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MOLECULAR BIOLOGY AND PHYSIOLOGY

Effects of Chilling Temperatures on Photosynthesis

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ABSTRACT

Environmental stress is an inescapable reality for most plants growing in natural settings. Conditions of sub- or supraoptimal temperatures, water deficit, water logging, salinity, and pollution can have dramatic effects on plant growth and development, and in agricultural settings, yield. In cotton, yield is a product of the number of mature bolls produced in a given area and the amount of cotton produced by each boll. Though cotton is among the most stress-tolerant crop plants, suboptimal environmental conditions limit the yields and quality of fiber and seed. The most significant effects of abiotic stress related to yield are on fertilization, boll retention, and boll filling. Maintenance of photoassimilate supply during fruit development is critical in achieving high yields in cotton. Because photosynthesis is the driving force behind plant productivity, although not the only factor that determines yield, plants have developed numerous mechanisms that serve to protect the photosynthetic apparatus during stressful conditions. Cotton is produced across a wide range of environments and management conditions, from hot and humid subtropical to semiarid environments. Although production is limited by varying environmental conditions across these environments, it is clear that the physiological resilience to abiotic stress is considerable. We present a review of our understanding of low-temperature limitations to photosynthesis and the impact on productivity. Additionally, we use the High Plains region of Texas as a case study to highlight potential key developmental aspects of low-temperature stress on yield.

The life cycle of an annual plant such as cotton occurs within a continuously variable thermal environment. Obviously, the majority of temperatures within these environments are suitable for growth, but in most production environments, there are some temperatures that are too low and some that are too high for optimal metabolic function. Although the existence of low- and high-temperature stresses is agreed upon, the identification of specific temperatures as too low and too high is problematic. The optimal temperature for cotton growth and development is considered to be approximately 28°C with a range of 23°C to 32°C often considered to be nonstressful (Burke et al., 1988; Upchurch and Mahan, 1988). In terms of the seasonal distribution of air temperatures below and above the optimum, temperatures experienced by cotton over a season potentially range from a minimum of 0°C at planting and/or harvest to a maximum of approximately 45°C. If we use 23°C as a lower limit and 32°C as an upper limit, the range of low temperatures experienced is 23°C (23 – 0°C) and the high temperature range is 8°C (45 − 32°C). It is apparent that high-temperature stress is limited to a narrower range than low-temperature stress. The assessment of high-temperature stress in cotton is complicated because transpirational cooling can reduce the leaf temperature substantially relative to the air (Burke and Upchurch, 1989; Salvucci and Crafts-Brandner, 2004). Low-temperature stress however, is different in that at air temperatures below 23°C, the temperature of the cotton plant is generally similar to that of the air.

Temperatures below and above the optimum affect metabolism differently. As temperatures rise above the optimum, reaction rates will increase up to the point where physical destruction of metabolic components begins to occur and reaction rates begin to decrease. Between the optimum and this physically destructive temperature, high-temperature thermal stress is generally reversible. As temperatures decline below the optimum, reaction rates decrease in a largely reversible manner, though below some temperature, oxidative stress and changes in membrane structure can result in nonreversible damage that requires repair before optimal metabolism can resume. Whereas severe or lethal low-temperature stresses are virtually guaranteed in most cotton

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production environments, severe and lethal high-temperature stresses, although entirely possible, generally are limited to water deficit conditions.

The exposure of cotton to temperatures that are sufficiently low enough to affect growth and development generally is referred to as chilling and the resultant chilling stress has been the subject of numerous studies over several decades. Historically, the temperature limits of chilling stress in cotton are not rigorously defined and this lack of a consensus often makes comparisons across studies difficult. It generally is accepted that photosynthesis in cotton is affected by chilling conditions in such a way that growth, development, yield, and quality can be adversely affected. Suboptimal temperatures have short-term (minutes) and long-term (hours or days) negative effects on photosynthesis in cotton, generally considered to be a chilling-sensitive species. Whereas the long-term effects will predominate when plants exposed to more than a day of constant chilling conditions, the relationship between only a few minutes of chilling temperatures during a day and longer term declines in photosynthesis are less understood. We present a review of the impact of suboptimal temperature exposure on cotton photosynthesis and cellular defense mechanisms that protect against chilling damage. We also present the results of an analysis of the incidence of chilling temperatures in the Texas High Plains, a major cotton production region of the U.S. and the impact of chilling on yield and fiber quality on a widely-grown present-day variety.

Impact of Suboptimal Temperature on Photosynthesis. When a plant is exposed to a suboptimal temperature after acclimation to an optimum or higher temperature, net carbon assimilation (A) declines immediately, whether the plant is able to acclimate eventually to lower temperatures or not (Hendrickson et al., 2004; Labate and Leegood, 1988; Pérez et al., 2001). Factors from the restriction of stomatal conductance (g_s) to leaf cell biochemical effects can be involved in this decline in A. The stomatal effects are evident even when the temperature of the roots of the plants is maintained at an optimum temperature to maintain water absorption while the shoots are being chilled (Allen and Ort, 2001; Bunce, 2000; Perera et al., 1995). However, biochemical factors often are more constraining than stomatal aperture, especially when the temperature is far below the optimum. Hendrickson et al. (2004) indicated that as the temperature falls from optimum to approximately 15°C, changes in A for grape involve Rubisco deactivation. Other studies have noted similar negative effects of chilling on Rubisco activation, either after an extended period of chilling (Holaday et al., 1992) or after night chilling (Allen et al., 2000). The deactivation of Rubisco could be related to a reduction in the availability of ATP from electron transport in the chloroplast. This ATP is needed by Rubisco activase in the process of removing inhibitory sugar phosphates from the active site of Rubisco, thus allowing Rubisco to be activated (Byrd et al., 1995). Acclimation to chilling by chilling-tolerant species involves an increase in the activation state of Rubisco and an increase in the total extractable activity of the enzyme (Campbell et al., 2007; Holaday et al., 1992; Hurry et al., 2000; Pérez et al., 2001).

With chilling, especially below 15°C, A is constrained, at least in the short term, by the decreased ability of the Calvin-Benson cycle to regenerate ribulose 1,5 bisphosphate (RuBP) for Rubisco (Hendrickson et al., 2004; Labate and Leegood, 1988; Leegood and Furbank, 1986; Perera et al., 1995; Sharkey et al., 1986; Silim et al., 2010). In such situations, CO_2 assimilation by C_3 plants becomes insensitive to changes in O_2 concentration and A saturates at a low intercellular CO_2 concentration, basically eliminating any constraint of stomatal conductance on A that might occur at slightly suboptimal temperatures. Studies with chloroplasts (Leegood and Walker, 1983; Mächler et al., 1984) and leaves (Hendrickson et al., 2004; Labate and Leegood, 1988; Leegood and Furbank, 1986, Sharkey et al., 1986; Silim et al., 2010) indicated that such exposure to a decline in temperature causes a phosphate limitation to A. Allowing excised leaves to accumulate phosphate prior to the exposure to chilling temperatures alleviates this limitation (Hendrickson et al., 2004). Phosphate is needed for ATP synthesis in the chloroplast to drive the regeneration of RuBP in the Calvin-Benson cycle. A slowing of the rate of the release of phosphate from phosphorylated sugars could restrict the amount of phosphate available in the chloroplast for ATP synthesis. The synthesis of ADP-glucose for starch synthesis by ADP-glucose pyrophosphorylase (AGPase) in the chloroplast is one such process (Hendriks et al., 2003). This enzyme uses glucose-1-phosphate as substrate along with ATP producing ADP-glucose and pyrophosphate, which can be cleaved to release phosphate. However, for spinach and wheat acclimation to low temperature, AGPase activity does not

increase (Martindale and Leegood, 1997; Savitch et al., 1997), suggesting that this pathway to release phosphate is not of major importance during chilling for these species. In contrast, cotton subjected to 15°C does increase the AGPase activity (Perera et al., 1995). Another process that releases phosphate is sucrose synthesis in the cytosol. The phosphate is shuttled into the chloroplast by the triose-phosphate translocator of the inner chloroplast envelope. Acclimation to chilling exposure increases the extractable activity of sucrose phosphate synthase and cytosolic fructose bisphosphatase (Guy et al., 1992; Holaday et al., 1992; Hurry et al., 2000; Lundmark et al., 2006; Pérez et al., 2001; Savitch et al., 1997) that are critical in sucrose synthesis. Reducing the expression for sucrose phosphate synthase reduces the ability of *Arabidopsis thaliana* (L.) Heynh. to acclimate to chilling (Strand et al., 2003). Also, in concert with an increase in sucrose synthesis, triose-phosphate exchange for phosphate appears to be an important process to upregulate during chilling (Lundmark et al., 2006). These changes during acclimation could improve phosphate cycling to the chloroplast.

Another major biochemical problem that could restrict RuBP regeneration is an inactivation of the stromal fructose bisphosphatase (sFBPase) and sedoheptulose bisphosphatase (SBPase) in the Calvin-Benson cycle (Allen and Ort, 2001; Holaday et al., 1992; Payton et al., 1997; Pérez et al., 2001; Sassenrath et al., 1990). These enzymes are activated in the light by the reduction of disulfide bonds utilizing reducing power ultimately from the light-absorbing reactions (Scheibe, 1990). During chilling, the critical sulfhydryl groups of sFBPase and SBPase become more oxidized, which alters the kinetic properties of the enzymes. These enzymes in chilling-tolerant plants tend to deactivate to a lesser degree in the short term (Pérez et al., 2001). The ability to acclimate to chilling conditions and improve A involves at least full activation of sFBPase (Holaday et al., 1992) and an increase in the extractable activity of both sFBPase and SBPase (Holaday et al., 1992; Hurry et al., 2000; Pérez et al., 2001).

Despite the apparent sensitivity of photosynthesis to chilling, photosynthate (carbohydrate) accumulates in the leaf with time at low temperature (Campbell et al., 2007; Hurry et al., 2000; Paul et al., 1992; Pérez et al., 2001; Venema et al., 1999). Over several days, an increase in leaf carbohydrate is known to cause a downregulation of genes for certain photosynthetic proteins of the Calvin-Benson cycle and light absorption (Koch, 1996; Paul and Foyer, 2001; Strand et al., 1997). Thus, plants of chilling-sensitive species likely would suffer further reductions in A with long exposures to chilling if the export of carbohydrate from leaves could not be improved. Although this carbohydrate accumulation occurs for most plants, whether they are able to acclimate to chilling or not, it does not appear to affect negatively gene expression for chilling-tolerant plants, such as *A. thaliana*, during the acclimation process (Strand et al., 1997). In fact, the gene expression for many critical enzymes is increased as part of the acclimation process, consistent with the change in the extractable activities of key enzymes of carbon metabolism. Interestingly, during acclimation to low temperature, respiration rates reach a maximum before rates of A do (Campbell et al., 2007), suggesting that the metabolic function is aimed at improving the processes that utilize carbohydrate before carbohydrate synthesis increases.

Cotton photosynthesis has been shown to be sensitive to reductions in temperature below optimum (DeRidder and Crafts-Brandner, 2008; Königer and Winter, 1993; Payton et al., 1997; Perera et al., 1995; Winter and Königer, 1991). Even a temperature of 20 to 21°C can cause a substantial reduction of A in the short term (DeRidder and Crafts- Brandner, 2008; Winter and Königer, 1991). In addition, growth at 20°C reduces leaf area, further reducing the total carbon gain (Winter and Königer, 1991). When researchers utilize plants in pots for their analysis, a large decrease in g_s often is observed in the short term, possibly due to the chilling of the root system that reduces water availability to the leaves (DeRidder and Crafts-Brandner, 2008; Perera et al., 1995). Keeping the roots at optimum temperature during the chilling period maintained g_s and improved A in one experiment (DeRidder and Crafts-Brandner, 2008) but had no effect on A in another experiment (Perera et al., 1995). These effects of chilling in the light on gas-exchange parameters for cotton, especially on g_s, can extend into a subsequent period of optimum temperature, as might occur in the morning following a cool night (Zhang et al., 2012). However, there appears to be genotypic variation in the sensitivity to a period of chilling and the rapidity with which photosynthesis recovers at optimum temperature (Wu et al., 2012).

In addition to a reduction in g_s with chilling, biochemical problems have been noted for cotton photosynthesis in a growth chamber experiment

under a moderate photon flux density (PFD) (450 to 540 μmol m^{-2} s^{-1}) and a constant 15°C, but primarily after 4 to 8 d of chilling (Perera et al., 1995). Thus, a brief period of moderate chilling with a moderate PFD, such as occurs during a cool morning, might not cause substantial biochemical disruptions to carbon assimilation. Initially, Rubisco activity (not activated in vivo) remained high, and the total extractable activity and the activation state of sFBPase rose, likely factors in keeping A from declining more than 13% at 15°C the first day the plant is exposed to 15°C. The lack of a substantial decrease in the O_2 sensitivity of A until day four suggests that there was no major problem, initially, with RuBP regeneration. Thus, with respect to the early responses to 15°C and a moderate PFD, aspects of cotton photosynthesis are insensitive to this temperature and mimicked many of the acclimation responses of chilling-tolerant plants. However, exposures to a much lower temperature in full sun (35 min at 5°C and 1700 μmol photons m^{-2} s^{-1}) can cause the activation state of sFBPase in cotton leaves to decline (Payton et al., 1997). Perera et al. (1995) showed that, with a long-term (8 d) exposure to 15°C, A did diminish for cotton by nearly 50%. The Rubisco initial activity declined approximately 25%, and the sFBPase activity and activation state declined during this period. One possible cause of this considerable further decline in A and changes in enzyme activity after day one of the experiment could have been the maintenance of high leaf sucrose and hexose (glucose plus fructose) contents that could have signaled a downregulation of gene expression for photosynthetic enzymes. Also, although increases in AGPase, cytosolic FBPase, and glucose-1-phosphate uridylyltransferase (UDP-glucose pyrophosphorylase) occurred with chilling, sucrose phosphate synthase activity declined, suggesting that eventually, A became increasingly constrained by the phosphate supply to the chloroplast, consistent with the decline in the O_2 sensitivity of A to 4% from 33% in the 8-d period. However, it is also possible that there were increasing problems of maintaining electron transport and the redox state of the chloroplast.

When more light energy is absorbed than can be utilized by the Calvin-Benson cycle during chilling, problems with components of the light-absorption apparatus and oxidative state of the chloroplast can develop (Kornyeyev et al., 2001; Payton et al., 2001; Perera et al., 1995). In such a situation, photoinactivation of photosystem II (PSII) and photosystem I (PSI) might occur, and redox-sensitive enzymes, such as sFBPase and SBPase, might inactivate. The extent of inactivated PSII complexes can be estimated from chlorophyll a fluorescence analysis (the variable to maximal fluorescence, F_v/F_m) after leaves or leaf discs have been allowed to remain in the dark for 30 to 60 min. With time in moderate to high PFD during chilling (10-15°C), F_v/F_m declines for cotton leaves, indicating an inactivation or damage to PSII complexes (Kornyeyev et al., 2001; Perera et al., 1995). The inactivated PSII complexes might not recover quickly once the leaves warm to an optimum temperature. For the cotton plants subjected to 15°C, the complete recovery of F_v/F_m values required 2 d at 28°C (Perera et al., 1995). The following section addresses this problem of oxidative stress in cotton leaves during chilling, what mechanisms the plants employ to reduce the negative effects on photosynthesis, and the potential that cotton has to subdue its occurrence in the field.

Cellular Mechanisms to Protect Against Chilling Damage and Oxidative Stress. Numerous studies suggested that photooxidative damage by reactive oxygen intermediates (ROIs) is a major cause in the decrease in A following exposure to a variety of environmental stresses, including excess light and suboptimal temperature (reviewed in Allen, 1995; Alscher et al., 1997; Bowler et al., 1992; Königer and Winter, 1993; Payton et al., 1997, 2001; Smirnoff, 1995). Previous studies in cotton showed significant impacts of low temperature on A in short-term acute exposures (35 min at 5°C and a PFD of 1700 μmol m^{-2} s^{-1}) (Payton et al., 1997) or more moderate stress (20°C and full sun for 1 d) (Königer and Winter, 1993). Both of these studies showed rapid decreases in A as well as significant lag times in recovery of A after re-exposure to optimal temperatures.

ROIs are generated in cellular reactions, such as electron transport in mitochondria and chloroplasts, where electron transfer to molecular oxygen can occur. Under normal conditions, oxidative damage is minimal due to the metabolism of active oxygen species by both enzymatic and nonenzymatic mechanisms. However, during exposure to environmental stress, the mechanisms that normally scavenge toxic oxygen species could become overwhelmed, resulting in membrane damage, pigment bleaching, enzyme inactivation, and decreased A or photoinhibition (Allen, 1995; Bowler et al., 1992; Foyer et al., 1994; Smirnoff, 1995; Van Camp et al., 1996). The damage caused by ROIs and their products is known as oxidative stress.

Chloroplasts are highly susceptible to oxygen toxicity for many reasons: (1) they have a high internal O_2 concentration during exposure to light; (2) they contain several molecules, such as reduced ferredoxin, that can reduce O_2 to superoxide anions (O_2^-); (3) lipids in the chloroplast membranes have a high percentage of unsaturated fatty acid tails that are susceptible to peroxidation; and (4) excited chlorophyll can generate singlet oxygen resulting in protein damage (Halliwell and Gutteridge, 1989). During photosynthesis, the photochemical oxidation of H_2O generates O_2 and electrons. Noncyclic electron flow occurs when PSII transfers these electrons to PSI via intermediate electron acceptors and results in the reduction of ferredoxin, which is then used to reduce $NADP^+$ on the stromal side of the thylakoids. A proton gradient across the thylakoid membrane is established as protons are released in the chloroplast lumen during electron transport. This proton gradient is used by a thylakoid-bound ATP synthetase to generate ATP by photophosphorylation of ADP and is also a regulator of electron transport rate and PSII photochemistry (Foyer, 1996). When NADPH/NADP ratios increase, formation of O_2^- via pseudocyclic electron flow to O_2 could serve to maintain electron flow through photochemistry and protect the transthylakoid gradient (Osmond and Grace, 1995; Schreiber and Neubauer, 1990). However, the O_2^- and subsequently formed H_2O_2 could react in the presence of Fe^{2+} or Fe^{3+} to form highly toxic hydroxyl radicals (OH) and must be scavenged to prevent cellular and subcellular damage (Bowler et al., 1992; Halliwell and Gutteridge, 1989). Additionally, excited chlorophyll can transfer energy to O_2 and generate singlet oxygen if the energy is not dissipated by transfer to reaction centers or lost as fluorescence (Demmig-Adams and Adams, 1996). Aside from the damaging effects of OH, H_2O_2 can inactivate several enzymes in the Calvin-Benson cycle, notably the bisphosphatases, as mentioned previously (Buchanan, 1980; Kaiser, 1979). Furthermore, increasing concentrations of H_2O_2 can cause damage to metal-containing enzymes, including superoxide dismutase and ascorbate peroxidase (Bunkelmann and Trelease, 1996; Ishikawa et al., 1996). Thus, the primary role of the ROI scavenging mechanism is to remove O_2 and H_2O_2 to prevent the formation of OH and prevent uncontrolled fluctuations in redox state of the cell.

For chilling-sensitive plant species, decreased photosynthesis in response to low temperature and high light results from stomatal limitations, decreased activity of enzymes involved in carbon assimilation, and inorganic phosphate limitation to ATP synthesis (Holaday et al., 1992; Labate and Leegood, 1988; Perera et al., 1995; Sassenrath et al., 1990). A considerable amount of attention has been focused on the role of the xanthophyll cycle in nonphotochemical dissipation of excess energy (reviewed by Demmig-Adams and Adams, 1994). One postulate is that nonphotochemical quenching (NPQ) involves the direct transfer of energy from excited chlorophyll a to de-epoxidized xanthophyll pigments, zeaxanthin and antheraxanthin, located in the light-harvesting antenna complexes of PSII and PSI (Demmig-Adams and Adams, 1996). NPQ decreases the efficiency of PSII, which slows energy entry into the electron transport chain to rates at which the products of electron transport (e.g., NADPH, ATP) can be used by the leaf. Although it has been suggested that other mechanisms also might contribute to NPQ of chlorophyll fluorescence (Adams et al., 1990; Johnson et al., 1993), this xanthophyll-cycle activity is thought to account for most of the NPQ. Additionally, Sonoike (1996) characterized a novel type of photoinhibition at PSI in chilling-sensitive plants in which ROIs damage the Fe-S centers on the acceptor side of P700. This inactivation of PSI could lead to conditions where electron transport intermediates downstream from PSII remain reduced, increasing rates of PSII inactivation (Sonoike, 1996). Grace and Logan (1996) showed that despite increases in the xanthophyll cycle pool size and in the rate of NPQ, the rate of O_2 photoreduction increased in plants exposed to increasing growth PFD. They concluded that increases in leaf antioxidants, specifically superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), ascorbate, and glutathione protect against this potential oxidative stress. Although several isozymes of SOD, APX, and GR exist in most subcellular compartments, the majority of their activity is concentrated in the chloroplast (Alscher, 1993; Edwards et al., 1994; Foster and Edwards, 1980; Foyer, 1993; Foyer and Halliwell, 1976; Gillham and Dodge, 1986; Hossain et al., 1984). SOD is a major scavenger of O_2^-, and its enzymatic activity results in the production of H_2O_2. In the chloroplast, the H_2O_2 is eliminated by APX (stromal and thylakoid-bound) via the peroxidation of reduced ascorbate (AsA) yielding monodehydroascorbate (MDHA) and H_2O. The MDHA radicals can disproportionate spontaneously into AsA and dehydroascorbate (DHA) or be reduced by ferredoxin or by monodehydro-ascorbate reductase (MDHAR) using NAD(P)H. The reduction of DHA to

AsA by dehydroascorbate reductase (DHAR) is dependent on reduced glutathione (GSH) which is, in turn, maintained by the NADPH-dependent activity of GR. Additionally, GSH plays a role in enzymatic detoxification of other electrophilic compounds in reactions catalyzed by glutathione S-transferases (GSTs). AsA and GSH can also directly serve as reducing agents for nonenzymatic reduction of peroxides and free radicals (Creissen et al., 1996; Foyer et al., 1994).

Genetically Engineering Stress Tolerance. Given that plants are known to increase endogenous levels of antioxidative enzymes, as well as altering rates of protein synthesis or repair (Edwards et al., 1994; Malan et al., 1990; May and Leaver, 1993; Mittler and Zalinskas, 1994; Smirnoff, 1993), one would hypothesize that engineering over-expression of ROI scavengers could enhance chilling tolerance (reviewed by Allen, 1995). A number of studies on transgenic plants that express GST, SOD, APX, and/or GR, as well as other ROI scavengers, have reported enhanced tolerance to multiple stresses (Gill and Tuteja, 2010). In cotton, our group published a number of reports describing the effects of over-expression of ROIs (Korneyev et al. 2001, 2003; Light et al., 2005; Logan et al., 2003; Payton et al. 1997, 2001; Roxas et al., 2000). In general, constitutive over-expression of SOD, APX, or GR alone or co-expression of the transgenes showed downstream biochemical effects that could be attributed to decreased oxidative stress (Korneyev et al., 2003; Payton et al., 2001). However, the intensity and duration of the stress event had significant effects on whether ectopic expression was sufficient for enhanced stress tolerance in the form of protection of the photosynthetic machinery or maintenance of A. For example, short-term, acute exposures to what we defined as moderate stress events (leaf temperatures above 12°C) over-expression of APX and/or GR showed some protection of A in transgenic plants (Korneyev et al., 2001; 2003; Payton et al., 2001). However, in experiments using long-term exposure (Logan et al., 2003) or severe stress events (leaf temperature below 10°C) (Payton et al., 1997), over-expression of ROI scavengers had no significant effect on A. More importantly perhaps, under field conditions or simulated field conditions, over-expression GR had no effect on cold tolerance (Logan et al., 2003; Mahan et al., 2009). In a study of seasonal variation of ascorbate and glutathione pools, Mahan and Wanjura (2005) concluded that although seasonal variation of antioxidants was statistically significant in some instances, the endogenous metabolic capacity for ROI scavenging was sufficient to ameliorate the temperature-related oxidative stresses under field conditions. Furthermore, we postulate that ROI scavenging and antioxidant homeostasis is of such importance in a large number of cellular reactions, that endogenous control of these reactions and metabolite pools supersedes the ability to positively affect scavenging via ectopic expression of these enzymes in cotton.

CHILLING STRESS IN PRODUCTION ENVIRONMENTS— A TEXAS HIGH PLAINS EXAMPLE

Considering the limited agronomic success of ROI scavenger over-expression in cotton, and based on reports by Logan et al. (2003), Mahan and Wanjura (2005), and Mahan and Mauget (2005), the primary question relating to photosynthetic susceptibility of cotton to low temperatures and the impact on yield is: How often is cotton exposed to potentially damaging low-temperature events that might impact yield under relevant production conditions? We present a case study examining the incidence of daytime low-temperature stress in an expanded cotton production season (beginning 1 April, approximately 45 d prior to traditional sowing) and the impact on yield and fiber quality on the Texas High Plains. Cotton has been grown on the Texas High Plains for approximately 70 yr. The region is characterized by a relatively high altitude (~ 100 m) and a potentially short cotton growing season (~ 150 d). The relatively short growing season results from a typical planting date of 15 May and a desire to achieve crop maturity prior to the average fall first freeze date of 31 October.

Low-temperature stress is widely discussed and acknowledged as a potential limiter of cotton production. As documented in the preceding sections, chilling sensitivity generally refers to a specific range of low temperatures that are defined with respect to a specific crop and a physiological or agronomic outcome. As with most crops that are grown in temperate and subtropical environments, cotton is generally cultivated with a growing season that is bounded on both ends by lethally low temperatures. In the interval between the lethal low temperature in the beginning of the growing season and those at season's end, there are planting dates that will almost certainly result in the exposure of the crop to low-temperatures stress at planting, at the end of the season, and, in some locations such as the Texas High Plains, both within a single season.

Low-temperature chilling stress is a direct outcome of the thermal dependence of the metabolic and physiological characteristics of the crop. In a cotton production system, the inherent thermal dependence of the crop becomes largely an agronomic issue that is a consequence of human actions that impose the planting date and the subsequent growing season of approximately 150 d. The vast majority of studies involving low-temperature effects on cotton report the response of cotton (generally seedlings) to controlled low-temperature regimes in growth chambers or temperature cabinets. Such controlled experiments are useful in developing a mechanistic understanding of the source of metabolic limitations at low temperatures. However, under production conditions, the severity, patterns, and effects of low temperatures on cotton are much more complex. Within a continuously variable field environment cotton plants are exposed to a range of temperatures in a diurnal cycle that when viewed over time comprises the seasonal pattern of temperature and chilling stress. There are few examples of low-temperature stress studies under field conditions for cotton (Mahan and Mauget, 2005; Steiner and Jacobsen, 1992).

Chilling stress is associated with air temperatures that result in a reduction in the growth and development of cotton seedlings. Chilling temperatures for cotton that have been addressed in the literature generally are < 12°C. Further, the exacerbation of low-temperature effects on cotton by moderate-to-high light intensities suggests that daytime low temperatures might have negative effects that do not occur during night hours. On this basis we analyzed air temperatures < 12°C as: (1) daily-chilling stress and (2) daylight-chilling stress.

One aspect of low-temperature stress in cotton that has not been explored in detail is the description of low-temperature stress, in terms of severity, duration, and frequency for cotton production systems. Chilling stress can occur during the period immediately after planting and at the end of the growing season. Early- and late-season chilling stresses are both known to adversely affect yield and quality in cotton. Thus the exposure of cotton to low-temperature stress will be a function of both the region's climate and the season end and start dates as determined by planting dates. Cleary, if cotton is planted early enough, seedling low-temperature stress will be guaranteed to occur and, if it is planted late enough, seedling chilling will be absent. In a similar manner, cotton that is planted sufficiently late will not be subject to seedling chilling but often will experience late-season chilling. The potential tradeoff is clear.

Low-Temperature Stress Categories. The relationships between planting date and early- and late-season chilling stresses were investigated by analyzing archival air temperature measurements for Lubbock, Texas (33° 35'37.04"N, 101°53'57.45"W; elevation, 988 m) from 2003 to 2015. Daily-chilling stress was defined as air temperatures < 12°C and daylight-chilling stress was defined as a combination of air temperatures < 12°C and irradiance > 100 W m^{-2}. Early-season chilling stresses were defined as thermal events experienced by cotton seedlings during the first 30 d after planting and late-season chilling stresses were defined as thermal events experienced by cotton plants during the last 30 d of the growing season. The beginning of 30-d end-of-season period, based on a 153-d growing season, was 123 d after sowing. The first and last 30 d of the season were used to calculate the frequency of daily chilling and daylight chilling for 1 April, 1 May, and 1 June planting dates. Figures 1 and 2 show the frequency of chilling air temperatures (daily chilling and daytime chilling) for each year across the three planting dates.

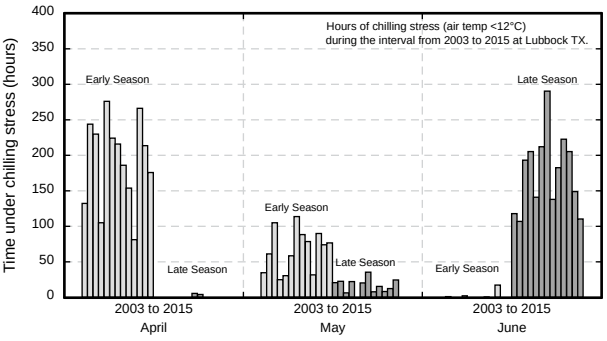

Figure 1. Hours of early- and late-season chilling stress (air temperatures < 12°C) for three planting dates (1 April, 1 May, and 1 June) from 2003 to 2015 for Lubbock, Texas.

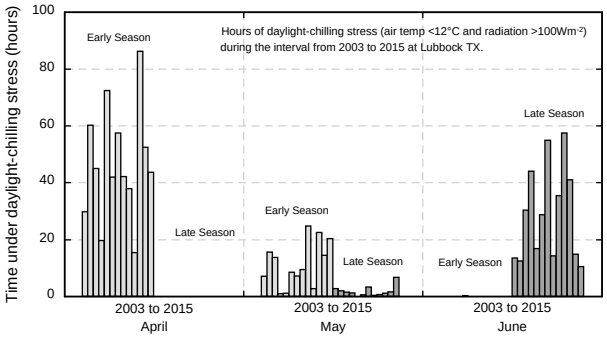

Figure 2. Hours of early- and late-season daylight-chilling stress (air temperatures < 12°C and radiation > 100 W m^{-2}) for three planting dates (1 April, 1 May, and 1 June) from 2003 to 2015 for Lubbock, Texas. Note the scale difference from Fig. 1.

Early-Season Chilling Stress. Early-season daily chilling varied across years and planting dates (Fig. 1). The variation across years appears random, although there is a clear effect of planting date on the number of early-season daily-chilling hours. The April planting had the most hours of early-season daily chilling (81-276 h), May had fewer (24-113 h), and June the fewest (0-17 h). The number of hours of early-season daily chilling on a per day basis was estimated by dividing the hours of daily chilling by 30 or 31 d. On this basis, early-season daily chilling for the April planting experienced the most with an average from 2.7 to 9.2 h/d. The May planting experienced fewer with an average of 0.8 to 3.6 h/d of early-season daily chilling and the June planting experienced the least with an average of 0.2 to 0.5 h/d of early-season daily chilling.

Early-season daylight chilling varied across year and planting dates (Fig. 2). The variation across years appears random, although there is a clear effect of planting date on the number of early-season daylight-chilling hours. The April planting ranged from 0.5 to 3.2 h/d. The May planting experienced an average of 0.03 to 0.8 h/d of early-season daylight chilling and June experienced an average of 0 to 0.008 h/d of early-season daylight chilling.

Late-Season Chilling Stress. Late-season daily chilling varied across years and planting dates (Fig.1). The variation across years appears random, although there is a clear effect of planting date on the number of late-season daily-chilling hours. The April planting had the fewest hours of late-season daily chilling (0-5.6 h), May had fewer (0-35 h), and June the most (107-290 h). The number of hours of late-season daily chilling on a per day basis was estimated by dividing the hours of daily-chilling by 30 or 31 d. On this basis, late-season daily chilling for the April planting ranged from 0 to 0.2 h/d. The May planting experienced an average of 0 to 1.1 h/d of late-season daily chilling and the June planting experienced an average of 3.5 to 9.6 h/d of late-season daily chilling. For late-season daylight chilling (Fig. 2), the April planting experienced no late-season daylight chilling. The May planting experienced 0 to 0.2 h/d of late-season daylight chilling and the June planting experienced an average of 0.32 to 1.9 h/d of late-season daylight chilling.

Planting-Date Chilling Stress Interactions and the Impact on Yield. The data demonstrate the interactions among low-temperature stress, season length, and planting date for cotton within a given environment. On the Texas High Plains, an early planting (April) increases the potential for early-season daily-chilling and daylight-chilling stresses and reducing the potential for late-season daily-chilling and daylight-chilling stresses. A May planting serves to balance the potential stresses and a June planting reduces early-season daily-chilling and daylight-chilling stress at the expense of an increased chance of late-season daily-chilling and daylight-chilling stress.

Figure 3 shows mean yield of multiple sowings from 1 April through 2 July across a range of irrigation levels for cropping years 2012 and 2014 in Lubbock, Texas. In the cases of rainfed and deficit irrigation production scenarios (low and medium rates), despite the fact that early plantings (1-15 April) are exposed to early-season chilling stress (Fig. 2), yields remain relatively stable. In fact, the yields are somewhat stable across the entire range of planting dates (1 April-2 July). However, under full irrigation, whereas early-season planting dates yield similar to traditional planting dates, the late-season planting yields are decreased. This is most likely a function of impaired boll maturation due to late-season chilling temperatures rather than a direct effect on A alone. Nevertheless, the striking point here is the early-season plantings exposed to significantly more hours of chilling in the light, and one would assume decreased A and photooxidative damage during seedling growth, apparently are able to recover from these stressful events and the impact on yield is small, especially under rainfed conditions.

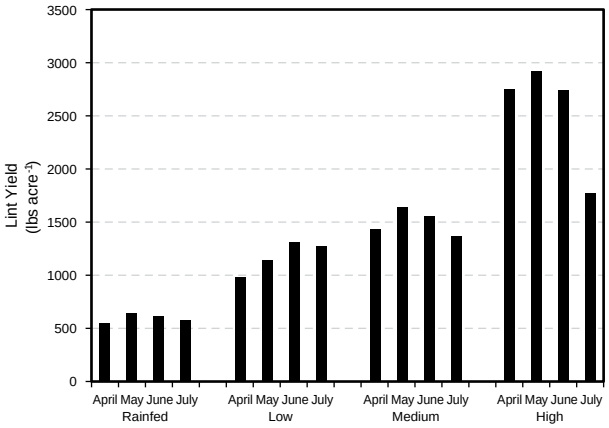

Figure 3. Average lint yield for FiberMax 9180 planted at 4-wk intervals beginning 1 April through 2 July and grown under rainfed, deficit (low, medium), and high irrigation levels in Lubbock, Texas in 2012 and 2014. Bars are combined average yields for each month (two plantings, except July) both years.

The hours of low temperatures vary across the combinations of years, planting dates, and types of chilling stress in a rough pattern. However it is difficult to evaluate the effect of an hour of a given type of chilling stress on agronomic factors of importance in cotton. Many chilling-stress studies have used exposures to low temperatures over the course of hours (Payton et al., 2001) to multiple days (Bange and Milroy, 2004; Bradow, 1991; Christiansen, 1967; Christiansen and Thomas, 1964; Rikin et al., 1979; Sofalian, 2013. Interpreting these controlled studies in terms of field performance of cotton under chilling is problematic at best.

Early-season chilling stresses affect the growth and development of the seedling and thus have the potential to ultimately affect yield and quality. Late-season chilling stresses primarily affect the fruit and can potentially alter yield and quality, but appear to have a larger impact on total yield. The general balance between early-season and late-season chilling stresses seen in this analysis should be true to some extent in any cotton growing region. In regions with longer frost-free periods, the importance of the balance of early- and late-season chilling stresses will be characteristic of the environment. There might be regions where it is important and others where it is agronomically irrelevant.

CONCLUSION

The availability of continuously measured environmental conditions collected with automated weather stations is increasing daily. Researchers now have routine access to such data that were unavailable as recently as a decade ago. Analyses of low-temperature conditions for multiple cotton growing regions over multiple years might be valuable in directing future efforts to develop germplasm and management systems that would make cotton production more resilient.

Given the indeterminate character of cotton, we would contend that the plant has a greater potential to offset negative effects of delayed seedling development under low-temperature growth conditions than it has to offset negative effect on fruit in the days before an end-of-season freeze. This could be a direct function of the resilience of the cotton photosynthetic machinery and endogenous protection mechanisms. Although cotton is considered a chilling-sensitive species, it has a suite of robust mechanisms to cope with excessive light stress and some capacity to acclimate photosynthesis and related processes to chilling that would occur under most production scenarios, most notably early planting dates.

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