

Water Stress in Cotton (*Gossypium hirsutum* L.)

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Summary

Among the abiotic stresses, water stress is perhaps the most yield limiting factor in cultivated crops including cotton. A number of studies showed that drought tolerance is complex multi-genic agronomic trait. Previous researchers proposed modifying root systems (robust root), water use efficiency, stomatal conductance, photosynthetic rate, leaf water content, carbon isotope discrimination, canopy temperature (T, °C), initial water content, the rate of excised leaf water loss, and compatible solutes (osmoprotectans) as a selection criterion for drought tolerant cotton improvement program. Thus, if appropriate plant morphology could be combined with the physiological characters for drought tolerant plant model by using crosses or gene transfer method, it could express superior adaptation to dry land environments.

Key words: Cotton, water stress, physiological and morphological mechanisms.

Introduction

Water availability is a determining factor in plant growth and yield of all agricultural commodities. While demands on water resources for agricultural purposes is increasing, declining water availability, changing climate conditions, and increasing human demands are limiting its availability for agriculture (Reddy et al., 1996). Drought tolerance is a complex agronomic trait with multi-genic components which interact in a holistic manner in plant systems (Ingram and Bartels, 1996; Cushman and Bohnert, 2000). Water deficit (drought) is one of the common stress conditions that adversely affect plant growth and yield. Decreasing ground water supplies and high energy cost affect production of irrigated cotton. Therefore, selection for drought tolerance is a major interest of plant breeders in cotton, as

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well as other agricultural commodities. Previous drought tolerant studies have focused on either modifying root systems to increase water use efficiency or determining morpho-physiology of plants, and the effects of plant growth regulators on cotton roots for increasing drought resistance (Bland and Dugas, 1989; Xu and Taylor, 1992; McCarty et al., 1993; Ball et al., 1994; Nepomuceno et al., 1998; Pace et al., 1999; Howard et al., 2001). The process of leaf expansion is affected very early from the water stress, but photosynthetic activity is much less affected. Inhibition of leaf expansion reduces consumption of carbon and energy, and a greater portion of the plant's assimilates can be distributed to the root system. Thus, root growth is less sensitive to drought than shoot growth according to Malik et al. (1979), Ball et al. (1994), and McMichael et al., (1999). Root characteristics can be important in determining the response of plants to drought. Water deficit not only decreases shoot growth rate, plant height, and yield, it also affects root growth. Pace et al. (1999) reported that drought-stressed cotton seedlings showed some increase in root length but reduced diameter. Ball et al. (1994) and Prior et al. (1995) showed that inadequate soil moisture reduced cotton root elongation while Plaut et al. (1996) found reduced root length density at 42 and 70 days after emergence. Malik et al. (1979) reported an effect of drought stress on root distribution for cotton.

The effect of water stress on yield depends on the timing and severity of the drought. Krieg (1997) indicated that the crop growth rate was reduced by water stress through a reduction in size and number of leaves produced and in reduction of photosynthesis. He also indicated that the period from square initiation to first flower represents the most critical development period in terms of water supply affecting yield components. The peak flowering period was the most sensitive to drought and at this time water stress led to the greatest decrease in yield. Under water stress, decrease in seed cotton yield is primarily due to the reduction in number of bolls (Pettigrew, 2004). Water stress prior to flowering reduces fruiting site number. Water stress also may affect the hormonal balance in squares and bolls that could contribute to shedding (Guinn et al., 1990). Water stress affects lint quality in numerous ways, especially during the fiber elongation period results in a decrease in fiber length and fiber immaturity. In cotton, water stress in late-bloom stages, will reduce late-developing bolls and fiber strength in midcanopy bolls and increase micronaire of existing bolls. Fiber length is most affected at 16 to 20 days after flowering. Fiber

strength is most affected 25 to 30 days into boll development through three to four days prior to boll opening (McWilliams, 2004).

Mechanism of Drought Tolerance

Previous studies reported that there is genetic variability for drought response in cotton subjected to water deficient (Cook and El-Zik, 1993; Lacape et al., 1998). A number of different morpho-physiological traits have been suggested as important selection criteria relative to drought tolerance in cotton. These include: distance from transition zone to the first main lateral root, taproot weight, number of lateral roots, seedling vigor, rapidity of root system development, and root/shoot ratio (Cook, 1985); longer taproot length (Pace et al., 1999); reduced transpiration (Quisenberry et al., 1982); stomatal conductance and photosynthetic rate (Nepomuceno et al., 1998); leaf water content and carbon isotope discrimination (Leidi et al., 1999), and canopy temperature ($T^{\circ}c$) (Lacape et al., 1998). Water deficiency involves multiple components that influence plants at the morphological, anatomical, cellular and molecular levels.

Root Morphology

Since some of the more important physiological process, such as nutrition uptake and assimilation, stress signals, and water movement occurs in the plant root, root characteristics logically play an important role in determining the response of plants to drought. Cotton root growth follows a typical sigmoidal curve and continues to grow and increase until about the time when maximum plant height is achieved soon after flowering (Taylor and Klepper, 1974). Since cotton has taproot system, overall root density and exploring the available soil volume for water and nutrients depend on the development of lateral roots. The number of lateral roots produced depends on the number of xylem poles in the taproots of cotton seedling (McMichael et al., 1999). As the number of vascular bundles increased, high branching intensities of lateral roots also increased in 7-day-old seedlings of exotic cotton (McMichael et al., 1987). Thus, modifying root system would be one of the ways to increase water use efficiency for drought resistance in cotton. Quisenberry et al. (1981) reported significant variability for taproot length and number of lateral roots among exotic cotton germplasm in greenhouse-grown, 35-day-old plants. Basal et al. (2003) indicated that the day-neutral converted race stocks (CRS) accessions have useful genetic variability for root growth parameters which were

root length (RL), lateral root number (LRN), root fresh weight (RFW), lateral root dry weight (LRDW) and total root dry weight (TRDW).

Water deficit has different affect on root growth. Pace et al. (1999) reported that drought-stressed cotton seedlings showed some increase in root length but reduced diameter. Ball et al. (1994) and Prior et al. (1995) showed that inadequate soil moisture reduced cotton root elongation while Plaut et al. (1996) found reduced root length density at 42 and 70 days after emergence. Incorporation of increased seedling vigor rapid root system establishment and lower root-to-shoot ratios were recommended to improve drought tolerance in cotton by Cook and El-Zik (1993).

In addition to modifying plant root system, application of plant growth regulators have been used to improve cotton yields under water stress. Xu and Taylor (1992), suggested a potential for using mepiquat chloride (M.C; 1,1-dimethylpiperidinium chloride) to increase root length and root dry weight, and to increase drought resistance of cotton seedlings under greenhouse condition. Zhao and Oosterhuis (1997) reported that PGR-IV has the potential to alleviate partially the detrimental effects of water stress on photosynthesis and dry matter accumulation.

Plant Physiology

Another important aspect of drought tolerance may be the plant's ability to reduce water loss by early stomata closure or leaf morphological structures. Therefore, many studies have emphasized the association of drought resistance with the rate of excised leaf water loss, stomatal closure, abscisic acid (ABA) accumulation in the plants under water deficient conditions, and accumulate a variety of small organic metabolites that are referred to collectively as compatible solutes (osmoprotectans).

An important physiological indicator of water stress is reduced leaf transpiration including stomatal transpiration (TR^{st}) and cuticular transpiration (TR^{cu}) (Osmond et al., 1987). Under water stress conditions, stomatal transpiration (TR^{st}) is controlled by stomatal conductance, and cuticular transpiration (TR^{cu}) is affected by the leaf surface characters such as the thickness of the wax layer and morphological structure (Richards et al., 1986). Lewitt (1980) reported that plants could avoid drought by stomatal closing.

Stomatal opening and closing are modulated by guard cells. Stomatal closing are controlled by guard cells in two ways either direct

water loss from guard cells, which is called hydropassive closure, or water loss from whole leaf, which is called hydroactive closure. Stomatal response to water stress is also controlled by messengers from the root system. Reports have noted that stomatal closure under drought stress is controlled essentially by the concentration of ABA transported in the xylem from the root to shoot and perceived at the guard cell apoplast (Ackerson, 1980; Hartung et al., 1998; Schroeder et al., 2001; Borel and Simonneau, 2002). In cotton (*G. hirsutum* L.), stomatal response to water stress is affected by ABA accumulation or ABA redistribution (Radin and Hendrix, 1988).

In addition to the stomatal behavior, initial water content (IWC) and the rate of excised leaf water loss have been proposed as a simple but relatively reliable indicator of drought resistance in wheat (Yang et al. 1991), in cotton (Quisenberry et al., 1982) and in sorghum (Jordan et al., 1984). Genotypes adapted to dryland exhibits high IWC and /or low rate of water loss from excised leaf suggesting that both characters may contribute to the maintenance of leaf water loss during periods of drought. In cotton, Quisenberry et al. (1982) reported that there was a significant correlation between relative water content (RWC) at mean stomatal closure (MSC) time and growth rates of the cotton genotypes when grown under water stress field conditions. This correlation demonstrated that field productivity tended to be greater in those genotypes which closed their stomata at lower RWC values. On the other hand, they did not detect correlation between RWC at MSC and growth rates under optimal water conditions. Thus, the ability of a genotype to keep its stomates open at low RWC was not an advantage under favorable water conditions. Also, carbon isotope discrimination (Leidi et al., 1999), canopy temperature (T , °C), and maintaining higher water potential (Lacape et al., 1998) during water stress were suggested as a selection criterion for drought tolerant in cotton.

Several stresses such as salt, high temperature and water stress lead to overproduction of reactive oxygen species (e.g. peroxide, superoxide), causing extensive cellular damage and inhibition of photosynthesis. This phenomenon is called oxidative stress and is known as one of the major causes of plant damage as a result of environmental stresses (Sunkar et al., 2003). Plants have evolved systems to combat oxidative stress. Different enzymes aid in reducing the active oxygen species in order to protect the plant cell from damages (Yamaguchi-Shinozaki et al., 2002). It is well known that when plants are subjected to the environmental stress (abiotic stress)

such as drought, salt, low or high temperature, plant cells accumulate a variety of small organic metabolites that are referred to collectively as compatible solutes (osmoprotectants) to protect themselves from stress (Bohnert et al., 1995).

Osmoprotectants such as proline, glycine betaine (GB), and mannitol occur commonly in plants. Earlier studies indicated that GB is a common compatible in many different organisms, including higher plants, and some plant species accumulate GB in response to drought (Koheil et al., 1992). Naidu et al., (1998) reported that the cotton plant has the naturally ability to accumulate GB. They indicated a genotypic difference exists for this character. They found that Tamcot HQ and Tamcot Sphinx, which are released for drought-affected conditions in Texas, accumulated higher GB than the Siokra L-23, Siokra 1-4, Siokra S-101, Siokra V-16, Sicot 189, CS 50 cotton cultivars that are released for irrigation conditions.

Biochemical studies have revealed that through osmotic adjustment (osmotically-active metabolites or osmolytes) compound such as praline-types sugars and polyols (myo-inositol and its derivatives) accumulated under abiotic stress conditions (Bohnert et al., 1995). Accumulated osmolytes protect biological proteins and membranes and also act as scavengers of reactive oxygen intermediates. Single gene transformation studies with the *imt 1* gene, when incorporated into model system such as tobacco and *Arabidopsis*, have demonstrated that increased osmolyte accumulation produces a higher level of drought tolerance in comparison to the wild type (Bohnert et al., 1995). The incorporation of genes for anti-oxidant enzymes (osmotic protection), Ps-APX (ascorbate peroxidase) and At-GR (glutathione reductase), represents a significant addition in countering oxidative stress in plants grown under water deficiency (Cushman and Bohnert, 2000). These transgenes will enhance the existing levels of osmotically-active osmolytes (*imt 1*) and incorporate additional scavenging capability (Ps-APX and At-GR) for reactive oxygen intermediates (Allen, 1995; Cushman and Bohnert, 2000). Nepomuceno et al. (2000) identified and isolated messenger RNAs differentially expressed during water deficit. They also indicated the cloned transcript A12B15-5, a NADP(H) oxidase homologue during the water deficit stress and only in Siokra L-23, a drought tolerant genotype.

Genetically engineered cotton plants containing the oxidative stress-related gene for the production of the enzyme ascorbate

peroxidase (APX) were already tested in field trials, and in dryland agriculture, the altered plants showed increased production (Moffat, 2002). After the trials on cotton, the ascorbate peroxidase encoding gene and a further gene that encodes the production of another enzyme called glutathione peroxidase were introduced into tobacco plants. Both enzymes are supposed to mop up peroxide in the cells. In greenhouse trials the transgenic tobacco plants maintained near-normal rates of photosynthesis during stressful conditions while photosynthesis in non-altered plants was reduced by one-half (Moffat, 2002). Voloudakis et al. (2002) searched four Greek cotton varieties for molecular response to drought in terms of the expression drought-tolerance-related genes. They reported that Heat-shock protein calmodulin-binding homolog was induced by water stress in drought-tolerant varieties Eva, Siokra L23, and Zeta 2.

Genetic mapping technologies have been used for a decade or more for many major crops. Several investigators have identified quantitative traits loci (QTLs) responsible for improved productivity under arid conditions. Also QTLs have been reported that confer physiological variations that are thought to be associated with stress tolerance, such as osmotic adjustment (Morgan and Tan, 1996), abscisic acid level (Tuberosa et al., 1998), stomatal conductance (Ulloa et al., 2000). Saranga et al. (2004) detected 33 QTLs for five physiological variables (osmotic potential, carbon isotope ratio, canopy temperature, chlorophyll a and b, and 46 QTLs for five measures of crop productivity (dry matter, seed cotton yield, harvest index, boll weight, and boll number) in two generation of progeny from a cross between *Gossypium hirsutum* and *Gossypium barbadense*.

New Gene Source

Plant breeders primarily use current and obsolete cultivars along with public germplasm in developing new cultivars. Thus, it is essential to add new (novel) alleles from exotic genotypes in order to expand genetic diversity for drought avoidance or resistance. Roark and Quisenberry, (1977) suggested that the genetic variability in current cotton cultivars potentially is low for many drought tolerant traits, since most of the current cultivars have been selected under humid and high rainfall conditions. The primitive race stocks of upland cotton have been identified as potential sources of traits associated with drought tolerance (Quisenberry et al., 1981, and Basal et al., 2003). Basal et al. (2003) reported that robustness of seedling rooting parameters can be

recovered easily, and that seedling rooting robustness can be improved by crossing robust rooting parents. If an extensive root system could be combined with the ability to maintain high leaf water content, it could express superior adaptation to dry land environments (Hurd and Spratt, 1975). Basal et al. (2004) indicated that the robust rooted CRS lines, having high initial water content (IWC) and low excised leaf water loss (ELWL) which has been proposed as reliable drought selection criteria for different plant species including cotton, could be used to expand genetic diversity for drought tolerant source in cotton.

Conclusion

In order to accomplish to increase plants' drought tolerance, plant breeders should combine classical breeding method with genetic and metabolic engineering. It is clear that a multidisciplinary approach including breeding, physiology, and biotechnology is required for efficient improvement for greater drought tolerance in cotton.

Özet

Pamukta (*Gossypium hirsutum* L.) Su Stresi

Pamuğun da içinde yer aldığı bitkilerde, kuraklık (su stresi) verimi en çok sınırlayan abiyotik stres faktörleri arasında yer almaktadır. Bir çok çalışma, kurağa dayanıklılığın çoklu gen etkilerinin etkisinde kompleks bir agronomik özelliğe sahip olduğunu göstermiştir. Daha önce yapılan araştırmalarda güçlü kök sistemi, su kullanım randımanı, stoma iletkenliği, fotosentez oranı, karbon izotop ayırımı, kanopi sıcaklığı, yaprak su içeriği, yaprak su kaybı ve osmotik düzenleyiciler'in kurağa dayanıklı pamuk ıslahı çalışmalarında seleksiyon kriteri olarak önerilmiştir. Böylece, kurağa dayanıklılık yönünden uygun morfo-fizyolojik özellikler klasik melezleme veya biyoteknolojik olarak bir bitki modelinde birleştirildiğine bu bitkilerin kurak alanlara uyum sağlayabilecekleri söylenebilir.

Anahtar sözcükler: Pamuk, su stresi, fizyolojik ve morfolojik mekanizmalar.

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