Chapter 9

COTTON SEEDLING GROWTH AND DEVELOPMENT RESPONSES TO TEMPERATURE AND DROUGHT STRESS

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INTRODUCTION

The United States is the third leading cotton (*Gossypium hirsutum* L.) producing country in the world with its production mainly concentrated in the southern states of Texas, Georgia, Arkansas, Louisiana, and Mississippi (Meyer, 2018). Cotton farmers in the southern US region favor early planting of cotton (Wrather et al., 2008), with a peak planting window from April 27 to the first week of May. Early planting provides the advantage of early season rainfall, minimizes late-season pest problems, and minimizes the risk of premature termination of the cotton crop by freezing temperatures in the fall (Bradow, 1991; Pettigrew, 2002). In addition, cotton planted in the early spring receives maximum solar radiation from emergence to squaring which promotes early vegetative growth and development and finally, cotton yield (Pettigrew, 2002). However, the early growth of cotton, seed germination and seedling development, is influenced by genotype x environment interactions. Temperature and soil moisture are the predominant abiotic factors that affect the early growth of cotton (Singh et al., 2018). Cotton is a warm temperature-requiring crop that needs a temperature of about 30°C for optimal seed germination and seedling development (Barpete et al., 2015). Early season planting always carries a risk of uncertainty in weather forecasting, potentially increasing the chance of chilling injury during the early growth stages. Low soil temperatures (<20°C) cause radicle abortion and necrosis of root tips, potentially leading to uneven stand establishment, poor seedling development, and decreased fiber yields (Bradow and Bauer, 2010). The average farm size for operations categorized as small and large in the USA ranges from 200 acres to 1500 acres, respectively. Farmers using a single cotton variety consider staggering planting dates to plant large acreage farms that can potentially expose the early growth stages of cotton to low temperatures. Also, above or below optimum soil moisture conditions combined with cool temperatures more negatively impact seedling development than either stress in isolation (Wanjura et al., 1971; Wanjura and Buxton, 1972a, b). Therefore, the objective of this chapter is to provide an overview of the effects of temperature and moisture stress on early growth and development of cotton seedlings.

TEMPERATURE

Shoot Growth and Development

Crop growth describes an irreversible increase in dry mass or volume, and development involves differentiation of cells into specific tissue types or organs, and both are controlled by environmental and genetic factors. Sub or supra-optimal temperature has been considered as a most damaging stress factor, especially during reproductive development of cotton (Reddy et al., 1992b; Reddy et al., 1992c; Oosterhuis, 2002). Cultivar-specific optimum temperatures are different for different growth stages, including seed germination, seedling establishment, leaf area and canopy development, flowering, boll development, and maturation (Pearson et al., 1970; Reddy et al., 1992b; Reddy et al., 1992c; Reddy et al., 1992a; Barpete et al., 2015; Singh et al., 2018), and are determined by ecotypes. Cotton cultivars grown in tropical parts of the world are well adapted to higher temperatures especially in south Asia, where summer temperatures can potentially rise above the optimum and reach around 48-50°C during the cotton growing season. Recent studies have reported the effect of day/night temperatures on late vegetative and reproductive growth in cotton (Oosterhuis, 2002; Kakani et al., 2005; Singh et al., 2007; Snider et al., 2011). Morphologically, higher temperatures (>30°C) significantly reduce leaf area, stem elongation, and biomass accumulation during early growth stages (Reddy et al., 1992a). Declines in pollen viability and germination (Saini et al., 1983; Kakani et al., 2005; Jain et al., 2007; Snider et al., 2011), and square and boll retention (Reddy et al., 1991; Reddy et al., 1992c) in response to heat stress during reproductive growth have been reported in Upland cotton. Similar but more pronounced responses were observed in Pima cotton (*Gossypium barbadense* L.) with increasing temperature (from 30/22°C to 40/32°C) during reproductive growth (Reddy et al., 1992b; Reddy et al., 1995). Upland cotton developed a significantly higher number of fruiting branches than Pima cotton at higher temperatures (Reddy et al., 1995). Reddy et al. (1995) also observed that Pima cotton required more heat units than Upland cotton to produce the first square at 30°C, based on which Pima cotton was concluded to be less heat tolerant during reproductive growth. Various physiological changes have been observed in response to varying temperatures in cotton at late vegetative and reproductive growth stages. These include a decline in photosynthesis due to an increase in photorespiration (Perry et al., 1983), primarily caused by reduced chlorophyll contents (Reddy et al., 2004; Snider et al., 2009; Snider et al., 2010), decrease in actual quantum yield of photosystem II (Φ_{PSII}) and maximum photochemical efficiency (F_v/F_m) (Bibi et al., 2008; Snider et al., 2009; Snider et al., 2010), inhibition of Rubisco activase, and increased membrane leakage (Bibi et al., 2008). Also, the rapid increase in dark respiration at higher temperatures can limit the accumulation of carbohydrates, especially fructose and glucose in the source (leaves) and their translocation to the final sink (bolls) (Arevalo et al., 2008). This trend of decreasing photosynthesis with increasing temperatures could substantially lower cotton yields.

As evident from the above review, there is extensive information on heat stress effects during the reproductive phase of growth, but few studies have focused on heat tolerance at germination and early seedling growth in cotton. Ashraf et al. (1994) found significant genotypic differences for seedling growth among cotton cultivars when subjected to 48°C for a 21-day period after incubating the seeds at 30°C. The authors further identified cultivars B-557 and MNH-93 had higher percent germination, dry biomass, leaf soluble sugars, proline sugars, and lower relative injury compared to cultivars CIM-70, NIAB-78, and S-12. The study, however, found no germination of seeds incubated at 50°C. Reddy et al. (1992a) observed plant height, leaf area, and main stem elongation rate in Upland cotton were relatively less sensitive to temperature regime (20/12 - 40/32 °C day/night) during seedling growth for the first two weeks after emergence than after that time. Similar responses were observed in Pima cotton to the temperature regime were during seedling growth (Reddy et al., 1992b).

Brand et al. (2016) identified low temperatures as the most damaging to seedling growth and development while studying root and shoot morphological responses to multiple stresses (carbon dioxide, ultraviolet-B radiation, and temperature). Low temperatures have also been associated strongly with seedling diseases like damping off, which are the primary reasons for root deterioration under chilling conditions (Brown and McCarter, 1976). Brown and McCarter (1976) also reported low temperature as the major factor that impacts the degree of damage by pathogens like *Rhizoctonia* and *Pythium* in cotton seedlings. Significant increases in the number of vegetative branches, especially in Pima cotton were found at low temperatures (Reddy et al., 1992a; Reddy et al., 1992b). Fully emerged seedlings of cotton, when exposed to suboptimal temperatures in the late spring, showed a significant reduction in seedling development and subsequent yield (Bradow and Bauer, 2010). Seedling emergence and development rates can determine cultivar sensitivity to cool temperatures under controlled conditions (Arndt, 1945; Pearson et al., 1970; Reddy et al., 1992a; Reddy et al., 1992b; Singh et al., 2018) and relative performance under field conditions (Steiner and Jacobsen, 1992). Moreover, leaf or cotyledon area, leaf dry weight, shoot and root dry weight, and plant height can substantially determine early vigor in modern cultivars and advanced cotton breeding lines (Reddy et al., 1992a; Reddy et al., 1992b; Liu et al., 2015; Brand et al., 2016; Singh et al., 2018). The genotypic difference in early vigor recovery from post-emergence chilling stress often informs the selection of cultivars for early planting when soil temperatures are cool. Singh et al. (2018) observed the seedling growth of nine elite cotton lines obtained from different breeding programs was more sensitive to low temperature (22°C) than drought stress (50% of optimum moisture). Further, the study reported significant differences in the response and degree of tolerance to low temperature among the cotton lines during seedling growth. The identified tolerant lines might, however, yield similar to other lines under late planting conditions when temperatures are optimal.

Physiological indicators of heat tolerance in a plant include membrane leakage, chlorophyll fluorescence, and antioxidant enzyme activity (Oosterhuis et al., 2008). Consequently, a thermotolerant plant shows relatively less leakage, higher photochemical efficiency of PS II and greater antioxidant enzyme activity under heat stress than a thermo-sensitive plant (Oosterhuis et al., 2008). For rapid screening purposes, fluorescence and membrane leakage assays, are heavily applied in previous studies determining cotton responses to high and low temperatures (Murphy and Noland, 1982; Cottee et al., 2007; Bibi et al., 2008, BÖLEK et al., 2013). These techniques aid in the selection of germplasm for improvement in cold or heat tolerance among commercial cultivars and advanced breeding lines (Oosterhuis et al., 2008).

Root Growth and Development

One of the major problems during early season planting of cotton is lack of uniform stand establishment because cool soil temperatures can substantially reduce root elongation rate, which determines root length (Pearson et al., 1970). Because of the difficulty associated with root phenotyping, most of the previous studies were only concentrated on studying root length (Newman, 1966; Reicosky, 1970). The studies concluded that suboptimal temperatures could substantially reduce root growth and simultaneous hydraulic conductance during early growth stages, even if soil moisture was optimum (Pearson et al., 1970, Radin, 1990, Bolger et al., 1992). Bradow (1991) observed a significant decline in root and shoot growth of 10-day old seedlings at low temperatures (10 to 25°C) in cotton. Christiansen et al. (1970) reported a significant loss of amino acid and sugars like glucose, fructose, and sucrose from the roots under chilling temperature (5°C) and the amount of loss increased linearly with increasing duration of chilling temperature. The study also identified marked differences among cotton cultivars in their capacity to recover from post-emergence chilling stress. The cultivar-specific differences in cotton were also observed for shoot and root water content under moderate chilling conditions (>15°C) (Bradow, 1991). Bauer and Bradow (1996) found greater emergence rate and root length in early maturing varieties than late maturing varieties at suboptimal temperatures. However, slower root growth in the late maturing varieties may be advantageous when low soil moisture and cool conditions prevail in the field (Bauer and Bradow, 1996).

DROUGHT

Drought can be defined as a prolonged period of below-average precipitation in a given region that can be measured by collecting historical data on precipitation and other weather parameters. It can severely limit agricultural productivity by providing insufficient soil moisture for proper growth and development at a given time. Agricultural drought is typically determined by plant available soil water in the root zone area, which is the amount of water that a typical soil retains between field capacity and permanent wilting point. Furthermore, researchers have imposed water deficit conditions either based on volumetric soil moisture content (m^3. m^{-3}), soil water tension, or evapotranspiration. In general, when soil moisture tension exceeds 30 to 50 centibars, depending on soil type, drought stress can occur (Perry et al., 2012).

Shoot Growth and Development

Cotton is mainly (about 65%) grown under dryland conditions particularly in the southeastern regions of the U.S., while irrigated cotton (about 35%) is concentrated in the arid southwestern U.S. (Perry et al., 2012). However, where dryland cotton is produced, the crop can receive less than the optimum average precipitation over the cotton growing season which significantly reduces the region-specific yield potential, and necessitates identifying cultivars that perform well under drought conditions. Cotton is most sensitive to water stress from a period of late squaring to early bloom when the water requirement ranges from 0.5 to 0.7 cm of water per day in the southeastern US (Perry et al., 2012). Low water availability during this period may cause a reduced number of bolls per plant, fiber quality, and seed cotton yield. Because the reproductive stage is considered the most sensitive to drought in cotton, most of the shoot morphological and physiological growth characteristics in response to drought stress have been studied during late vegetative and reproductive growth stages (Ackerson et al., 1977; Saini and Lalonde, 1997; Pettigrew, 2004a; Pettigrew, 2004b; Chastain et al., 2014; Chastain et al., 2016). These studies have used various growth traits such as leaf folding, plant height, leaf area, leaf size and stem elongation (Singh et al., 2018; Jordan et al., 1975; Turner et al., 1986; Ball et al., 1994; Pettigrew, 1994; Pace et al., 1999), node number and plant dry weights (Pace et al., 1999), and squaring and boll production (Grimes and Yamada, 1982; McMichael and Hesketh, 1982; Turner et al., 1986; Gerik et al., 1996; Pettigrew, 2004a) to quantify the effects of drought on cotton seedlings.

Certain changes in response to drought stress may occur at cellular levels like reduced cell expansion, changes in grana, thylakoid membrane, mitochondria, chloroplast membrane integrity, and also modification in chemical compositions like formation of long-chain alkanes, decreased glycolipids and phospholipids, and increased triacylglycerol levels in epicuticular wax of water-stressed leaves (Loka et al., 2011). Though these above changes may not objectively specify drought tolerance. Singh et al. (2018) classified nine elite cotton lines developed from nine different breeding groups into different degrees of drought tolerances, ranging from very low to very high tolerance, based on the morphological growth of seedlings. Secondly, they observed differential responses of seedling growth to cold and drought stresses among the cotton lines, with low temperatures were more damaging than drought stress. The adverse effect of drought stress on photosynthesis (Jordan and Ritchie, 1971; Turner et al., 1986; Ephrath et al., 1994; Pettigrew, 2004b) may be caused by decreasing relative water content (Lawlor and Cornic, 2002) and leaf water potential (Lawlor and Cornic, 2002; Chastain et al., 2014). However, results for decreasing photosynthetic rates under water deficit conditions are contradictory in that some studies have concluded stomatal conductance to be a major limiting factor for reduced leaf photosynthetic rates under mild water stress, while others concluded non-stomatal limitations are the primary cause for downregulating leaf photosynthesis under severe water stresses (Ennahli and Earl, 2005). Many past studies found that decreasing leaf water potential may cause stomatal closure that limits carbon dioxide diffusion into the mesophyll cells, and thus reduces carbon fixation and photosynthetic rates (Chaves, 1991; Flexas et al., 2004; Chastain et al., 2014). Jordan (1970) observed a low level of stomatal resistance in field-grown cotton cultivar Lankart 57 even when leaf water potential was reduced to -30 bars. Others have recognized that non-stomatal limitations such as inhibition of metabolic processes like ribulose-1,5-bisphosphate carboxylase synthesis, Rubisco activity, and adenosine triphosphate synthesis can also play a role in reducing photosynthetic rates under drought stress (Gimenez et al., 1992; Medrano et al., 1997; Tezara et al., 1999). Ennahli and Earl (2005) observed that lowered CO_2 concentrations in leaves at moderate water stress (15% relative soil water content) were recovered back to normal levels upon hydration, but photosynthetic rates remained low even after a drought recovery period, which was caused due to non-stomatal inhibition. Also, the results obtained under field conditions for changes in PSII quantum efficiency (Φ_{PSII}) and PSII electron transport in response to water stress were contradictory to greenhouse studies. Certain field experiments showed little change in PSII quantum efficiency (Φ_{PSII}) and PSII electron transport under moderate stress levels than what was observed by the greenhouse and other field studies (Chastain et al., 2014; Kitao and Lei. 2007; Zhang et al., 2011). Pettigrew (2004b) explained the variability in physiological response to drought stress based on the time of the day. The CO_2 exchange rates (CER) and light-adapted photosystem II quantum efficiency in dryland leaves were greater in the morning than in the afternoon, and these results differed from what was observed in irrigated plants. Photosynthetic tolerance to moisture stress strongly correlates to leaf development and growth stage in cotton (Karami et al., 1980; Chastain et al., 2016). Karami et al. (1980) observed cotton was more photosynthetically tolerant to drought during reproductive stages than during the vegetative stage. Also, Chastain et al. (2016) identified younger leaves were more photosynthetically tolerant to drought stress than mature leaves in cotton. The authors also found that net photosynthesis remained unchanged in younger leaves but had declined in mature leaves later in the season. Significant declines in the photosynthetic capacity and carbon fixation under drought stress could result in increased photorespiration and reactive oxygen species production (Foyer et al., 1997; Faria et al., 1999) that can cause oxidative damage to lipids, proteins, carbohydrates, and nucleic acids (Monk et al., 1987; Gigon et al., 2004; Deeba et al., 2012).

Dark respiration rates do vary with water stress, but the results of field studies differed from environmentally controlled studies (Loka et al., 2011). Genotypic differences have been reported for drought tolerance based on morphological parameters (Hatfield et al., 1987; McMichael and Quisenberry, 1991; Lopez et al., 1995; Singh et al., 2017b; Singh et al., 2018) and physiological parameters (Nepomuceno et al., 1998; Leidi et al., 1999; Burke, 2007; Rahman et al., 2008). Identifying variability in photosynthetic rate (Pn), stomatal conductance (gs), transpiration rate (E), and PS II thermostability among cotton genotypes grown in drought conditions could aid in selection of the genes for drought tolerance (Rahman et al., 2008; Snider et al., 2013). Thus, water efficient cotton genotypes selected based on morphological and physiological responses to water-deficit regimes would have stable lint yields in the environments having variable soil moisture contents (Turner et al., 1986). Cotton response to water stress greatly depends upon plant age, leaf size and position, time of day, growth stage, and genotype. Therefore, understanding of such parameters is a prerequisite while conducting drought tolerance studies at different growth stages of cotton. The interaction of agronomic practices, environments and MG are well studied in the past. Planting early to medium maturing varieties of cotton crop is a common practice to obtain quite stable yields under dryland conditions (Rosenow et al., 1983). To study the response of the plant in later stages of the life is very complex because of overlapping detrimental effects of drought stress and underground competition for space with neighboring plants (Blum, 1996). Thus, observing the response in the early growth stages for drought stress is a convenient way to avoid such errors, especially for field experiments of early planting.

Root Growth and Development

Despite a broad investigation on cotton responses to drought stress, few have focused on seedling growth characteristics (Jordan, 1970; Jordan et al., 1975; Kawakami et al., 2010; Singh et al., 2018). However, cotton sensitivity to drought stress at the time of seedling growth was closely associated with dry biomass and root morphology (Pace et al., 1999; Basal et al., 2005; Singh et al., 2018). Early growth stages of cotton primarily consist of a tap root system unless an injury to the primary root has increased the number of secondary and tertiary roots. Although it has been quite difficult to evaluate the performance of cultivars based on root growth and development (McMichael, 1986), a significant amount of data has been reported in the past for an impact of drought stress on root growth in the seedling stage. This involved the use of various techniques and methods with advancement in technology over time to accurately measure root morphology (Newman, 1966; Reicosky et al., 1970; Reicosky et al., 1972; Taylor and Klepper, 1979; Bohm, 1979; Heen, 1980). At present, the use of a WinRhizo root scanner has been described as one of the most convenient methods to analyze the root characteristics during early growth stages in various crops (Narayanan et al., 2014; Wijewardana et al., 2015; Singh et al., 2017b, Singh et al., 2018). Steudle (2000) explained that the transport of water in the roots occurs through apoplastic and/or symplastic pathways, regulated by hydraulic and osmotic modes of action, respectively, depending upon the presence or absence of transpiration. Plants under drought stress show slowed root growth and symplastic flow of water characterizing roots hydraulic resistance that limits water loss from the roots to the soil. (Steudle, 2000).

Root growth has been found to be less sensitive to water deficits than shoot growth which is primarily due to osmoregulation that allow cells in root hairs to maintain lower osmotic potential (Oosterhuis and Wullschleger, 1987). The lowered osmotic potential allows consistent turgor pressure in the cells despite decreasing soil water potential which maintains root growth under water stress. This also allows partitioning of total biomass more towards roots than shoots and thus, results in higher root-shoot ratio under drought stress conditions (Oosterhuis and Wullschleger, 1987; McMichael and Quisenberry, 1991; Ball et al., 1994; Singh et al., 2017b; Singh et al., 2018). Ball et al. (1994) identified the significance of the position of roots within the soil profile while assessing any root traits against water stress conditions. The authors observed a greater number of medium roots (0.62 mm mean diameter) than small sized roots (0.30 mm mean diameter) in the upper zone, while the lower zone contained an equal number of both types of roots under drought as well as during the recovery period. The study explained the reason behind such a phenomenon was that the lower zone consistently held more water than the upper zone during stress periods. The study also provided the significance of studying variability in root size in response to drought stress.

Certain plant growth regulators, PGR-IV and Mepiquat Chloride, have been recognized as alleviating the damaging impact of drought stress through altered root growth characteristics in cotton. Zhao and Oosterhuis (1997) observed significantly higher stomatal conductance (g_s), leaf net photosynthetic rate, and root dry weight in water-stressed plants treated with PGR-IV compared to untreated plants. Furrow application of PGR-IV also showed an enhanced seedling growth regarding root length, root dry weight, lateral root numbers per plant, and final yields in cotton (Oosterhuis, 1995). Iqbal et al. (2005) observed accelerated root growth in cotton seedlings after treating the seeds with Mepiquat Chloride. Pace et al. (1999) observed a significant increase in root length and root thickness in drought-treated cotton seedlings compared to untreated seedlings at the end of drought recovery period. The use of polyethylene glycol (PEG) is another method to identify drought tolerance among genotypes during seed germination and seedling growth in different crops (Nepomuceno et al., 1998; Seepaul et al., 2012; Singh et al., 2017a). Nepomuceno et al. (1998) identified the difference in photosynthetic rate, stomatal conductance, transpiration, and dry weights using PEG 6000 for drought tolerance among cotton cultivars. Past studies have reported differential growth responses between root and shoot growth to drought stress, and concluded root growth was more sensitive to drought and cold than the shoot (Pace et al., 1999; Singh et al., 2018). Thus, it is essential to study root patterns either independently or in combination for drought tolerance in cotton. Cotton genotypes or breeding lines exhibited significant variability for seedling root-shoot ratio, root length, root dry weights, root diameters, root numbers, root surface area, root length per unit volume, and other root parameters under drought stress (Quisenberry et al., 1981; Basal et al., 2005; Singh et al., 2018). Therefore, studying root morphological characteristics of cotton seedlings in response to drought conditions has been identified as an important method in breeding programs for improving drought tolerance in cotton.

MOLECULAR STUDIES

Studies that characterize cotton cultivars for cold tolerance using molecular approaches are limited in the literature. Phospholipases (PLDa) have been found to play a significant role in the cold stress response in cold tolerant species (Kargiotidou et al., 2010). Kargiotidou et al. (2010) observed the induction of two PLDa genes, PLDa1 and PLDa2, under cold stress (10°C or less) in cotton. However, the levels of two isoforms significantly changed under varying temperature and light conditions. Glycine betaine, an effective osmoprotectant, has been exploited for improving drought tolerance in several crops like cotton, wheat, barley, and corn. Naidu et al. (1998) identified increased amounts of glycine betaine in all cotton cultivars under water deficit conditions. The author further identified genotypic variations for glycine betaine levels, where the highest levels were found in the cultivar Tamcot Sphinx, adapted to dryland conditions, and the lowest levels were observed in the cultivar Siokra S101, adapted to irrigated conditions. Also, seed treatment with glycinebetaine along with foliar application after emergence and at the squaring increased cotton yield under rainfed conditions (Naidu et al., 1998). Transgenic *GF14λ*-expressing cotton plants displayed the "stay green" phenotype and improved tolerance to water deficit conditions because of increased photosynthesis and stomatal conductance regulated by GF14λ (Yan et al., 2004).

SUMMARY

Cotton researchers are interested in studying the early growth of cotton in response to suboptimal temperatures and soil moisture conditions. Low temperatures and variable soil moisture contents are the major abiotic factors influencing seed germination and early seedling growth. Genotype x environment interactions do exist among cotton cultivars that aid in selecting cultivars for regions with variable temperature and moisture conditions. Screening techniques based on growth and physiology can successfully screen commercial cotton cultivars for early season cold and drought tolerance. Further, the early maturing cultivars have shown greater shoot and root growth at low temperatures and drought conditions compared to late maturing cultivars. Therefore, early maturing and cold tolerant cultivars can be selected by cotton breeding programs for developing cold stress tolerance. However, there is also a need to focus on molecular mechanisms contributing to stress tolerance in diverse cotton germplasm that could provide long-term benefits. Thus, developing resistant commercial varieties could ensure uniform and even stand establishment, and subsequent vigorous shoot and root growth under varying temperatures and moisture conditions when cotton is planted early in the season.

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