Natl. Cotton Counc. of Am., Memphis, Tenn.

Lin, Z.F., and J. Ehleringer. 1982. Effects of leaf age on photosynthesis and water use efficiency of papaya. Photosynthetica. 16:514-519.

Livingston, S.D., D.J. Anderson, L.B. Wilde, and J.A. Hickey. 1992. Use of foliar applications for PIX, PGR-IV and PHCA in low rate multiple applications for cotton improvement under irrigated and dryland conditions. pp.1055-1056. *In*: D.J. Herber and D.A. Richter, (eds.) Proc. of the Beltwide Cotton Prod. Res. Conf. Natl. Cotton Counc. Am., Memphis, Tenn.

Liu, F., C.R. Jensen, and M.N. Andersen. 2004. Drought stress effect on carbohydrate concentration in soybean leaves and pods during early reproductive development: its implication in altering pod set. Field Crops Res. 86:1-13.

Loka, D.A., and D.M. Oosterhuis. 2011. Effect of 1-MCP on the cotton flower under water-deficit stress. *In*: D.M. Oosterhuis (ed.). Summaries of Arkansas Cotton Res. Ark. Agri. Exp. Sta. In press.

Longenberger, P.S., C.W. Smith, S.E. Duke, and B.L. McMichael. 2009. Evaluation of chlorophyll fluorescence as a tool for the identification of drought tolerance in upland cotton. Euphytica. 166:25-33.

Lopez, M., J.C. Gutierrez, and E.O. Leidi. 1995. Selection and characterization of cotton cultivars for dryland production in the South West of Spain. Eur. J. Agron. 4:119-126.

Lopez-Castaneda, C., R.A. Richards, G.D. Farquhar, and R.E. Williamson. 1996. Seed and seedling characteristics contributing to variation in early vigour between wheat and barley. Crop Sci. 36:1257-1266.

Loveys, B.R., M. Stoll, and W.J. Davies. 2004. Physiological approaches to enhance water use efficiency in agriculture: exploiting plant signaling in novel irrigation practice. pp. 113-141. *In*: M.A. Bacon (ed.) Water Use Efficiency in Plant Biology. Blackwell Publishing, Oxford, and CRC Press, Boca Raton.

Lu, Z., J. Chen, R.G. Percy, M.R. Sharrifi, P.W. Rundel, E. Zeiger. 1996. Genetic variation in carbon isotope discrimination and its relation to stomatal conductance in Pima cotton (*Gossypium barbadense* L.). Aust. J. Plant Physiol. 23:127-132.

Lv, S., A. Yang, K. Zhang, L. Wang, and J. Zhang. 2007. Increase of glycine betaine synthesis improves drought tolerance in cotton. Mol. Breed. 20:233-248.

Mahan, J.R., and D.F. Wanjura. 2005. Seasonal patterns of glutathione and ascorbate metabolism in field-grown cotton under water stress. Crop Sci. 45:193-201.

Makela, P., K. Jokinen, M. Kotturi, P. Peltonen- Sainio, E. Pheu, and S. Somersalo. 1998. Foliar application of glycine betaine a novel product from sugar beet as an approach to increase tomato yield. Ind. Crops. Prod. 7:139-148.

Malik, R.S., J.S. Dhankar, and N.C. Turner. 1979. Influence of soil water deficits on root growth of cotton seedlings. Plant Soil. 53:109-115.

Marani, A., and A. Amirav. 1971. Effects of soil moisture stress on two varieties of upland cotton in Israel. The Coastal Plain Region. Exp. Agric. 7:213-224.

Massaci, A., S.M. Nabiev, L. Petrosanti, S.K. Nematov, T.N. Chernikova, K. Thor, and J. Leipner. 2008. Response of the photosynthetic apparatus of cotton (*Gossypium hirsutum* L.) to the onset of drought stress under field conditions studied by gas-exchange analysis and chlorophyll fluorescence imaging. Plant Physiol. Biochem. 46:189-195.

Matsuda, K., and A. Riazi. 1981. Stress-induced osmotic adjustment in growing regions of barley leaves. Plant Physiol. 68:571-576.

McCree, K.J., C.E. Kallsen, and S.G. Richardson.1984. Carbon balance of sorghum plants during osmotic adjustment to water stress. Plant Physiol. 76:898-902.

McMichael, B.L., W.R. Jordan, and R.D. Powell. 1972. An effect of water stress on ethylene production by intact cotton petioles. Plant Physiol. 49:658-660.

McMichael, B.L., W.R. Jordan, and R.D. Powell. 1973. Abscission processes in cotton: Induction by plant water deficit. Agron. J. 65:202-204.

McMichael, B.L., and J.D. Hesketh. 1982. Field investigations of the response of cotton to water deficits. Field Crops Res. 5: 319- 333.

McMichael, B.L., and J.E. Quisenberry. 1991. Genetic variation for root-shoot relationship among cotton germplasm. Environ. Exp. Bot. 31:461-470.

Meek, C., D.M. Oosterhuis, and J. Gorham. 2003. Does foliar applied glycine betaine affect endogenous betaine levels and yield in cotton J. Crop Management p. 9. www.plantmanagementnetwork/pub/cm/research/betaine/

Meek, C.R., D. M. Oosterhuis, and J. M. Stewart. 2010. Physiological and molecular responses of common cotton cultivars under water-deficient conditions. Amer. J. Plant Sci. Biotech. 2:109-116.

Meyer, S., and Y. de Kouchovsky. 1992. ATPase state and activity in thylakoids from normal and water-stressed lupin. FEBS Letters 303:233-236.

Mittler, R. 2002. Oxidative stress, antioxidants, and stress tolerance. Trends Plant Sci. 7:405-410.

Monk, L.S., K.V. Fagernstedt, and R.M.M. Crawford. 1987. Superoxide dismutase as an anaerobic polypeptide. A key factor in the recovery from oxygen deprivation in Iris pseudacorus. Plant Physiol. 95:72-82.

Morgan, J.M. 1984. Osmoregulation and water stress in higher plants. Annu. Rev. Plant Physiol. 35:299-319.

Morgan, J.M. 1987. Differences in osmoregulation between wheat genotypes. Nature. 270:234-235.

Morgan, J.M. 1992. Osmotic components and properties associated with genotypic differences in osmoregulation in wheat. Aust. J. Plant Physiol. 19:67-76.

Nepomuceno, A. L., D.M. Oosterhuis, and J.M. Stewart. 1998. Physiological responses of cotton leaves and roots to water deficit induced by polyethylene glycol. Environ. Exp. Bot. 40: 29-41.

Neumann, D., O. Licthenberger, D. Gunther, K. Tschiersch, and L. Nover. 1994. Heat-shock proteins induce heavy-metal tolerance in higher plants. Planta. 194:360-367.

Noctor G., and C.H. Foyer. 1998. Ascorbate and glutathione: keeping active oxygen under control. Annu. Rev. Plant Physiol. Plant Mol. Biol. 49:249-279.

Oosterhuis, D.M., and S.D. Wullschleger. 1987. Osmotic adjustment in cotton (*Gossypium hisrsutum* L.) leaves and roots in response to water stress. Plant Physiol. 84:1154-1157.

Oosterhuis, D.M. and Wullscheleger, S.D. 1988. Drought tolerance and osmotic adjustment of various crops in response to water stress. Arkansas Farm Res. 37(1):12.

Oosterhuis, D.M., Wullschleger, S.D., and Stewart, J.M. 1987. Osmotic adjustment in commercial cultivars and wild types of cotton. Agronomy Abstracts. p. 97.

Oosterhuis, D.M., R.E. Hampton, and S.D. Wullschleger. 1991. Water deficit effects on cotton leaf cuticle and the efficiency of defoliants. J. Agron. Prod. 4:260-265.

Oosterhuis, D.M., and D. Zhao. 1994. Increased root length and branching in cotton by soil application of the plant growth regulator PGR-IV. Plant Soil. 167:51-56.

Oosterhuis, D.M. 1995. Effects of PGR-IV on the growth and yield of cotton: a review. pp. 29-39. *In* Proc. First World Cotton Research Conf. Brisbane, Australia. CSIRO, Canberra.

Orgaz, F., L. Mateos, and E. Fereres. 1992. Season length and cultivar determine optimum evapotranspiration deficit in cotton. Agron. J. 84:700-706.

Pace, P.F., H.T. Crale, S.H.M. El-Halawany, J.T. Cothren, and S.A. Senseman. 1999. Drought induced changes in shoot and root growth of young cotton plants. J. Cotton Sci. 3:183-187.

Pallas, J.E., B.E. Michel, and D.G. Harris. 1967. Photosynthesis, transpiration, leaf temperature, and stomatal activity of cotton plants under varying water potentials. Plant Physiol. 42:76-88.

Pandey D.M., C.L. Goswami, B. Kumar, and S. Jain. 2002. Effect of growth regulators on photosynthetic metabolites in cotton under water stress. Biol. Plant. 45:445-448.

Papageorgiou, G.G., and N. Murata. 1995. The unusually strong stabilizing effects on glycine betaine on the structure and function in the oxygen evolving photosystem II complex. Photosyn. Res. 44:243-252.

Parida, A.K., V.S. Dagaonkar, M.S. Phalak, G.V. Umalkar, and L.P. Aurangabadkar. 2007. Alterations in photosynthetic pigments, protein and osmotic components in cotton genotypes subjected to short-term drought stress followed by recovery. Plant Biot. Rep. 1:37-48.

Parkhi, V., V. Kumar, G. Sunilkumar, L.M. Campbell, N.K. Singh, and K.S. Rathore. 2009. Expression of apoplastically secreted tobacco osmotin in cotton confers drought tolerance. Mol. Breed. 23:625-639.

Pelham, H. 1986. Speculations on the major heat shock and glucose regulated proteins. Cell 46: 959-961.

Pettigrew, W.T. 2004. Moisture deficit effects on cotton lint yield, yield components, and boll distribution. Agron. J. 96:377-383.

Pettigrew, W.T. 2004. Physiological consequences of moisture deficit stress in cotton. Crop Sci. 44:1265-1272.

Pettigrew, W.T., and W.R. Meredith. 1994. Leaf gas exchange parameters vary among cotton genotypes. Crop Sci. 34:700-705.

Pettigrew, W.T., J.J. Heitholt, and K.C. Vaughn. 1993. Gas exchange differences and comparative anatomy among cotton leaf-type isolines. Crop Sci. 33:1295-1299.

Pham Thi, A.T., C. Borrel-Flood, J.V. DaSilva, A.M. Justin, and P. Mazliak. 1985. Effects of water stress on lipid metabolism in cotton leaves. Phytochemistry. 24:723-727.

Pinheiro, C., M.M. Chaves, C.P.P Ricardo. 2001. Alterations in carbon and nitrogen metabolism induced by water deficit in the stem and leaves of *Lupinus albus* L. J. Exp. Bot. 52:1063-1070.

Plaut, Z. and E. Federman. 1991. Acclimation of CO_2 assimilation in cotton leaves to water stress and salinity. Plant Physiol. 97:515-522.

Plaut, Z., M. Ben-Hur, and A. Meiri. 1992. Yield and vegetative growth as related to plant water potential of cotton irrigated with a moving sprinkler system at different frequencies and wetting depths. Irrig. Sci. 13:39-44.

Quisenberry, J.E., and B.L. McMichael. 1991. Genetic variation among cotton germplasm for water-use efficiency. Environ. Exp. Bot. 31:453-460

Quisenberry, J.E., and B. Roark. 1976. Influence of indeterminate growth habit on yield and irrigation water-use efficiency in upland cotton. Crop Sci. 16:762-765.

Quisenberry, J.E., B. Roark, and B.L. McMichael. 1982. Use of transpiration decline curves to identify drought-tolerant cotton germplasm. Crop Sci. 22:918-922.

Quisenberry, J.E., W.R. Jordan, B.A. Roark, and D.W. Fryrear. 1981. Exotic cottons as genetic sources for drought resistance. Crop Sci. 21:889-895.

Rabadia, V.S., V.S. Thaker, and Y.D. Singh. 1999. Relationship between water content and growth of seed and fibre of three cotton genotypes. J. Agron. Crop Sci. 183:255-261.

Radin, J.W. 1984. Stomatal responses to water stress and to abscisic acid in phosphorus-deficient cotton plants. Plant Physiol. 76:392-394.

Radin, J.W., and R.C. Ackerson. 1981. Water relations of cotton plants under nitrogen deficiency: III. Stomatal conductance, photosynthesis, and abscisic acid accumulation during drought. Plant Physiol. 67:115-119.

Radin, J.W., J.R. Mauney, L.L. Reaves, and O.F. French. 1992. Yield enhancement by frequent irrigation during fruiting. Agron. J. 84:551-557.

Radin, J.W. 1992. Reconciling water-use efficiency of cotton in field and laboratory. Crop Sci. 32:13-18.

Rahman, M., I. Ullah, M. Ashraf, J.M. Stewart, and Y. Zafar. 2008. Genotypic variation for drought tolerance in cotton. Agron Sustain. Dev. 28:439-447.

Raymond, P., and A. Pradet. 1983. Adenine nucleotide ratios and adenylate energy charge in energy metabolism. Annu. Rev. Plant Physiol. 34:199-224.

Rawson, H.M., and G.A. Constable. 1980. Carbon production of sunflower cultivars in field and controlled environments. I. Photosynthesis and transpiration of leaves, stems and heads. Aust. J. Plant Physiol. 7:565-573.

Reddell, D.L., J.F. Prochasca, and A.J. Cudrak. 1987. Sequential water stress in cotton: a stress day index model. ASAE 87, 2080, 23.

Reddy, A.R, K.V. Chaitanya, and M. Vivekanandan. 2004. Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. J. Plant Physiol. 161:1189-1202.

Reddy, V.R., K.R. Reddy, and H.F. Hodges. 1995. Carbon dioxide enrichment and temperature effects on cotton canopy photosynthesis, transpiration, and water-use efficiency. Field Crops Res. 41:13-23.

Reich, P.B., A.W. Schoettle, and R.G. Amundson. 1985. Effects of low concentrations of O_3, leaf age and water stress on leaf diffusive conductance and water use efficiency in soybean. Physiol. Plant. 63:58-64.

Ribas-Carbo, M., N.L. Taylor, L. Giles, S. Busquets, P.M. Finnegan, and D.A. Day. 2005. Effects of water stress on respiration in soybean leaves. Plant Physiol. 139:466-473.

Ritchie, G.L., J.R. Whitaker, C.W. Bednarz, and J.E. Hook. 2009. Subsurface drip and overhead irrigation of cotton: A comparison of plant boll distribution in upland cotton. Agron. J. 101:1336-1344.

Rhodes, D., and A.D. Hanson. 1993. Quaternary ammonium and tertiary ammonium compounds in higher plants. Ann. Rev. Plant Physiol. Plant Mol. Biol. 44:357-384.

Roark, B., J.E. Quisenberry, and J.E. Friesen. 1975. Rate of water loss from detached leaves of cultivars of upland cotton.p.72. *In*: Proc. Beltwide Cotton Prod. Res. Conf., Natl. Cotton Counc. of Am., Memphis, Tenn.

Roark, B., and J.E. Quisenberry. 1977. Evaluation of cotton germplasm for drought resistance. p. 49-50. *In*: Proc. Betlwide Cotton Prod. Res. Conf. Natl.Cotton Counc. Am., Memphis, Tenn.

Rosenow, D.T., J.E. Quisenberry, C.W. Wendt, and L.E. Clark. 1983. Drought tolerant sorghum and cotton germplasm. Agric. Water Manage. 7:207-222.

Saini, H.S. 1997. Injuries to reproductive development under water stress, and their consequences for crop productivity. J. Crop Prod. 1:137-144.

Saini, H.S., and M.E. Westgate. 2000. Reproductive development in grain crops during drought. Adv. Agron. 68:59-96.

Sakamoto, A., and N. Murata. 2002. The role of glycine betaine in the protection of plants from stress: clues from transgenic plants. Plant Cell Environ. 25:163-171.

Saranga, Y., N. Sass, Y. Tal, and R. Yucha. 1998. Drought conditions induce mote formation in interspecific cotton hybrids. Field Crops Res. 55:225-234.

Saranga, Y., I. Flash, and D. Yakir. 1998. Variation in water-use efficiency and its relation to carbon isotope ratio in cotton. Crop Sci. 38:782-787.

Saranga, Y., I. Flash, A.H. Paterson, and D. Yakir. 1999. Carbon isotope ratio in cotton varies with growth stage and plant organ. Plant Sci. 142:47-56.

Saranga, Y., C.X. Jiang, R.J. Wright, D. Yakir, and A.H. Paterson. 2004. Genetic dissection of cotton physiological responses to arid conditions and their inter-relationships with productivity. Plant Cell Environ. 27:263-277.

Schussler, J.R., and M.E. Westgate. 1991. Maize kernel set at low water potential. II. Sensitivity to reduced assimilates at pollination. Crop Sci. 31: 1196-1203.

Schussler, J.R., and M.E. Westgate. 1995. Assimilate flux determines kernel set at low water potential in maize. Crop Sci. 35:1074-1080.

Sharkey, T.D., and J.R. Seeman. 1989. Mild water stress effects on carbon reduction cycle intermediates, ribulose bisphosphate carboxylase activity, and spatial homogeneity in intact leaves. Plant Physiol. 89:1060-1065.

Sheoran, I.S., and H.S. Saini. 1996. Drought induced male sterility in rice. Changes in carbohydrate levels and enzyme activities associated with inhibition of starch accumulation in pollen. Sex Plant Reprod. 9:161-169.

Singh, S.P. 1975. Studies on the effects of soil moisture stress on the yield of cotton. Indian J. Plant Physiol. 18:49-55.

Singh, B., and K. Usha. 2003. Salicylic acid induced physiological and biochemical changes in wheat seedlings under water stress. Plant Growth Regul. 39:137-141.

Smirnoff, N. 1993. The role of active oxygen in the responses of plants to water deficit and desiccation. New Phytol. 125:27-58.

Socias, F.X., M.J. Correia, M.M. Chaves, and H. Medrano. 1997. The role of abscisic acid and water relations in drought responses of subterranean clover. J. Exp. Bot. 48:1281-1288.

Stockton, J. R., L.D. Doneen, and V.T. Walhood. 1961. Boll shedding and growth of the cotton plant in relation to irrigation frequency. Agron. J. 53:272-275.

Sun, W., M.V. Montagu, and N. Vebruggen. 2002. Small heat shock proteins and stress tolerance in plants. Biochem. Biophys. Acta. 1577:1-9.

Sung, F.J.M., D.R. Krieg. 1979. Relative sensitivity of photosynthetic assimilation and translocation of 14C to water stress. Plant Physiol. 64:852-856.

Tezara, W., V.J. Mitchell, S.D. Driscoll, D.W. Lawlor. 1999. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. Nature. 401:914-917.

Timpa, J.D., J.J. Burke, J.E. Quisenberry, and C.W. Wendt. 1986. Effects of water stress on the organic acid and carbohydrate composition of cotton plants. Plant Physiol. 82:724-728.

Turner, N.C. Further progress in crop water relations. Adv. Agron. 58:293-338.

Turner, N.C., J.E. Begg, and M.L. Tonnett. 1978. Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on the water potential at which stomata close. Aust. J. Plant Physiol. 5:597-608.

Turner, N. C., and P.J. Kramer, (eds.) 1980. Adaptation of Plants to Water and High Temperature Stress. Wiley, New York.

Turner, N.C., A.B. Hearn, J.E. Begg, and G.A. Constable. 1986. Cotton (*Gossypium hirsutum* L.) physiological and morphological responses to water deficits and their relationship to yield. Field Crops Res. 14:153-170.

Trolinder, N.L., B.L. McMichael, and D.R. Upchurch. 1993. Water relations of cotton flower petals and fruits. Plant Cell Environ. 16:755-760.

Van Iersel, M.W., and D.M. Oosterhuis. 1996. Drought effects of the water relations of cotton fruits , bracts and leaves during ontogeny. Exp. Environ. Bot. 36:51-59.

Vierling, E. 1991. The role of heat shock proteins in plants. Annu. Rev. Plant Physiol. Plant Mol. Biol. 42:579-620.

Wardlaw, I.F. 1967. The effect of water stress on translocation in relation to photosynthesis and growth. I. Effect during grain development in wheat. Aust. J. Biol. Sci. 20: 25-39.

Warren, C.R., N.J. Livingston, and D.H. Turpin. 2004. Water stress decreases the transfer conductance of Douglas-fir (*Pseudotsuga menziensii*). Tree Phys. 24:971-979.

Waseem, M., H.U. Athar, and M. Ashraf. 2006. Effect of salicylic acid applied through rooting medium on drought tolerance of wheat. Pak. J. Bot. 38:1127-1136.

Weber, H., U. Heim, S. Golombek, L. Borisjuk, U. Wobus. 1998. Assimilate uptake and the regulation of seed development. Seed Sci. Res. 8:331-345.

Whitaker, J.R., G.L. Ritchie, C.W. Bednarz, and C.I. Mills. 2008. Cotton subsurface drip and overhead irrigation efficiency, maturity, yield, and quality. Agron. J. 100:763-768.

Wilson, R.F., J.J. Burke, and J.E. Quisenberry. 1987. Plant morphological and biochemical responses to field water deficits. II. Responses of leaf glycerolipid composition in cotton. Plant Physiol. 84:251-254.

Wullschleger, S.D., and D.M. Oosterhuis. 1989. Water use efficiency as a function of leaf age and position within the cotton canopy. Plant Soil 120:79-85.

Wullschleger, S.D., and D.M. Oosterhuis. 1990. Photosynthetic and respiratory activity of fruiting forms within the cotton canopy. Plant Physiol. 94:463-469.

Wullschleger, S.D., and D.M. Oosterhuis. 1991. Photosynthesis, transpiration, and water-use efficiency of cotton leaves and fruit. Photosynthetica. 25:505-515.

Xing, W., and C.B. Rajasekar. 1999. Alleviation of water stress in beans by exogenous glycine betaine. Plant Sci. 148:185-195.

Yakir, D., M.J. DeNiro, and J.E. Ephrath. 1990. Effects of water stress on oxygen, hydrogen and carbon isotope ratios in two species of cotton plants. Plant Cell Environ. 13:949-955.

Yancey, P.H., M.E. Clark, S.C. Hand, R.D. Bowlus, G.N. Somero. 1982. Living with water stress: evolution of osmolyte systems. Science 217:1214-1222.

Yang, J., S. Peng, S.Gu, R.M. Visperas, and Q. Zhu. 2001a. Changes in activities of three enzymes associated with starch synthesis in rice grains during grain filling. Acta Agron. Sin. 27:157-164.

Yang, J., J. Zhang, Z. Wang, Q. Zhu, L. Liu. 2001b. Water-deficit induced senescence and its relationship to the remobilization of pre-stored carbon in wheat during grain filling. Agron. J. 93:196-206.

Younis, H.M., J.S. Boyer, and Govindjee. 1979. Conformation and activity of chloroplast factor exposed to low chemical potential of water in cells. Bioch. Biophys. Acta. 548:328-340.

Zhao, D., and D.M. Oosterhuis. 1997. Physiological response of growth chamber-grown cotton plants to the plant growth regulator PGR-IV under water-deficit stress. Environ. Exp. Bot. 38:7-14.

Zhu, J. P.M. Hasegawa, and R.A. Bressan. 1997. Molecular aspects of osmotic stress in plants. Crit. Rev. Plant Sci. 16:253-277.

Zinselmeier, C., J.R. Schussler, M.E. Westgate, and R.J. Jones. 1995. Low water potential disrupts carbohydrate metabolism in maize ovaries. Plant Physiol. 107:385-391.

Zinselmeier, C., B.R. Jeong, and J.S. Boyer. 1999. Starch and the control of kernel number in maize at low water potentials. Plant Physiol. 121:25-35.

Zur, B., and J.W. Jones. 1984. Diurnal changes in the instantaneous water use efficiency of a soybean crop. Agric. For. Meteorol. 33:41-51.