ASSESSING PHYSIOLOGICAL RESPONSE TO DROUGHT AND EVALUATING WATER USE-EFFICIENT IRRIGATION SCHEDULING FOR COTTON GROWN IN GEORGIA

by

CALVIN DOUGLAS MEEKS

(Under the Direction of John Snider)

ABSTRACT

Cotton irrigated acreage is predicted to increase 89 percent in Georgia by 2050. Research was conducted to 1) define early season soil-moisture thresholds for improving irrigation management 2) evaluate agronomic and physiological effects of plant–based irrigation thresholds in combination with high biomass rye cover crops and 3) assess physiological effects of various early season drought durations on multiple modern cotton cultivars in a greenhouse setting. Field experiments were conducted at Stripling Irrigation Research Park (SIRP) near Camilla, GA in 2014 and 2015, at the Lang-Rigdon Research Farm near Tifton, GA during 2014 and 2015, and in greenhouses on the UGA campuses near Athens in 2014 and near Tifton in 2016. The studies reported on in the current dissertation 1) define soil moisture-based irrigation thresholds that decreased early season water use without penalizing yield, 2) demonstrate increased water potential for cotton planted into a high biomass rye cover crop but did not demonstrate a yield or water use benefit, and 3) identify the overriding physiological factors contributing to poor early season growth under drought.

INDEX WORDS: Cotton, Drought Avoidance, Irrigation, Water, Soil Moisture

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INTRODUCTION AND LITERATURE REVIEW

This literature review summarizes the importance of efficient irrigation for cotton in Georgia, and the effects of water stress on cotton (*Gossypium hirsutum*) physiology, growth, and yield. The utility of remote sensing of row crops (cotton in particular) for assessing canopy development and drought stress detection, particularly via aerial imagery, are highlighted. Additionally, the potential for cover crop utilization and alternative irrigation strategies to improve water use efficiency and impact cotton yields and physiological processes are discussed. Agricultural production and processing consumes approximately 70% of all freshwater usage by modern civilization, more than twice the amount of industrial, municipal, and other users (Clay, 2004). Another factor expected to further exacerbate the strain on fresh water resources is that global populations are predicted to approach 9 billion by 2050 (McKenna, 2012). Current predictions indicate that even more water will be required since population growth by 2050 to 9 billion would require a 60% to 70% increase in food production (McKenna, 2012). Current crop water use efficiencies (WUE) do not lend well to this increase in food production due to the fact 70% is already being utilized for agricultural production and processing and increasing crop dry matter 60 to 70% would require an additional 2.76 kg/ha per mm of applied water for rice alone. Cotton currently has a WUE of 6.8 kg/ha per mm of water applied compared to WUE 17.2 for corn and WUE 4.6 for rice (Fageria, 2012). Therefore, cotton yields alone indicate substantial yield losses if the amount of irrigation available were reduced (60.8 kg loss per hectare by a mere 10 mm loss in applied water). The 60 to 70% increase in production would in turn require a 50%

increase in agricultural water usages on top of the current usage (Clay 2004) which is an unsustainable prospect. Locally, population growth in the state of Georgia and episodic drought typical of the region's summer climate has greatly increased the demand of groundwater resources in the state of Georgia. Irrigation in Georgia accounted for 41% of total state water usage in 2004 (Hutson, 2004), and irrigation of many crops is now seen as a necessity by producers in order to minimize risk and allow for sustainable and profitable operations due to declining commodity prices. In order to increase yields at current water usage levels, WUE must be maximized by utilizing alternative irrigation techniques and methods that have been developed but are not currently in widespread use. In order for this to happen, more intensive research and increased grower education will be required as well. The climates of the humid southeastern United States, as well as similar regions, receive total rainfall during a typical growing season that can provide adequate moisture for profitable crop production (Ritchie et al., 2009); however, supplemental irrigation can lead to increased lint yield and greater yield stability, especially in years with less than normal summer rainfall or during summers with low rainfall specifically during periods of high water demand by the crop (Ritchie et al., 2009). The benefits of supplemental irrigation are recognized by producers in the region who tend to irrigate as needed; however, determinations of when to irrigate are usually not based on plant or soil based sensing methods (Bednarz et al., 2002). Due to competition for water resources with municipalities and other industries and limits on surface and groundwater withdrawals such as the set minimum flows for both surface and groundwater resources in the Flint River basin of Georgia, increased WUE is a must in order for producers to maintain profitability in the future (Hook et al., 2001, Corn et al., 2008).

In addition to using better irrigation scheduling methods, a number of other production practices exhibit the potential to improve WUE in row crop production and include alternative irrigation practices (e.g. deficit irrigation, partial root-zone drying, primed acclimation), altered row spacing, enhanced soil management, improved soil water retention through cover cropping, etc. (Hatfield et al., 2011, Ritchie et al., 2009, Rowland et al., 2012). As an example, conservation tillage with a cover crop such as cereal rye (*Secale cereal*) has been touted to save up to 14% percent more water compared to conventional tillage methods (Sullivan et al. 2007). It is, therefore, expected that WUE could be maximized in cotton production systems if more accurate plant or soil-based irrigation scheduling triggers were coupled with alternative irrigation scheduling methods or the use of high-biomass cover crops. Thus, we plan to evaluate the use of plant-based water potential measures, coupled with heavy rye cover crops for use in modification of traditional irrigation management to maximize WUE. Furthermore, remote sensing via aerial imagery as well as soil water potential sensors will be evaluated as methods for detecting optimum irrigation scheduling thresholds and water management strategies.

Cotton growth and water stress

Water is the main component of actively growing plants, ranging from 70 to 90 percent of total fresh plant mass and is essential for nutrient transport, chemical reactions, cell enlargement, and transpiration (Gardner et al., 1984). Massacci et al (2008) observed daily declines in stomatal conductance that occurred at significantly greater rates for cotton leaves that were stressed as compared to leaves from well watered cotton plants. Because the availability of water to a plant has a significant impact on a large number of physiological processes, all plants can be negatively affected by soil moisture deficit which leads to inhibited plant growth and development, hindered cell expansion, altered enzyme activities, and eventually decreased respiration, photosynthesis, and assimilate translocation (Loka et al., 2010). Lokhande and Reddy (2014) determined that water deficient cotton had low photosythetic rates which stemmed from stomatal reductions and significant reductions in seed cotton produced per plant.

Drought spells cause devastation within agricultural production (Wilhite, 2000; Humphries and Baldwin, 2003), and past agricultural societies have collapsed due to extended drought periods (Kennett et al., 2012). Domestic upland cotton (*Gossypium hirsutum* L.) ancestors were viny perennial plants with an indeterminate growth habit that were native to semi-arid, sub-tropical environments that experienced periodic drought and temperature extremes which these plants adapted to (Kohel et al., 1974). These wild cotton cultivars produced abundant vegetative growth under favorable growing conditions, which included adequate water and nutrients (Ritchie et al., 2007). Vigorous vegetative growth allows for greater light interception early during the growing season, but excessive vegetative growth can decrease the total number of bolls that are produced since resources are diverted away from reproductive growth and toward vegetative growth instead (Loka et al., 2010), which can limit lint and seed production (Ritchie et al., 2009). These characteristics of cotton influence how cotton is to be managed, as commercial production in the U.S. requires cotton to be produced as an annual crop through maximizing production and retention of harvestable fruit within a single season. Although cotton is classified as a crop species with an indeterminate growth habit, for commercially grown cotton, cultivars with more “determinate” growth habits are desired to limit vegetative growth and enhance fruit production (Jost et al. 2006); however, limiting vegetative growth is usually achieved through the use of exogenously applied gibberellin-inhibiting plant growth regulators (e.g. mepiquat chloride) (Jost et al., 2006, Vellidis et al., 2009). Because cell expansion is the most sensitive physiological process to drought stress (Hsiao, 1973), it is not surprising that irrigation timing, rates, and methods have demonstrated utility in affecting vegetative growth (Ritchie et al., 2009). Thus, in addition to optimizing WUE, yield, and fiber quality, efficient irrigation practices also reduced the need for plant growth regulators via vegetative growth suppression (Whitaker et al., 2008).

Water requirements of cotton

Bednarz et al. (2002) found that cotton grown in Southern Georgia requires a minimum of 46 cm of water per growing season for maximum yields to be achieved. Rainfall data deceptively indicate adequate rainfall to meet these goals since Georgia received an average of 52.7 cm of rainfall during the typical growing season (1 May - 31 September) during 1971-2000, and more recently, an average of 46.3 cm from 2009-2012 (Georgia Automated Environmental Monitoring Network, 2013). This observation suggests that average seasonal rainfall should be sufficient for cotton production in this region; however, episodic drought and the course-textured, sandy soils that have poor water retention comprise the majority of cultivated land in Georgia (Chesworth et al., 2008). These factors can lead to suboptimal or insufficient soil moisture for the crop during periods of critical water demand and emphasize the need for supplemental irrigation in this region even though average seasonal rainfall suggests that cotton water requirements meet the criteria defined by Bednarz et al. (2002).

The environment of this region is also prone to heat stress or increased evaporation of needed water due to high temperatures during the growing season. For example, daily average temperatures during the typical growing season averaged 25.7 °C from 1971 to 2000 and 26.2 °C in more recent years (2009-2012). Average maximum daily temperatures were 32.0 °C from 1971 to 2000 and 32.6 °C from 2009 to 2012 (Georgia Automated Environmental Monitoring

Network, 2013). Yield losses due to increased boll abscission during heat stress have been observed (Reddy et al., 2002). High temperatures can also negatively impact pollen germination (Burke et al., 2004; Kakani et al., 2005), pollen tube growth (Burke et al., 2004; Kakani et al., 2005; Snider et al., 2011a), and fertilization efficiency (Snider et al., 2009; Snider et al., 2011b), which can limit the number of seed per boll and negatively impact yield (Oosterhuis and Snider, 2011; Pettigrew et al., 2008). Elevated air temperatures can increase evapotranspiration by increasing atmospheric demand leading to an increase in crop water requirements (Hargreaves and Allen, 2003). Although cotton has an exceptional ability to cool its canopy below air temperature when water is not limited (Upchurch and Mahan, 1988), drought stress decreases stomatal conductance (Baker et al., 2007; Conaty et al., 2012; Snider et al., 2014), which increases canopy temperature (Taiz and Zeiger, 2010) and reduces photosynthetic rates likely due to the synergistic, effects of high temperature (Law and Crafts-Brandner, 1999; Crafts-Brandner and Salvucci, 2000; Salvucci and Crafts-Brander, 2004; Wise et al., 2004) and drought (Baker et al., 2007, 2009; Chastain et al., 2014; Snider et al., 2014).

Whole plant physiological responses to drought

Drought stress has been shown to negatively affect boll retention, this reduced boll retention ultimately leads to reduced yield as well as reduced lint quality due to the fact that the greatest number of yield-contributing bolls and highest quality bolls are located on the lower nodes in the plant and usually on the first position of each node (Pettigrew, 2004). Drought stress prior to first bloom can result in abscission of young squares; flowers are insensitive to drought stress and will not abscise. However, after flowering, young cotton bolls are quite sensitive to drought stress which leads to abortions if water deficit is experienced while the bolls are young and green (Loka et al., 2011; Loka and Oosterhuis, 2012). Periods of water deficit also cause vegetative growth to slow which in turn causes plant height/terminal growth to increase at a slower rate as compared to well watered conditions (Ritchie et al., 2009). This reduced height increase/terminal growth also decreases the rate of node development (Ritchie et al., 2009) thereby limiting upward development of effective fruiting sites. Maturity, as measured by nodes above the first square and nodes above the uppermost first-position white flower (Bourland et al., 1992; Bourland et al., 2001; Brown and Oosterhuis, 1992), is hastened under drought due to reduced upward growth. Hastened maturity can potentially lead to early "cutout", i.e. the premature cessation of vegetative growth. Premature cutout tends to adversely affect yields by limiting the number of fruiting sites per plant. Fruit loss due to mild-to-moderate water stress occurring later in the growing season has been documented with plants that produce and retain fewer upper bolls due to boll sheds on nodes near the top of the plant (Cetin and Bilgel, 2002). Drought has been shown to decrease stem height, stem dry weight, leaf area, leaf dry weight, and total number of main stem nodes in cotton as well (Pace et al. , 1999; Ritchie et al. 2007).

Vegetative above ground physiological responses

Growth is the most sensitive physiological process to drought stress due to declines in cell turgor pressure which limits cell expansion (Hsiao, 1973; Ball et al., 1994). Leaf expansion has been observed in the past to be more sensitive to water deficits than the root expansion (Ball et al., 1994). However, this response can increase the ratio of root growth compared to above ground shoot growth such that boll abscission increases and harvestable lint yield is reduced for dryland cotton (Cook and El-Zik, 1992). Thus, the results of the aforementioned studies provide abundant reason to avoid drought stress in order to maximize yield and profitability. Leaf expansion limitations from drought stress were also observed by a number of authors (Matsuda and Riazi, 1981; Masle and Passioura, 1987; Cutler et al., 1977). This is especially important due to the fact that leaf expansion declines have been observed in as little as 2 days of drought stress (Ball et al., 1994). Ball et al., (1994) noted as well that a rebound in leaf expansion was observed 5 days after drought stress was alleviated; however, water deficit treatments had significant reductions in leaf area index (LAI) at season's end.

Total above ground carbon assimilation has been shown to be dependent upon leaf area and photosynthetic efficiency (Gardner et al. 1985; Kreig and Sung, 1986; Turner et al. 1986). Net photosynthesis is negatively affected by drought stress in cotton (Pettigrew 2004; Ennahli and Earl, 2005; Snider et al. 2014; Chastain et al., 2014). Canopy-level carbon assimilation (total source strength) is primarily limited under drought due to decreased total leaf area which causes reduced light interception by photosynthetic surfaces (Wells and Stewart, 2010; Kreig and Sung, 1986; Turner et al. 1986). It is well-established that photosynthetic efficiency of drought stressed individual leaves decreases compared to well watered plants (Pettigrew 2004; Ennahli and Earl, 2005; Snider et al. 2014; Chastain et al., 2014); however, individual leaf photosynthesis has been observed to be less sensitive to both soil and leaf water deficits than leaf area development (Turner et al., 1986). Increasing leaf area has been indicated to lead to more productive plants in general (Hirose et al., 1997).

Fiber quality effects due to drought stress

Fiber quality is significantly affected by drought stress, with fiber length and thickness reductions being observed in situations of less than optimal moisture (Pettigrew et al., 2004). Leaf water potential reductions from drought stress have been reported to cause linear reductions in fiber length and strength (Lokhande and Reddy 2014). This study also demonstrated fiber uniformity reductions when leaf water potentials declined and that fiber strength was highly impacted by low water potential (Lokhande and Reddy 2014). Similar results were observed for fiber quality parameters by a number of other authors as well (Krieg, 2002; Reddy et al., 1992, Wanjura et al., 2002). The three stages of fiber development prior to maturation: fiber initiation, fiber elongation, and fiber thickening take a substantial amount of time to complete with initiation occurring on the day of anthesis and continuing into the elongation phase which occurs immediately following initiation and continues for 20-30 days. Fiber thickening overlaps with the elongation phase and concludes approximately 42 days past anthesis; therefore, a substantial time period is available for drought stress to negatively affect fiber development and lint yield (Oosterhuis, 1991; Gokani and Thaker 2002, Lee et al., 2007).

Physiological responses to excessive irrigation

Providing excess irrigation can result in yield reductions due to increased fruit shed (Cetin and Bilgel, 2002). Specifically, over-irrigating beyond what is required by cotton, often causes excessive vegetative growth which can potentially cause boll losses at lower nodes on the plant (Cetin and Bilgel, 2002; Ritchie et al., 2007, 2009). However, larger plants allow for more fruiting sites and greater leaf area which potentially could compensate for poor fruit retention on lower nodes if the growing season is sufficiently long. This situation can be advantageous in some situations if optimal fruit set lower in the plant is lacking. However, this effect can be problematic when excessive irrigation leads to lower nodes losing critical fruit (Ritchie et al., 2007, 2009). Full-season climates can avoid some of the adverse yield effects of shifting boll production to the upper nodes due to longer periods of suitable heat unit accumulation, though the upper bolls tend to produce lint of lower quality whereas bolls on lower nodes tend to produce higher quality lint (Cetin and Bilgel, 2002; Ritchie et al., 2007). However, even in regions such as southern Georgia, the growing season can be limited by cooler late-season weather and periodic frost events, which would prevent compensation for poor early season fruit retention. (Ritchie et al., 2009). Preventing excessive irrigation also alleviates the lodging concerns that can come from a tall plant with a top heavy boll load especially in an environment that is subject to tropical weather systems and the high winds associated with those systems.

Another concern with irrigated cotton is that overhead (OVHD) irrigation can cause pollen rupture which in turn leads to fruit loss (Burke 2003). Subsurface Drip Irrigation (SDI) is currently used in Texas and other arid environments due to its increased efficiency and the problematic issues associated with declining aquifer levels (Bordovsky et al., 2000). The state of Georgia is currently involved in its own water war with its neighboring states which makes this technology more appealing**.** In areas of Texas where irrigation water is supplied by the Ogallala aquifer, over 100,000 ha of SDI is currently used (Colaizzi et al., 2008), whereas the applications of SDI in row crop production have been much more limited in Georgia. SDI systems in TX include yield improvements as well as water savings when compared to OVHD systems, which holds great promise for producers in other states to increase their WUE (Bordovsky and Porter, 2003; Colaizzi et al., 2004, 2005, 2006). Currently 45% of cotton in GA is irrigated yearly (Guillebeau, 2006), mostly with OVHD systems due to the simplicity of these systems, the longevity, and the nonexistent limits on tillage methods. Therefore, WUE must be maximized with the OVHD systems in current use to ensure efficiency while protecting yield potential as well as producer profitability.

Environment-based irrigation triggering methods

Proper irrigation scheduling should allow a producer to decide when to irrigate a crop as well as the amount of water needed to maximize WUE while not limiting yield. A “checkbook” approach has been utilized in Georgia is recommended by the University of Georgia Cooperative extension service (Collins et al., 2013).

This approach has been well documented as an effective method for irrigating cotton (Lundstrom and Stegman, 1983; Allen et al. 1998; Fisher and Udeigwe, 2012, Meeks et al. 2013, Chastain et al,., 2014). Checkbook approaches to managing irrigation simply utilize irrigation as a supplement to the rainfall received per week. The UGA checkbook is based on weekly amounts needed by cotton plants based on the weekly growth stage so that moisture is not a limiting factor. Producer observations have indicated this practice to be effective for maximizing yield (Meeks et al., 2013). Previous results when compared to soil moisture, however, highlight the need for flexibility to be added to this approach since utilizing soil moisture sensors have led to similar yields with significantly higher WUE (Meeks et al., 2013). Thus, irrigation scheduling decisions could be adjusted based on in field parameters such as temperature and soil moisture levels, which could lead to higher WUE. Other adjustments should be made due to the fact that soil moisture sensors give an accurate soil moisture measurement versus just a rainfall amount since the rainfall amount cannot take into account runoff, especially from episodic severe thunderstorms. If more advanced methods to irrigation scheduling could be done in a producer-friendly manner, WUE improvements would likely be embraced by producers due to reduced cost from irrigation while saving critical water resources.

Evapotranspiration (ET) estimates have demonstrated utility in irrigation scheduling with the simple UGA EASYpan device that has produced results within 5 mm of Watermark granular matrix soil water sensors (Thomas et al., 2004; Thomson and Fisher 2006). The drawback with this system is the amount of maintenance required since it must remain level and at the same height with the crop canopy. Soil moisture sensors can help capture variation in soil moisture throughout a field (Leib et al., 2003; Jones, 2007; Meeks et al., 2013) and tend to be advantageous due to the ability to access soil moisture data remotely from personal computers or smartphones.

Plant-based irrigation triggering methods

From the physiologist's perspective, irrigation triggers that use the plant to sense its environment offer advantages over the water balance approaches discussed previously because the cotton plant integrates soil, atmospheric, and plant factors such that the need to irrigate can be accurately determined from the water status of the plant (Jones 2007; Chastain et al., 2014). Leaf water potential (Ψ_l) is a direct method of measuring plant water status, though variability in readings is possible due to environmental factors (Jones, 1990; So, 1979; Chastain et al., 2014). Grimes and Yamada (1982) demonstrated relatively stable and maximum water potentials predawn within the 2 hours prior to sunrise and observed values at their minimum in the afternoon (1200 to 1500 h). For those not inclined to be in the field during predawn hours, convenience would dictate that midday readings would be the most likely to be utilized. Optimum yield was observed by Grimes and Yamada to occur if -1.8 MPa to -2.0 MPa readings were used to trigger irrigations (1982). Fiber-elongation was observed to be stable until -2.8 MPa was reached which lead to rapid decreases in elongation leading Grimes and Yamada (1982) to conclude that fiber growth may be a preferred sink when the plant encounters high levels of drought stress. Optimal square retention was observed by maintaining midday leaf water potentials above -1.4 MP (Hake and Grimes, 2010; Hake et al., 1996), Photosynthesis is negatively impacted at levels of midday leaf water potential below -1.9 MPa (Turner et al. 1986; Pettigrew, 2004; Ennahli and Earl, 2005; Snider et al., 2013). Though far less convenient, predawn water potential (Ψ_{PD}) has been determined to be an excellent indicator of plant stress due to being influenced to a lesser degree by environmental factors (Ameglio et al., 1999, Chastain et al., 2014). Utilizing canopy temperature measurements such as those from a thermal camera mounted to an unmanned aerial vehicle, however, would allow for a more rapid measurement. These temperature measurements have been suggested as a method to estimate water potential levels (Jones, 1999; Saha et al., 1986). One problem with the aforementioned plant-based methods is that they do not give a measure of the amount of water to be applied to relieve the drought stress (Jones 2004). Estimates of daily water use by the crop will likely need to be coupled with plant-based triggers to ensure that water is received when it is needed and in the amount needed.

Cover crop benefits

Glyphosate-resistant Palmer amaranth has caused many producers to abandon conservation tillage and revert back to tillage and cultivation along with herbicides (Shurley et al., 2013). However, since conservation tillage has been touted to save up to 14% percent more water compared to conventional tillage methods, (Sullivan et al. 2007), methodologies should be developed to protect cover crop-derived water savings, while also maintaining control over glyphosate resistant Palmer amaranth. A high-biomass rye cover crop (heavy biomass) to control glyphosate resistant Palmer amaranth in a conservation tillage system planting a Roundup-Ready Flex® variety has been demonstrated by Stanley Culpepper at UGA(Shurley et al., 2013). The heavy rye cover provides savings in herbicide expense, but these savings were more than offset by other costs such as the seed required for the cover crop, additional nitrogen required by the cover crop, and the additional fuel for rolling of the rye (Shurley et al., 2013). Irrigation efficiency has yet to be examined with this system; however, multiple location studies in other states have demonstrated high residue conservation tillage systems as higher yielding than conventional tillage systems (Price et al. 2012). The possibility exists for higher yields and increased WUE to offset the costs of using such a system.

Conservation tillage (CT) has numerous environmental benefits, such as controlling soil erosion and reducing runoff, and increasing soil organic matter near the soil surface (Reeves 1994; Reeves 1997; Truman et al. 2003, Price et al., 2011; LeBissonnais 1990; Truman et al. 2005). Increasing soil organic matter directly affects soil water holding capacity because organic matter has nearly four times the water holding capacity of mineral soil (Hudson 1994). Cover crop residues also can be utilized to dissipate rain drop energy which leads to slower losses from runoff (Baumhardt and Lascano 1996, Price et al., 2011). Increasing soil aggregate formation and soil stability is a byproduct of CT (Bruce et al. 1992) which reduces the potential for crust formation and surface sealing. These soil improvements from CT lead to improved water infiltration leading to increased water storage in the soil profile (Kemper and Derpsch 1981; Bruce et al. 1992; Truman et al. 2003).

New herbicide technologies hold great promise for a return of producers to CT production (Wychen, 2013) which could increase their WUE in the long run. Additionally, since CT requires additional equipment, preplant spraying, and the rolling of the cover crop, increased WUE must be obtained to offset the additional labor and production costs in order to make the system attractive to producers (Shurley et al., 2013).

Primed acclimation

Irrigation management strategies have been developed that utilize deficit periods that are timed to coincide with certain crop developmental stages that allow for vegetative growth to be restrained while not negatively impacting crop yield (Girona et al., 1993, Rowland et al., 2012).

Regulated Deficit Irrigation (RDI) was a method developed by Mitchell et al. (1984); RDI utilizes reduced irrigation while the crop is in its vegetative growth stages, so that the crop has adequate water applied during critical reproductive stages, which maximizes WUE without reducing yield (Rowland et al., 2012). Some cotton producers in Georgia refuse to irrigate early during crop development in order to encourage root growth. This rationale has some credence since this approach could potentially increase root growth, allowing plants to utilize a deeper soil water profile (Rowland et al., 2012). Chaves and Oliveira (2004) demonstrated increased water productivity (WUE) by utilizing RDI to split irrigation, where the crop in vegetative stages received reduced irrigation and moisture, but received full irrigation during critical reproductive stages of growth. This technique (hereafter termed primed acclimation) has been successfully demonstrated to save water without reducing yield, in some cases actually increasing yield in peanut (*Arachis hypogaea* L.) (Rowland et al 2012). Plants produced under primed acclimation conditions have demonstrated improvement in their WUE as well as photosynthesis when compared to non-acclimated plants under drought stress (Flexas et al., 2006, Rowland et al., 2012). These acclimated plants have also been demonstrated to have a better optimization of water use (Chaves et al., 2003, Rowland et al., 2012). Physiological alterations resulting from prior exposure to stresses (one example being histone modification) are often retained by plants the entire growing season (Bruce et al. 2007). The primed acclimation irrigation strategy has not been tested in a typical cotton production setting. The key to successfully using this approach is to not place cotton under severe, yield-limiting stress during vegetative development (Perry et al., 2012). Research in Arizona has indicated that an optimum irrigation point can be defined using heat units accumulated after planting (HUAP, 86/55° F), where the first irrigation is triggered at a level of 800-1000 HUAP (Silvertooth et al., 2001). Physiologically, cotton plants in this environment develop first pinhead squares at 700 HUAP (usually on nodes 5-7) with matchhead squares developing by 900 HUAP (Silvertooth et al., 2001). Course soils require irrigation by 700 HUAP with negative yield impacts occurring by 1200 HUAP (Silvertooth et al., 2001). Advances in soil moisture sensing should allow researchers to accurately define early season soil moisture thresholds to prevent excessive plant stress while keeping WUE optimal. However, studies assessing sensor-based primed acclimation strategies for field grown cotton are, to our knowledge, nonexistent.

Remote sensing and new technologies for crop stress detection

High labor costs have made remote sensing platforms (e.g. satellites, airplanes, unmanned aerial vehicles, etc.) and ground-based platforms appealing from an agricultural standpoint. These platforms have been utilized to collect data on a far greater scale than conventional handheld measurements (Sui et al., 2005; Vierling et al., 2006; Yang et al., 2001; Yang et al., 2003; Ritchie, et al. 2007; Ritchie et al., 2010). These systems are particularly advantageous since they require little to no labor assistance once they are in place with the only disadvantage being their high cost of acquisition (Sui et al., 2005; Vierling et al., 2006; Yang et al., 2001; Yang et al., 2003; Ritchie, et al. 2007; Ritchie et al., 2010). Large aircraft and satellites tend to have resolution that is not adequate for detecting slight differences in plant canopies within a single field. Alternative platforms, such as tethered blimps, have demonstrated promise in imagery and spectrometry (Chen and Vierling, 2006; Vierling et al., 2006, Ritchie et al., 2010) in that they are both stable and economical. These units are also ground-tethered; therefore, licensing is not required for use. However, mobility is limited with tethered blimps. With the ever-increasing use of Unmanned Aerial Vehicles (UAV), remote sensing platforms are becoming economical enough for actual field use by a producer. A method using a UAV and image processing techniques (digital image derived indices discussed in subsequent sections) has demonstrated prediction with an average accuracy value of 89% as compared to handheld SPAD chlorophyll meter readings (Teoh et al., 2012). While these evaluations were based upon just three levels of nitrogen stress, the results noted above suggest that UAV's should be strongly considered as an alternative platform for remote sensing. Due to their stability and ease of use, quadrotor UAVs demonstrate the potential for use as low cost crop scouting tools, and the availably of these units are much greater than other remote sensing platforms (West 2014).

Remote sensing has often been used to provide crop growth estimates, which are primarily vegetation indices, such as the normalized difference vegetation index (NDVI) (Elvidge and Chen, 1995; Huete, 1988; Ritchie et al.; 2007, 2010; Rouse et al.; 1973). NDVI = (near infrared — visible)/(near infrared + visible), with observed wavelengths of 650nm to 750nm for the visible wavelength and 750 to 800 nm for near infrared. When attempting to use vegetation indices to estimate crop growth, soil reflectance effects as well as atmospheric effects must be accounted for (Ritchie et al., 2010). Therefore, vegetation indices were developed to measure ratios of visible and near-infrared reflectance because healthy green cover reflects substantially more near-infrared than the visible wavelengths as compared to drought-stressed green cover (Govaerts and Verhulst, 2010). These indices were utilized to distinguish between the two canopies (stressed and unstressed) as well as distinguish canopy from soil since soil reflects similar amounts of visible and near-infrared light (Asner et al., 2000; Ritchie et al., 2010). Stressed vegetation reflects significantly different levels of near-infrared compared to visible light when compared with a healthy plant canopy (Ritchie et al., 2010). These demonstrations indicate that vegetation indices can be used effectively to map crop growth characteristics as well as to detect general stress events in the plant canopy (Klassen et al., 2003; Osborne *et al.*, 2002; Plant *et al.*, 2000, Ritchie et al., 2010)

Spectral reflectance has been demonstrated to differ considerably with drought stressed vegetation in the near infrared region (700-1300 nm) and in the visible red range (550-700 nm) (Kumar and Silva, 1973; Govaerts and Verhulst, 2010). Due to the presence of chlorophyll, visible light reflectance is higher for green wavelengths than for blue and red (Govaerts and Verhulst, 2010). Thus, a green/red index can be determined from conventional images as demonstrated by Ritchie et al. (2007, 2010). This method, first discussed by Adamsen (1999), utilizes a ratio of the measured green hex values to red hex values as determined by a digital camera on the RGB scale of 0-255. This index could be applied to a UAV-based camera system to demonstrate a low cost aerial imagery-based measure of crop growth.

Although they do not qualify as remote sensing tools, portable chlorophyll fluorometers (CF) have been used to detect abiotic stress (including drought and high temperature stress as examples) and have been proposed as useful tools for high throughput drought or heat tolerance screening (Burke, 1990; Burke, 2007) due to rapidity of measurement (approximately 1 s per reading) and because they provide an accurate measure of photosynthetic processes *in vivo*. Some of the common parameters derived from chlorophyll a fluorescence measurements include maximum quantum yield of photosystem II in dark-adapted leaves (F_v/F_m), actual quantum yield of photosystem II in illuminated leaves (Φ_{PSII}), and photosynthetic electron transport rate (ETR) (Chastain et al., 2014; Flexas et al., 1999; Maxwell and Johnson, 2000; Snider et al., 2009, 2010; Valentini et al., 1995; Woo et al., 2008; Zhang et al., 2011). One major drawback to the use of some of the aforementioned parameters for stress detection in cotton is that F_v/F_m, Φ_{PSII}, and ETR are extremely tolerant to both drought and high temperature extremes (Chastain et al., 2014;

Snider et al., 2013, 2014). Thus, CF may have limited utility in detecting the early stages of drought or high temperature stress when traditional fluorescence parameters are utilized. More recently developed chlorophyll fluorescence parameters derived from “fast” or “OJIP” fluorescence analysis (O, J, I, and P are just used to indicate steps in the fluorescence trace and are not abbreviations for other terms; Strasser et al., 2000), have been touted as more sensitive indicators of drought and high temperature stress in other plant species (Boureima et al., 2012; Oukarroum et al., 2007, 2009; Tan et al., 2011). However, the utility of these novel methods for detecting early drought stress has not been evaluated for field-grown cotton. It is anticipated that combining novel CF measurements with RGB derived vegetation indices should be highly predictive of crop performance since one method measures photosynthetic efficiency and the other method measures canopy development.

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Chapter 1

ASSESSING THE UTILITY OF PRIMED ACCLIMATION FOR IMPROVING WATER SAVINGS IN COTTON USING A SENSOR-BASED IRRIGATION SCHEDULING SYSTEM[1]

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[1] Meeks, C.D., J.L. Snider, W.M. Porter, G. Vellidis, G.L. Hawkins, and D.L. Rowland. 2017. *Crop Science*. 57:1–13.
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Abstract

This study addressed the potential of reduced prebloom irrigation, referred to as primed acclimation (PA), to increase agricultural water-use efficiency (WUE) using a soil-moisture-based irrigation scheduling system in cotton (Gossypium hirsutum L.). To address this, a study was conducted near Camilla, GA, under a variable-rate, center-pivot irrigation system using a Watermark-based automated soil moisture potential sensing approach to measure soil water potential (SWP) and impose varying irrigation scheduling treatments during the prebloom stage of development. Early season thresholds were −20 (Treatment 1), −40 (Treatment 2), −70 (Treatment 3), to −100 kPa (Treatment 4) prior to flowering. Reductions in prebloom irrigation of up to 17% were noted in this study for the driest thresholds (−100 kPa) with no reduction in lint yield relative to the −20 and −40 kPa thresholds. In some cases, prebloom irrigation was eliminated completely in the drier prebloom threshold treatments with no appreciable yield reductions. In rainfed treatments, episodic drought during flowering (2014) limited plant growth and node production, hastened cutout, decreased boll numbers per plant, produced a more compact boll distribution on the plant, and decreased yield and WUE relative to irrigated treatments. In contrast, season-long rainfed treatments exhibited the highest WUE in 2015 (a wet season). The results of this study conclude that prebloom irrigation thresholds between −70 and −0 (Treatment 3), to −100 kPa (Treatment 4) prior to flowering. Reductions in prebloom irrigation of up to 17% were noted in this study for the driest thresholds (−100 kPa) with nlity and WUE for cotton production in the southeastern United States.

Introduction

Irrigated crop land estimates have relatively stable irrigated acreage projections in the near future except for cotton, which is projected to increase in irrigated acreage two-fold by 2050 (Cai et al., 2010). Episodic drought in humid regions, like the southeastern United States, leads to additional irrigation being applied to supply the 460 mm of total season water needed for optimum yields of cotton (Bednarz et al., 2002). Global agricultural production and processing consumes ~70% of all freshwater, more than twice the amount of industrial, municipal, and other users combined (Clay, 2004). Another factor expected to further exacerbate the demand on fresh water resources is that global populations are predicted to approach 9 billion by 2050, which would require a 60 to 70% increase in food production (Mckenna, 2012). Agriculture irrigation accounted for 41% of the total water usage in Georgia for 2004 (Hutson et al., 2004), with irrigation of many crops now seen as a necessity for sustainable and profitable commercial farming. Episodic drought leads to significant yield losses with extended periods of drought causing devastation within agricultural production (Wilhite, 2000; Humphries and Baldwin, 2003). In an attempt to balance the need to conserve water resources with the need to irrigate to maximize yield and limit risk, recent research efforts have been aimed at improving the efficiency of irrigation management without penalizing yield (Whitaker et al., 2008).

Irrigation management strategies have been developed that use periods of deficit irrigation that are timed to coincide with specific crop developmental stages to restrain vegetative growth while not negatively impacting crop yield (Girona et al., 1993; Rowland et al., 2012). Regulated deficit irrigation (RDI) was a method developed by Mitchell et al. (1984), which uses water deficits timed to particular crop growth stages in an effort to conserve water while avoiding yield losses typically seen in season-long deficit irrigation schemes. Primed acclimation is a type of RDI that uses reduced irrigation while the crop is in its vegetative growth stage to elicit a priming response such that drought tolerance can be enhanced during critical reproductive stages, thereby maximizing WUE without reducing yield (Rowland et al., 2012). Fereres and Soriano (2007) demonstrated that RDI initiated during vegetative growth stages increased water productivity (agricultural product per unit of water supplied by rainfall and irrigation; Ali and Talukder, 2008; Chastain et al., 2016; also referred to as WUE by Whitaker et al., 2008) and producer profits when using deficits ranging from 60% to as high as 100% of evapotranspiration in fruit trees and vines (2007). This approach has some credence since it could potentially increase root growth, allowing plants to access water deeper in the soil profile (Rowland et al., 2012). Root growth is favored over shoot growth under water deficits (Sharp and Davies, 1979; Hsiao and Xu, 2000; Fereres and Soriano, 2007), and in some situations, C partitioning to fruit growth is not affected (Gucci and Minchin, 2002; Fereres and Soriano, 2007). Cotton has been shown to respond to drought during its vegetative growth stages by increasing the length of the taproot while decreasing taproot diameter to allow cotton plants to reach moisture deeper in the soil profile (Pace et al., 1991). The PA technique has also been used in perennial species such as grapevine (Vitis vinifera L.) where RDI was implemented during vegetative stages, followed by full irrigation during critical reproductive stages of growth, with a resulting increase in WUE (Chaves and Oliveira, 2004). In more typical agronomic crops, such as peanut (Arachis hypogaea L.), yield increases with PA have been observed when compared with fully irrigated plants (Rowland et al., 2012), thereby resulting in improved WUE. Plants produced using PA have demonstrated improved WUE as well as photosynthetic rates under drought stress when compared with nonacclimated plants (Flexas et al., 2006; Rowland et al., 2012).

A concern with the PA approach to irrigation scheduling is that sufficient water limitations need to be imposed on the crop to elicit an acclimation response without causing yield-limiting drought stress (Guinn et al., 1981; Perry Bauer et al., 2012). Guinn et al. (1981) demonstrated that stress developed during flowering in cotton is nearly always detrimental. If drought stress develops early during squaring, square retention is not affected, but boll abscission increases when stress is experienced after flowering, especially 5 wk after flowering (Bruce and Romkens., 1965; Guinn et al., 1981). More recent research from the High Plains of Texas has demonstrated that drought stress during squaring did not reduce yield; however, if the stress continued into the early bloom periods, significant yield loss was noted as well as reductions in fruit retention and fiber quality (Snowden et al., 2014). It should be noted that the vegetative stage of growth is not completely immune from the effects of drought, and if water deficit is severe enough during vegetative growth, it can limit root growth, leaf area development, and fruiting site development, which in turn limits yield (Loka et al., 2011; Loka and Oosterhuis, 2012). Thus, within the prebloom phenological stage of development, critical irrigation thresholds need to be clearly defined and based on actual measures of crop water status (plant or soil) if PA is to be adopted as a viable irrigation scheduling strategy. Advances in soil moisture sensing should allow for a more clear definition of these thresholds. For example, Vellidis et al. (2013, 2016) demonstrated the use of the University of Georgia Smart Sensor Array (UGA SSA) as a viable irrigation scheduling tool for cotton production. The UGA SSA is a wireless soil moisture sensing system that allows for a high density of sensor nodes. The term sensor node refers to the combination of electronics and sensor probes installed within a field at a one location. Each probe integrates three Watermark (Irrometer Company, Inc.) soil moisture potential sensors. For our study, the probes included three sensors, which, when installed, were at 30, 45, and 60 cm below the soils surface. Soil water potential data flow hourly from individual sensor nodes in the field via a base station to a web-based interface, which allows users to view their soil moisture data in various formats (Vellidis et al., 2013). Use of the UGA SSA allowed our study to clearly define growth-stage-specific SWP thresholds for irrigation scheduling purposes in field-grown cotton. Therefore, it was hypothesized that withholding early-season irrigation using an appropriate soil-water-potentials threshold that moderated crop stress level could lead to increased WUE by limiting or preventing yield loss relative to treatments maintained under well-watered conditions during the preflowering stage of development. Consequently, the main objective of this study was to measure the growth and agronomic responses of cotton to a wide range of early-season SWP to define suitable early-season soil moisture potential thresholds for efficient irrigation scheduling using a PA approach.

Materials and methods

A field study was established to assess the growth and yield response of cotton to a range of soil-water, potential-based irrigation thresholds established prebloom. At a site near Camilla, GA (31 16 48 N, 84 17 29 W), seeds of cotton cultivar FM 1944 GLB2 (Bayer CropScience) were sown at a 2.5 cm depth on 13 May 2014 and 11 May 2015. A 0.91-m interrow spacing and a target seeding rate of 13 seeds m−1 row were used. Plots were eight rows wide and 13.3 m long with 6.3-m bare-soil alleys between plots and 16-row buffer areas in between treatment areas to ensure overspray from the sprinklers was not an issue. The experimental design was a randomized complete block design with one cultivar and four irrigation treatments (n = 4). However, because of irrigation system limitations, rainfed plots (T5) could not be randomized with the other treatments. Treatment 5 was planted under one section of the irrigation pivot in four replicated plots in the same field as the remaining treatments. The entire study area was treated similarly when applying fertilizer and all other inputs other than irrigation applications. The soil type at the Camilla study site was a Lucy loamy sand (loamy, kaolinitic, thermic Arenic Kandiudults). All seedbed preparation, fertilization, and pest management was conducted according to University of Georgia Cooperative Extension Service recommendations (Collins et al., 2014). Uniform stand establishment and pre-emergent herbicide activation was obtained for all treatments by supplementing rainfall with sprinkler irrigation (2.54 cm applied within 3 d of planting both years). Plant stands averaged 12.5 plants m−1 row across all treatments, which is above the plant densities recommended to maximize yields (Collins et al., 2014).

Five different irrigation treatments were initiated on 1 June 2014 and 31 May 2015; each treatment is defined in Table 1.1. The treatments were implemented as follows: T1, a well-watered, SWP level of −20 kPa was used as the prebloom irrigation threshold; T2, plants were irrigated at a soil moisture potential threshold of −40 kPa prior to flowering; T3, plants were irrigated at a soil-moisture potential threshold of −70 kPa prebloom (a deficit irrigation threshold determined to be yield limiting from Meeks [2013]; Collins et al., 2011); T4, plants were irrigated at a soil-moisture potential threshold of −100 kPa prebloom (a deficit level assumed to be extremely severe); T5, rainfed with no supplemental irrigation provided beyond stand establishment. Treatments 1 through 4 were irrigated at a threshold of −35 kPa after the first-bloom growth stage. Plants were irrigated using a variable-rate, center-pivot irrigation system to allow for irrigation only in the plot area that required it. Irrigation decisions were made daily Monday through Friday based on treatment average SWP using the UGA SSA. As described earlier, UGA SSA probes contained Watermark sensors at depths of 30, 45, and 60 cm. A weighted average SWP for these three sensors was used to make irrigation scheduling decisions. Throughout the growing season, the weighting function was as follows: (0.5 x SWP at 30 cm) +

(0.3 x SWP at 45 cm) + (0.2 x SWP at 60 cm). Soil moisture potential was monitored in three of the four replicate plots and irrigation was triggered when a treatment average reached the threshold. Plots in which thresholds exceeded during Saturday and Sunday were irrigated on Monday unless rainfall occurred in sufficient quantity to lower water potential below predefined thresholds. At first open boll (when open bolls were first observed in 10% of 10 random plants in the latest maturing irrigation treatment), irrigation was terminated for all treatments. A sensor replacement in 2014 caused a brief spike in moisture readings on 1 Aug. 2014 because of the installation process. A rapid drop in SWP was observed immediately thereafter as a result of the soil being very dry at that point in the season. It is typical for the sandy soils of this region to dry rapidly because of the limited water holding capacity of the soil and high water demands of the crop at this point in the growing season.

Crop growth and development were assessed by measuring plant height, total number of mainstem nodes per plant, and the number of mainstem nodes above the first-position white flower (NAWF) every 2 wk after irrigation treatments were initiated. Collection of this data was done by sampling five plants from the center two rows of each plot and obtaining average values for each plot prior to statistical analysis. In-season data collection was terminated at NAWF < 2 in the earliest maturing treatment. At 65% open boll in the latest maturing treatment, plot harvest aides were applied to promote defoliation and boll opening to facilitate timely harvest. Plant mapping was conducted 10 d after defoliation for an accurate measure of harvestable bolls in a method similar to Ritchie et al. (2011). Plant mapping consisted of visual assessment of harvestable bolls on five consecutive plants in the center rows that were representative of the whole plot. Aborted plants, if present, were not used in this analysis. Harvestable boll number by position and node (1 if present and 0 if absent at a given node and position) were recorded using a Microsoft Excel Visual Basic Macro program (Tifton, Ga) on plants in the field at the time of assessment. Harvestable monopodial bolls were recorded as well for the same five plants per plot mentioned previously. Lint yield was determined at crop maturity by mechanically harvesting the two center rows with a John Deere 9930 cotton spindle picker modified with a bagging attachment to collect the samples. End of row effects were minimized by mowing the plot area to the correct length before harvest. Harvested samples were weighed on site using a hanging scale (Intercomp CS750, Intercomp) positioned immediately adjacent to the field and taken to the University of Georgia micro gin (Tifton, GA) to obtain a lint turnout percentage for each sample. Lint yield was expressed as kilograms per hectare, and a 454-g fiber sample was retained from each plot and taken to the local USDA classing office in Macon, GA, to obtain high volume instrument fiber quality measurements (Kelly et al., 2012). Agricultural WUE was calculated as follows: lint yield divided by total water received by the crop during the growing season (precipitation plus irrigation) (Whitaker et al., 2008).

Statistical analysis was conducted using JMP Pro 12 (SAS Institute, 2016) and graphs were constructed using SigmaPlot 11.0 (Systat Software Inc., 2008). In all instances where comparative analyses were performed, $\alpha = 0.05$. Effect of irrigation treatment on end-of-season fiber yield, total plant nodes, plant heights, NAWF, harvestable sympodial and monopodial bolls per plant, and fiber quality parameters was assessed using a mixed-effects ANOVA according to a randomized complete block design. Blocks represented random effects, whereas irrigation treatment was a fixed effect. Where significant main effects were observed, mean separation was performed using LSD post hoc analysis. For plant mapping observations, the interactive effects of mainstem node and position along a sympodial branch on boll number (values were an average of five plants per plot and could range from 0 to 1) were evaluated using a response surface analysis. The response surface model is a multiple, nonlinear regression model that uses a combination of linear and quadratic terms and cross-products of linear terms to describe the interactive effects of multiple independent variables (e.g., node and position) on a single dependent variable (boll number) (Freund et al., 2003). For each irrigation treatment, the response surface model was derived from 264 data points (22 mainstem nodes assessed [Nodes 5 through 26] x 3 positions x 4 replicate plots).

Results

Environmental data recorded in 2014 and 2015 at the field site near Camilla, GA, indicated similar trends for maximum (Tmax) and minimum (Tmin) daily temperatures in both years; however, differences in rainfall were noted between the two growing seasons (Figure 1.1). For example, average Tmin and Tmax was 20.2 and 32.3°C and 20.9 and 32.6°C in 2014 and 2015, respectively. The highest recorded daily temperatures occurred on 23 Aug. 2014 (37.3°C) and 17 July 2015 (36.6°C). In contrast to the ambient temperature conditions, the two growing seasons differed substantially in rainfall patterns and soil moisture conditions (Table 1.1; Figure 1.1, 1.2). For example, total rainfall was 32 cm in 2014 vs. 61cm in 2015 (Table 1.1). The 2014 growing season had more extended episodic drought periods, with the last 12 d of May 2014 having no measureable rainfall and severe water deficit conditions occurring between 1 and 16 July and 1 to 12 August. In 2015, there were fewer episodic drought periods than the 2014 season, with only one 7-d period without rainfall occurring the week of 31 May (Figure 1.1). Dryland differences in water availability are illustrated further by extended periods of −155 kPa soil moisture potential sensor readings occurring in 2014 (Figure 1.2), whereas 2015 never had SWP readings less than −100 kPa (Figure 1.2). The longest period of extreme drought (SWP less than or equal to −155 kPa) occurred during the first weeks of bloom in 2014 in T5 (rainfed) for an extended period of 16 d; this severity of drought stress was not present in 2015. For irrigated treatments, SWP was similar for T1 through T4 throughout 2014 and 2015 growing seasons, regardless of growth stage, where treatment average water potential differences between irrigated treatments were less than or equal to −20 kPa at any given point in the season for both years. However, in 2014, T5 plants were subjected to severe drought stress as evidenced by soil moisture potential levels being below the sensor's measureable range for extended periods during the season (Figure 1.2). Soil water potential was less than or equal to −155 kPa for T5 multiple times in 2014, with a brief 7-d period beginning prior to flowering and an extended period of soil moisture at this level for nearly 2 wk beginning at the first week of flowering. For irrigated plots, prebloom SWP minimums ranged from −50 kPa for T1 to −108 kPa for T4 in 2014. Soil moisture potential levels were not observed at this level in any treatment in 2015, although rainfed plots had water potentials that were as low as −80 kPa prior to flowering and −100 kPa after flowering. In contrast, the lowest prebloom water potentials in irrigated treatments in 2015 ranged from −75 kPa prebloom to −60 kPa during bloom.

During the 2014 growing season, T4 and T3 irrigation treatments had the same amount of irrigation water applied (15.2 cm), with a 3-cm reduction in applied irrigation compared with T1, which was irrigated at a −25 kPa threshold prior to flowering (Table 1.1). Treatment 4 (−100 kPa threshold) received no prebloom irrigation in 2015, resulting in a 5-cm reduction in applied irrigation compared with the well-watered regime T1 (Table 1.1). Additionally, the −100 kPa prebloom threshold eliminated seven irrigation events when compared with T1. The number of irrigation events triggered prebloom were seven for T1, two for T2, one for T3, and zero for T4 (Table 1.1). Postbloom irrigation was not substantially different between treatments even with the reduced prebloom irrigation applications for PA treatments with 13.7 cm applied in 2014 and 8.4 cm applied in 2015 to T1 through T4.

Plant heights were affected significantly by irrigation treatment, with T1 and T2 having similar heights on all sample dates; T3, T4, and T5, were shorter than T1 and T2 plants in 2014 with up to a 30 cm reduction in plant height when compared with T1 (Figure 1.3). For example, plant heights ranged from 120 cm for T2 to 80 cm for T5 on 25 Aug. 2014. In 2015, plant height formed two distinct groups by the end of the season with T1 and T2 plants being the tallest and having comparable heights (170 and 160 cm, respectively) and T3 through T5 being the shortest and all having comparable heights (120 cm for T3 to 100 cm for T5). Total plant nodes were similar among T1 through T4 in 2014, with T5 having an average of six fewer observed nodes on 25 Aug. 2014 (Figure 1.5). Total nodes in 2015 were similar for all irrigation treatments, averaging 21 mainstem nodes per plant during end of season measurements on 17 Aug. 2015 (Figure 1.3 1.5). Seasonal trends for NAWF were similar for all irrigated treatments (T1–T4) in both years of the study. In contrast, cutout was hastened in 2014 for rainfed cotton as evidenced by NAWF being highest in T5 at first flower but then rapidly declining to NAWF of zero on 5 Aug. 2014 when average NAWF in irrigated treatments was four. In 2015, NAWF was consistently lower in T5 than in all other irrigation treatments regardless of sample date (Figure 1.6).

No significant treatment effects were observed between any irrigated treatment in 2014 or 2015 concerning lint yield or WUE. For example, lint yields for all irrigated treatments ranged from 1482 (T3) to 1630 kg ha -1 (T2) in 2014 and 1315 (T2) to 1476 kg ha-1 (T1) in 2015 (Figure 1.4). Water-use efficiency showed a similar response to irrigation, averaging 28 and 15 kg ha-1 cm-1 for all irrigated treatments in 2014 and 2015, respectively (Figure 1.4). Yield and

WUE in the season-long rainfed treatment (T5) were strongly impacted by year. For example, in 2014, lint yield for T5 (400 kg ha−1) was 1200 kg ha−1 lower than the average yield of the irrigated treatments (Figure 1.4). Water-use efficiency showed a similar trend, with WUE being 53% lower for the rainfed treatment than the mean WUE of the irrigated treatments in the same field and under the same management practices (Figure 1.4). In 2015, rainfed yields were 1600 kg ha−1, roughly 100 kg ha−1 higher than the mean of irrigated treatments (Figure 1.4).

Fiber quality parameters were similar between all irrigated treatments in 2014 with no significant differences in color grade, fiber length, micronaire, fiber strength, or uniformity (data not shown). Despite some apparent numerical differences in fiber quality parameters between the rainfed and the irrigated treatments, the differences observed would not have resulted in an additional premium or penalty when comparing treatments. Plant mapping indicated no significant differences in bolls per plant in either 2014 or 2015 for treatments T1 through T4, ranging from 9.98 (T2) to 15.13 bolls plant−1 (T4) in 2014 (Table 1.2). Sympodial bolls ranged from 12.30 (T1) to 15.84 bolls plant−1 (T4) in 2015 (Table 1.2). However, T5 had substantially fewer bolls in both 2014 and 2015 with only 2.19 and 6.85 bolls plant−1, respectively. Boll distribution patterns illustrate peak boll numbers at the first sympodial position, regardless of treatment or year (Figure 1.5, 1.6). However, the mainstem node at which peak boll retention was observed for irrigated treatments ranged from Node 9 for T3 to Node 13 for T4 in 2014 and from Node 13 for T4 to Node 14 for T1 in 2015. Rainfed bolls peaked at Node 5 in 2014 and Node 12 for 2015 (Table 1.3). Furthermore, in 2014, rainfed plants had fewer bolls both by node and position compared with irrigated treatments (Figure 1.3). Plant mapping in 2015 indicated substantial differences in boll distribution with rainfed plants having fewer bolls both by node and position than irrigated treatments but a 100% increase in bolls by position and node than

2014 rainfed plants (Figure 1.3). Thus, within a given year, rainfed plots produced a more compact fruit load, fewer bolls, and had peak boll retention at nodes lower on the plant than irrigated treatments.

Discussion

The observations from 2 yr of field trials in Camilla, GA, demonstrated that the PA irrigation strategy is applicable to southeastern United States growing conditions in both favorable periods of high rainfall (2015) and periods of episodic drought (2014). This study hypothesized that PA treatments using prebloom SWP thresholds could lead to increased WUE over well-watered treatments; however, WUE did not differ statistically between any of our irrigated treatments, which does not support this hypothesis. Importantly, even though WUE was not affected, no significant yield loss (Figure 1.4) or decline in fiber quality was detected from using the prebloom triggers of −70 and −100 kPa when compared with the −20 and −40 kPa triggers. Furthermore, season-long irrigation water savings of 3 to 5 cm less applied irrigation were observed for the −70 and the −100 kPa triggers relative to maintaining a wet soil profile early in the growing season. Therefore, these results verify that lower SWP thresholds (i.e., higher soil water tension) of −70 kPa or lower could be used prior to flowering to conserve irrigation application while still providing a suitable environment for optimum yields (Figure 1.3). For example, Figure 1.3 illustrates similar yields for all four irrigated treatments in both years even with 25 cm less rainfall in 2014 than 2015. In contrast, substantial yield losses (yields below 400 kg ha−1) and declines in WUE are seen for the season-long rainfed check in 2014, illustrating the importance of supplemental irrigation to minimize drought risk in cotton production in the southeastern United States and highlighting the possibility of negative impacts of drought stress during the flowering period. However, 2015 harvest data indicated no yield increase over rainfed in the irrigated treatments, likely a result of the additional 25 cm of water received from precipitation. Table 1.1 illustrates that in the 2015 environment, while no yield increases over rainfed were noted, water savings of 5 cm were possible using the lower SWP thresholds of −70 and −100 kPa relative to the early-season treatments using greater water application rates. High precipitation in 2015 led to increased rainfed WUE observations in 2015, especially with sufficient rainfall during the last weeks of bloom when the postbloom −35 kPa threshold treatment likely applied excess irrigation. Overall, these observations are similar to the observations of Rowland et al. (2012) as well as Fereres and Soriano (2007) in which deficit irrigation during vegetative growth led to similar yields when compared with well-watered crops. Using a particular irrigation threshold does not necessarily mean that a given threshold was ever reached, and future prebloom irrigation triggers should be based on observed values. For example, the −100 kPa prebloom threshold was reached for a brief period of time in 2014 (−114 kPa), and the −70 kPa threshold was exceeded in both 2014 and 2015 (−101 and −75 kPa, respectively). Thus, it appears that prebloom water potential irrigation thresholds between −70 and −100 kPa may be feasible in the southeastern United States. Previously published reports by Meeks (2013) and Whitaker et al. (2008) indicated yield losses when using season-long irrigation thresholds of −70 kPa relative to −40 kPa trigger points. In contrast with the previously mentioned studies, the current experiment used thresholds of this nature for prebloom periods only then used thresholds of −35 kPa to supply adequate moisture during flowering and boll development. The previously noted work used a −40 kPa season-long threshold for a well-watered sensor-based method, which demonstrated similar yields to the well-watered "checkbook" method recommended by the University of Georgia Cooperative Extension Service

(Meeks, 2013; Whitaker et al., 2008; Collins et al., 2014). It appears that the cotton crop is able to tolerate lower irrigation thresholds than these as long as they are imposed prebloom.

In contrast, when water deficit occurs during flowering (Figure 1.2), a substantial yield penalty results. Multiple periods of episodic drought were observed during flowering in 2014, which caused the rainfed treatment to reach a SWP less than or equal to −155 kPa for extended periods of time (one period ~3 wk in duration) during the growing season, which is the practical measurement limit for these sensors in the soil type used in the present study (Figure 1.2). Irrigation events during bloom were similar for T1 through T4 in both 2014 and 2015 with minor differences in timing only. It has been demonstrated that drought stress occurring prebloom could result in shorter plants with fewer nodes than well-watered plants but, despite the decrease in plant height, could achieve comparable end-of-season lint yields (Bauer et al., 2012; Snowden et al., 2014). However, early flowering can be sensitive to water deficit, leading to lint yield reductions when compared with a well-watered crop. Snowden et al. (2014) demonstrated that drought stress in the early bloom stage led to fruit abscission, yield loss, reductions in boll numbers, and reductions in fiber quality. In this study, low SWP in rainfed plots during early bloom in 2014 and 2015 led to reduced plant heights (Figure 1.3), indicating physiological limitations to cellular expansion processes. Growth has long been regarded as the most sensitive physiological process to the onset of water deficit (Hsiao, 1973). Crop maturity, as measured by NAWF, was hastened in both years for rainfed plots relative to irrigated plots; T1 through T4 all had comparable NAWF throughout the season, indicating a cessation of new vegetative growth and fruiting site development. This effect was noted by Pettigrew (2004) as well, with irrigated plants maintaining vegetative growth longer after reproductive growth was undertaken by the plants. Additional nodes on the plants allowed for flowering to be sustained and for the production of more fruiting sites relative to stressed plants.

Figure 1.1 illustrates the season-long environmental conditions encountered in 2014 and 2015, with similar minimum and maximum temperature trends noted in both 2014 and 2015. However, precipitations patterns were substantially different, with extended drought periods in 2014 during the second half of the growing season. Rainfall events occurring in 2015 were more frequent and intense than 2014, with rainfall amounts at times reaching ~6 cm per event. The yield losses noted in 2014 for the rainfed treatment, despite a seasonal cumulative precipitation greater than 46 cm (an amount shown previously to maximize cotton yields in Georgia [Bednarz et al., 2002]), illustrates the importance of the timing of rainfall or irrigation events occurring during flowering. Figure 1.3 further reinforces the effects of drought periods during bloom on boll retention, with rainfed boll counts significantly lower per node and position in addition to rainfed plants having bolls distributed over fewer nodes and positions when compared with irrigated treatments. Bolls were also retained only at the first position along a sympodial branch in T5 during 2014. Thus, it is likely that limited boll distribution contributed to the significantly lower (500 kg ha−1) yield when compared with irrigated plots. Figure 1.3 illustrates an impact on bolls by node and position that is less severe for rainfed plants because of a higher amount of rainfall during 2015. Bolls were present on similar nodes as T1 through T4 but at nearly a 50% reduction in bolls per fruiting site. Decreased harvestable fruit at the higher nodes in the plant have been observed by Ritchie et al. (2009), Pettigrew (2004), and Guinn and Mauney (1984) who noted that nonirrigated cotton produces fewer fruiting structures higher in the plant and tends to set bolls lower on the plant as a result of a reduction in fruiting sites as compared with well-watered cotton plants. In 2015, it was observed that large amounts of crop seedcotton were lost as a result of stringout from rainfall (personal observation) in irrigated treatments more than rainfed. Specifically, high rainfall events (Figure 1.1) occurred after the plants were defoliated and mapped but prior to mechanical harvest. Harvest was delayed by 21 d because of inclement field conditions. Table 1.2 illustrates average bolls per plant with no significant differences in total monopodial or sympodial bolls in 2014 or 2015 between T1 through T4, whereas substantial reductions in sympodial boll numbers were observed in both years for T5. The harvest timing constraint could help explain the similar yields between T1 through T5 in 2015 because of crop seedcotton losses from excessive rainfall.

Conclusions

There are three major conclusions that can be derived from this study. First, when using the SWP monitoring system and methods defined herein, these results suggest that prebloom irrigation thresholds between −70 and −100 kPa can be used to reduce the number of prebloom irrigation events without penalizing yield relative to well-watered treatments using −20 or −40 kPa irrigation thresholds prior to flowering. Plant mapping data also reinforce the utility of using the lower −70 or −100 kPa triggers because of no pronounced differences in boll distribution between any of the four different prebloom irrigation thresholds. Second, episodic drought during flowering substantially limits yield by reducing the total number of bolls per plant through processes that may include the following: fruit abscission, a reduction in the total number of available fruiting sites, reductions in overall plant growth, decreased node development, and hastening of cutout. Lastly, despite the fact that the sensor-based approaches had higher WUE in a dry year (2014), WUE was substantially higher in rainfed plots during the 2015 season (a high rainfall year) than in plots irrigated using any of the sensor-based approaches; therefore, further studies are needed to better define growth-stage-specific, sensor-based irrigation thresholds at all developmental stages of the crop to maximize WUE irrespective of year-to-year variation in rainfall patterns.

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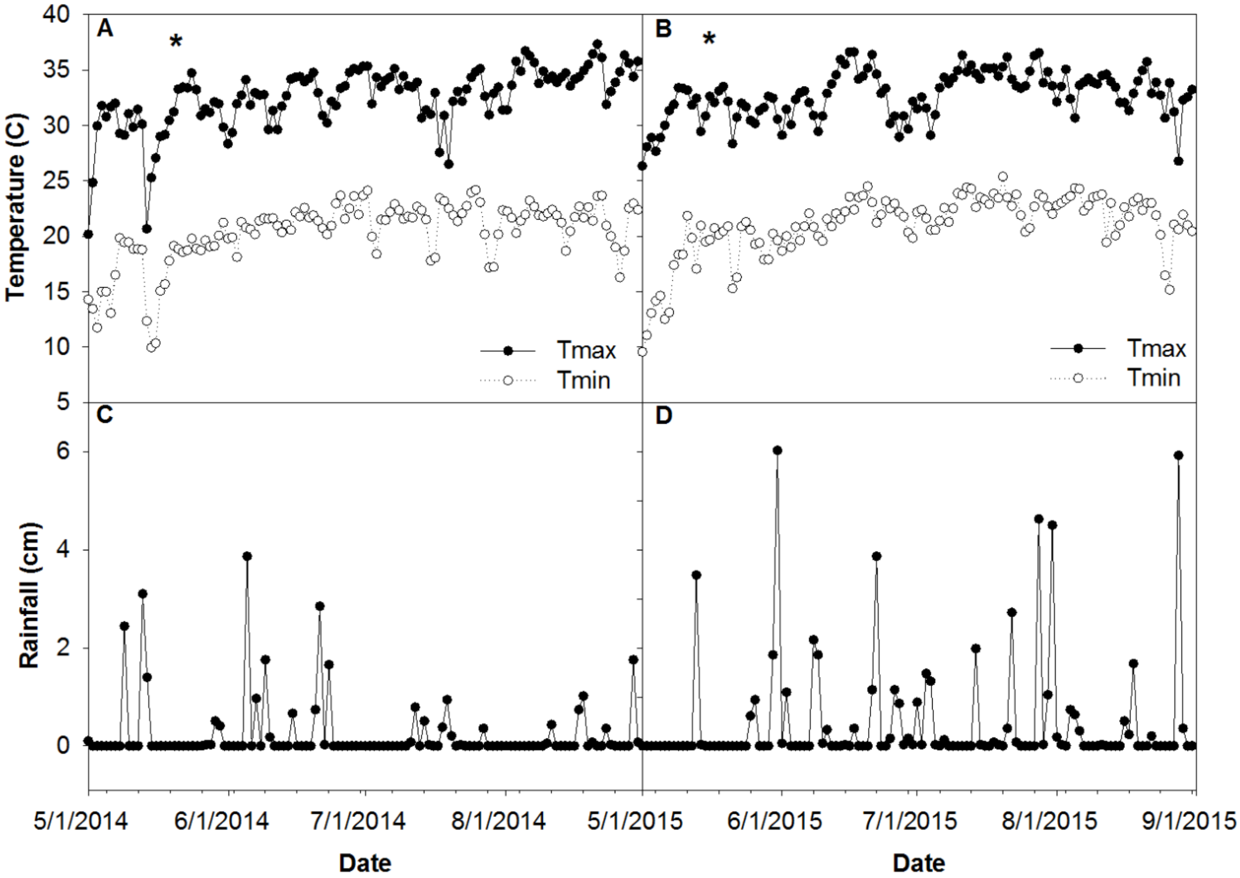

Figure 1.1. Environmental data for the 2014 and 2015 growing seasons near Camilla, GA, in 2014 and 2015. Data collected include maximum ($T_{\max}$) and minimum ($T_{\min}$) daily temperatures in (A) 2014 and (B) 2015 and rainfall events in (C) 2014 and (D) 2015. Asterisks in (A) and (B) indicate date of planting.

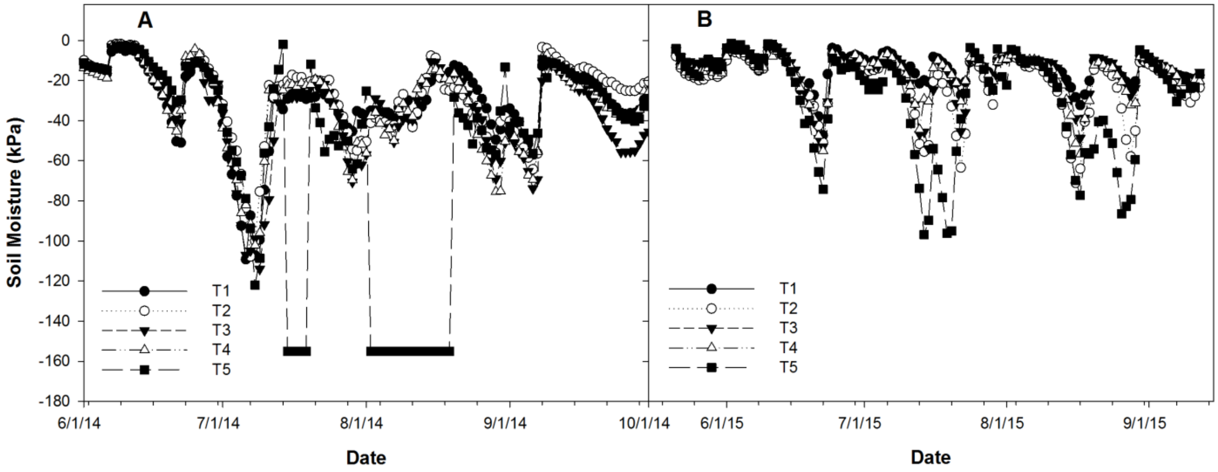

Figure 1.2. Watermark sensor-based soil water potential readings for irrigation regimes T1 through T5 during the (A) 2014 and (B) 2015 growing season near Camilla, GA. Values are means of sensor readings in three reps for each treatment. Prior to obtaining a mean for each treatment, a daily average soil water potential was obtained from each plot by differentially weighting values obtained at 30 (50%), 45 (30%), and 60 cm (20%).

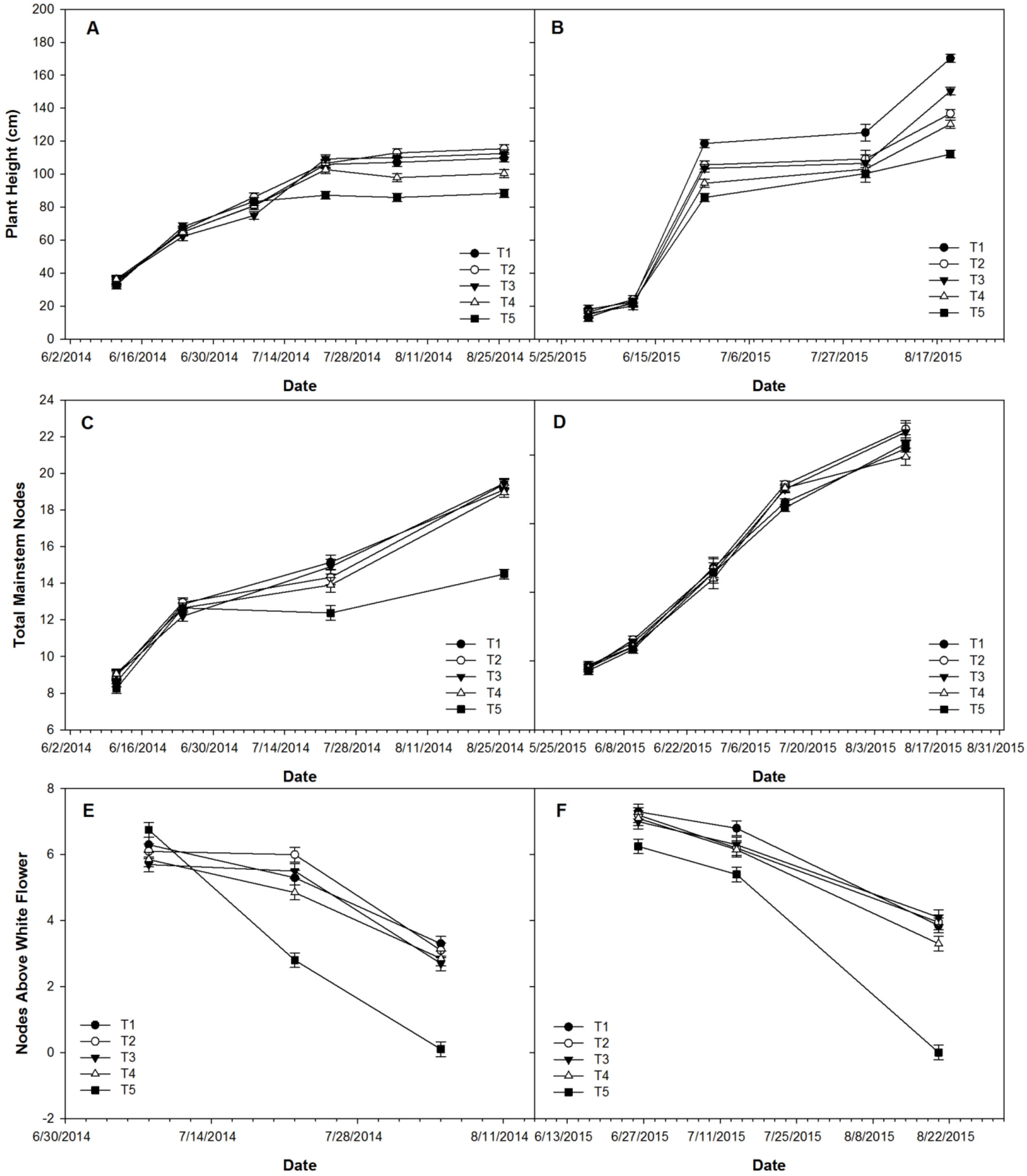

Figure 1.3. Plant heights for cotton grown in irrigation regimes T1 through T5 during the (A) 2014 and (B) 2015, total mainstem nodes for cotton grown in irrigation regimes T1 through T5 during the (C) 2014 and (D) 2015 and mainstem nodes above the first position white flower for cotton grown under irrigation regimes T1 through T5 during the (E) 2014 and (F) 2015 growing seasons at a field site near Camilla, GA. Values are means □ standard error (*n* = 4).

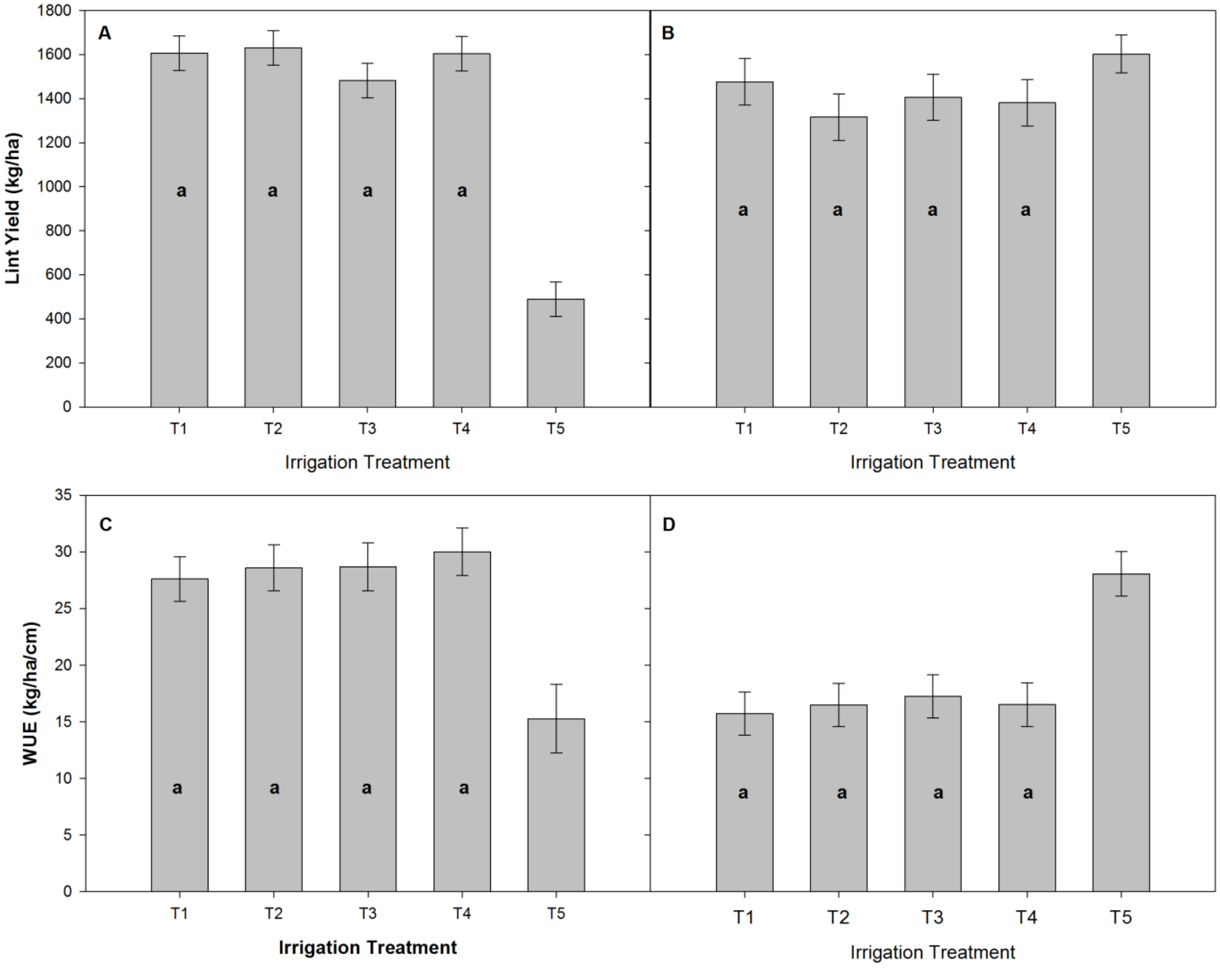

Figure 1.4. Lint yield in the (A) 2014 and (B) 2015 growing seasons (kg ha^{-1}) for irrigation regimes T1 through T5 and water-use efficiency (WUE) in the (C) 2014 and (D) 2015 growing seasons (kg ha^{-1} cm^{-1}) for irrigation regimes T1 through T5 in Camilla, GA. Values are means □ standard error ($n = 4$) and bars not sharing a common letter within a given year are significantly different ($P < 0.05$).

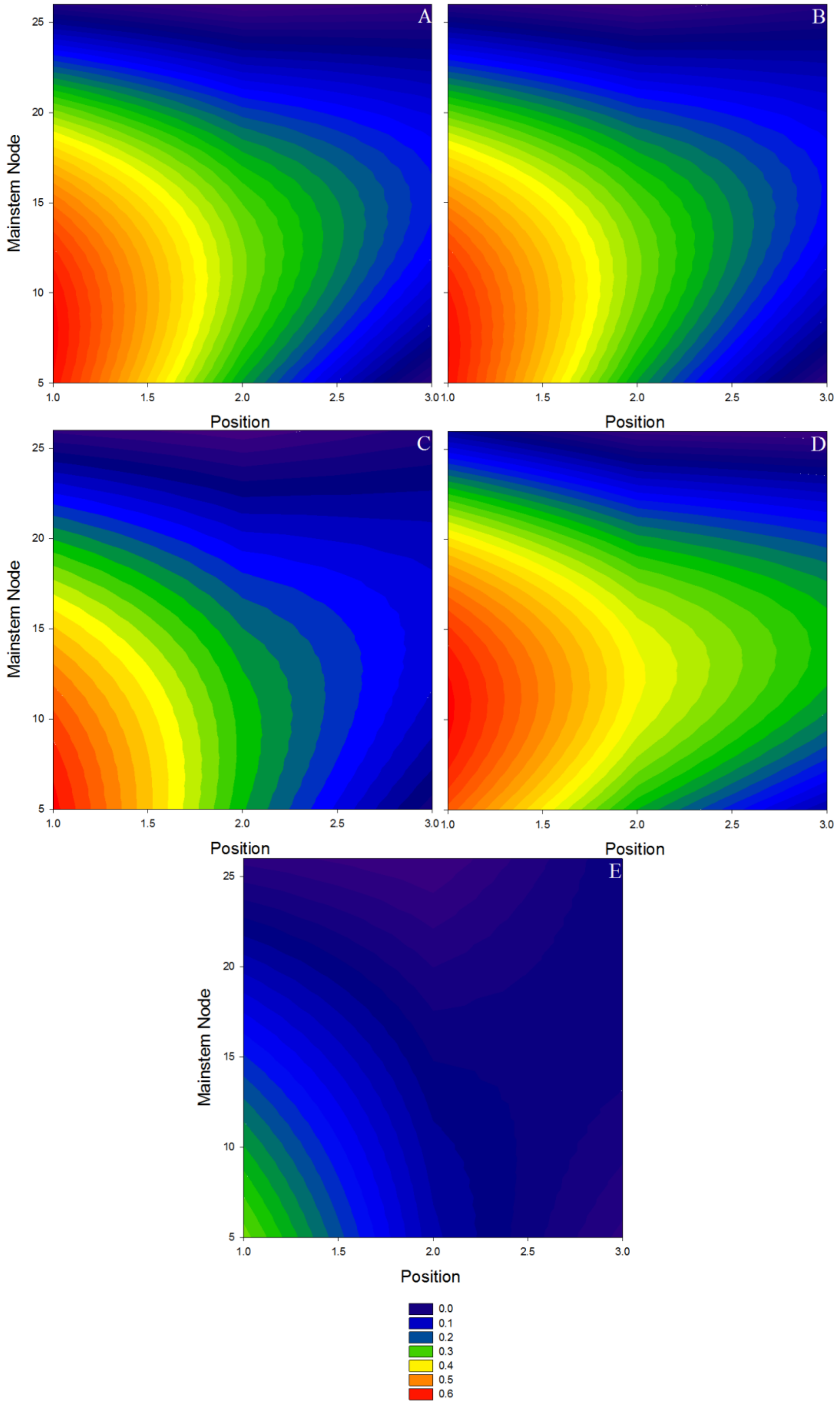
A
B
C
D
E
Mainstem Node
Position
25
20
15
10
5
1.0
1.5
2.0
2.5
3.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6

Figure 1.5. Plant mapping data for the 2014 growing season near Camilla, GA. Each graph represents a contour plot of a three-dimensional response surface model in which boll number is the response variable, and mainstem node (of sympodial branch attachment only) and position (horizontal position along a sympodial branch) are the dependent variables. Five plants were mapped per plot to obtain the average number of bolls per node and position (values between 0 and 1) prior to response surface analysis. Each graph represents the irrigation regimes (A) T1, (B) T2, (C) T3, (D) T4, and (E) T5. The color legend indicates the average number of bolls.

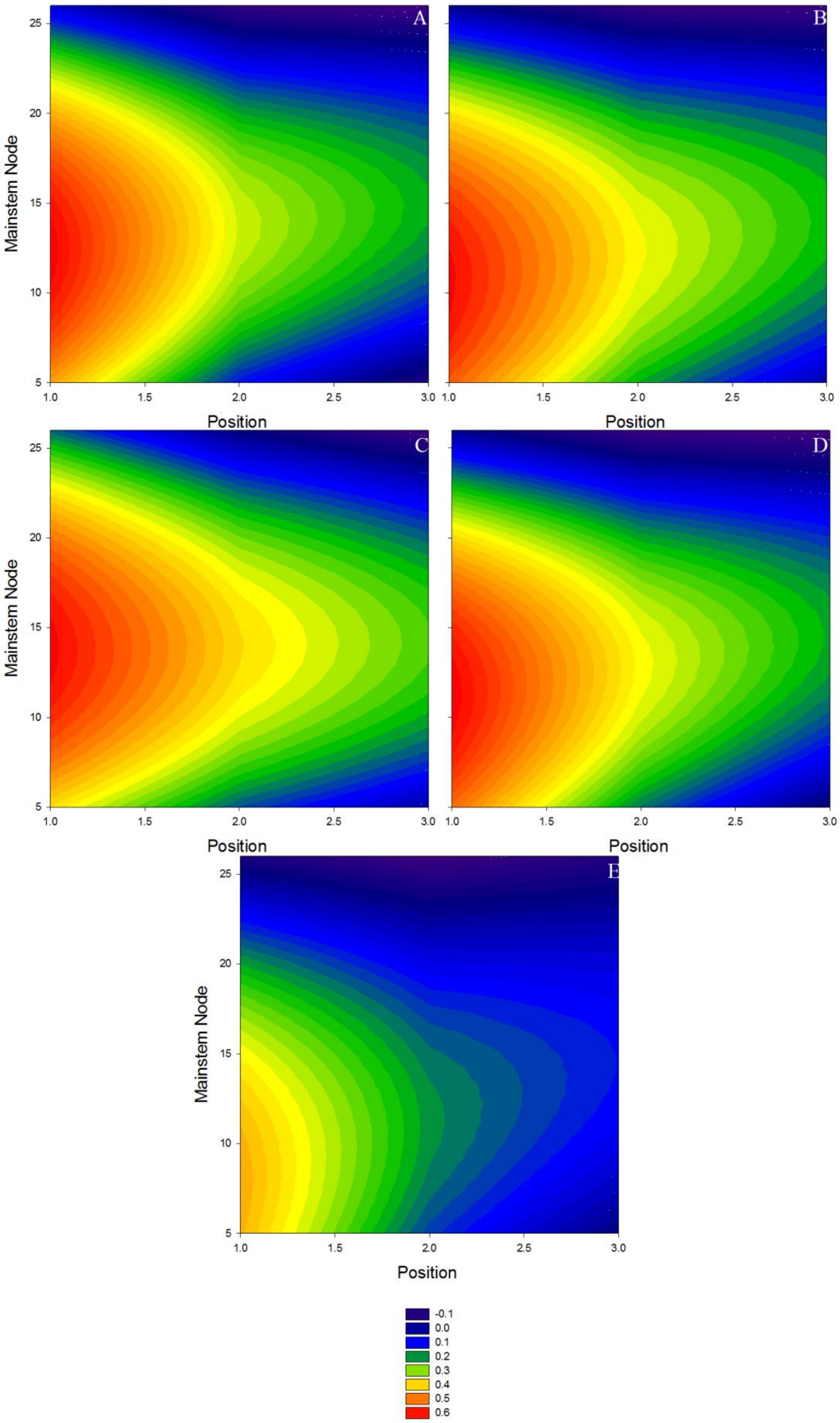A
B
C
D
E
Mainstem Node
Position
25
20
15
10
5
1.0
1.5
2.0
2.5
3.0
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6

Figure 1.6. Plant mapping data for the 2015 growing season near Camilla, GA. Each graph represents a contour plot of a three dimensional response surface model in which boll number is the response variable, and mainstem node (of sympodial branch attachment only) and position (horizontal position along a sympodial branch) are the dependent variables. Five plants were mapped per plot to obtain the average number of bolls per node and position (values between 0 and 1) prior to response surface analysis. Each graph represents the irrigation regimes (A) T1, (B) T2, (C) T3, (D) T4, and (E) T5. The color legend indicates the average number of bolls.

Table 1.1 Rainfall, irrigation, and total water received (in cm) by the cotton crop in irrigation Treatments 1 (T1) through 5 (T5) during the 2014 and 2015 growing seasons near Camilla, GA.

Year	**Treatment**	**Prebloom Threshold**	**Postbloom Threshold**	**Irrigation**	**Rainfall**	**Total**
		kPa			cm	
2014	T1	−20	−35	18.3	32.0	50.3
	T2	−40	−35	16.8	32.0	48.8
	T3	−70	−35	15.2	32.0	47.2
	T4	−100	−35	15.2	32.0	47.2
	T5	Rainfed	Rainfed	0.0	32.0	32.0
2015	T1	−20	−35	13.7	61.0	74.7
	T2	−40	−35	9.9	61.0	70.9
	T3	−70	−35	9.1	61.0	70.1
	T4	−100	−35	8.4	61.0	69.3
	T5	Rainfed	Rainfed	0.0	61.0	61.0

Table 1.2 Average number of bolls per plant determined from samples collected for plant mapping. Five plants were sampled per plot, and the average number of bolls per plant determined prior to performing comparative analyses. Data represent the means (*n* = 4) for each irrigation treatment (T1 through T5) during the 2014 and 2015 growing seasons. Values not sharing a common letter within a given year are significantly different ($P < 0.05$).

Year	**Irrigation treatment**	**Sympodial bolls plant^{-1}**	**Monopodial bolls plant^{-1}**
2014	T1	10.59a	0.50a
	T2	9.98a	0.30a
	T3	12.21a	0.40a
	T4	15.13a	1.10a
	T5	2.19	0.15
2015	T1	12.30a	0.88a
	T2	12.92a	0.33a
	T3	13.30a	0.92a
	T4	15.84a	1.44a
	T5	6.85	0.75

Table 1.3. The mainstem node of sympodial branch attachment (Node), horizontal position along a sympodial branch, and boll number at which the peak in boll distribution occurs on a plant for both years and all five irrigation treatments. Five plants were sampled per plot, and the average number of bolls by position and node determined prior to performing response surface analysis. The node and position at which maximum boll numbers were observed was derived from the response surface models illustrated in Figure 5 and 6.

Year	**Irrigation treatment**	**Node**	**Position**	**Boll number**	R^2	***P*-value**
2014	T1	12	1	0.285	0.71	<0.0001
	T2	12	1	0.231	0.71	<0.0001
	T3	9	1	0.306	0.68	<0.0001
	T4	13	1	0.319	0.69	<0.0001
	T5	5	1	0.066	0.47	<0.0001
2015	T1	14	1	0.168	0.66	<0.0001
	T2	13	1	0.286	0.71	<0.0001
	T3	13	1	0.321	0.65	<0.0001
	T4	13	1	0.371	0.70	<0.0001
	T5	12	1	0.188	0.53	<0.0001

CHAPTER 2

APPLYING PLANT-BASED IRRIGATION SCHEDULING TO ASSESS WATER USE EFFICIENCY OF COTTON FOLLOWING A HIGH-BIOMASS RYE COVER CROP [2]

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[2] Meeks, C.D., J. Snider, G.D. Collins, A.S. Culpepper and G. Hawkins. To be submitted to *Agronomy Journal*.

Abstract

This study addressed the potential of combining a high biomass rye winter cover crop with predawn leaf water potential (ΨPD) irrigation thresholds to increase agricultural water use efficiency (WUE) in cotton. To address this, a study was conducted near Tifton, Georgia under a manually-controlled, variable-rate lateral irrigation system using a Scholander pressure chamber approach to measure leaf water potential and impose varying irrigation scheduling treatments during the growing season. ΨPD thresholds were -0.4 MPa (T1), -0.5 MPa (T2), and -0.7 MPa (T3). A winter rye cover crop or conventional tillage were utilized for T1-T3 as well. Reductions in irrigation of up to 10% were noted in this study for the driest thresholds (-0.7 MPa) with no reduction in lint yield relative to the -0.4 and -0.5 MPa thresholds. Drier conditions during flowering (2014) limited plant growth and node production, hastened cutout, and decreased yield and WUE relative to 2015. We conclude that ΨPD irrigation thresholds between -0.5 MPa and -0.7 MPa appear to be viable for use in a ΨPD scheduling system with adequate yield and WUE for cotton production in the southeastern U.S. Rye cover positively impacted water potential at certain points throughout the growing season but not yield or WUE indicating the potential for rye cover crops to improve water use efficiency should be tested under longer-term production scenarios.

Introduction

Glyphosate-resistant Palmer amaranth has caused many cotton producers to abandon conservation tillage and revert back to conventional tillage and cultivation along with herbicides for control (Shurley et al 2014). Because conservation tillage has been touted to save up to 14% percent more water compared to conventional tillage methods, (Sullivan et al. 2007), methodologies should be developed to protect cover crop-derived water savings, while also maintaining control over glyphosate resistant Palmer amaranth. Utilizing a high-biomass rye cover crop along with herbicide resistant cotton cultivars and an appropriate herbicide program has been shown effectively control glyphosate resistant Palmer amaranth in a conservation tillage system (Shurley et al., 2014). The heavy rye cover provided savings in herbicide expense, but these savings were offset by other costs such as the seed required for the cover crop, additional nitrogen required by the cover crop, and the additional fuel for rolling of the rye (Shurley et al., 2014). Information on irrigation efficiency in this system is limited; however, multiple location studies in other states have demonstrated high residue cover crop systems as higher yielding than conventional tillage systems (Price et al. 2012). Therefore, the possibility exists for higher yields and increased water use efficiency (WUE) to offset the costs of using such a system.

To define the improvements in WUE that can be achieved through the use of a high biomass rye cover requires an understanding of irrigation scheduling approaches. Due to low soil water holding capacity soils and periods of episodic drought, supplemental irrigation is a necessity for Georgia cotton production. Although historical rainfall data from this region indicates an average amount (61.3 cm) May-September 2012-2015 (Georgia Automated Environmental Monitoring Network, 2016) sufficient to meet the required 46 cm of rainfall for maximum yields (Bednarz et al., 2002), episodic drought coupled with sandy soils that have poor water retention (Chesworth et al., 2008), often require supplemental irrigation to protect from yield losses. These periods of suboptimal or insufficient soil moisture tend to coincide with crop growth stages having the highest water demand. Proper irrigation scheduling should allow a producer to decide when to irrigate a crop as well as the amount of water needed to maximize WUE while not limiting yield. A water balance approach referred to as the “checkbook” method has been utilized in Georgia as noted in Table 2.1 and is recommended by the University of

Georgia Cooperative extension service (Collins et al., 2014). This approach supplements naturally occurring rainfall with irrigation to meet targeted weekly amounts of water specific to different stages of crop development. This method prevents water from being the limiting factor for cotton production systems in Georgia (Meeks et al., 2013; Chastain et al., 2014, 2016). However, from the physiologist's perspective, irrigation triggers that use the plant to sense its environment offer advantages over the water balance approaches discussed previously because the cotton plant integrates soil, atmospheric, and plant factors such that the need to irrigate can be accurately determined from the water status of the plant (Jones 2007, Chastain et al., 2014, 2016). Leaf water potential (Ψ_l) is a direct method of measuring plant water status, though variability in readings is possible due to environmental factors such as VPD and solar radiation (Jones, 1990; So, 1979; Chastain et al., 2014). Grimes and Yamada (1982) demonstrated relatively stable and maximum water potentials predawn within the 2 hours prior to sunrise and observed values at their minimum in the afternoon (1200 to 1500 h). Though conducted at a far less convenient measurement time, predawn leaf water potential (Ψ_{PD}) is an excellent indicator of plant water status and is not as greatly impacted by environmental fluctuations as midday measurements (Ameglio et al., 1999; Chastain et al., 2014). Ψ_{PD} has been correlated with predawn and midday physiological processes (Snider et al., 2014, 2015, Chastain et al., 2014) as well as end of season lint yield in cotton (Snider et al., 2015). Chastain et al. (2016) recently demonstrated Ψ_{PD} irrigation thresholds (Ψ_{PD} = -0.5MPa season long) could increase WUE relative to the checkbook method without penalizing yield. Using Ψ_{PD}-based irrigation scheduling should allow for a definitive assessment of the improvements in WUE attainable with high-biomass rye cover crops when compared with conventional tillage systems. There are currently no studies that the authors are aware of that have addressed WUE of high biomass rye tillage systems using plant-based irrigation scheduling.

If a rye cover crop increases Ψ_{PD} during episodic drought events relative to conventionally tilled treatments, rapid in-season physiological assessments should identify periods during the growing season where rye cover measurably improved plant performance. Previous reports have demonstrated the sensitivity of photosynthesis to plant water status in cotton (Snider et al., 2014, 2015; Chastain et al., 2016), and chlorophyll fluorescence has been used to detect abiotic stress by monitoring the efficiency of the thylakoid reactions of photosynthesis and have been proposed as useful tools for high throughput drought or heat tolerance screening (Burke, 1990; Burke, 2007). Some of the common parameters derived from chlorophyll a fluorescence measurements include maximum quantum yield of photosystem II in dark-adapted leaves (F_v/F_m), actual quantum yield of photosystem II in illuminated leaves (Φ_{PSII}), and photosynthetic electron transport rate (ETR) (Chastain et al., 2014; Flexas et al., 1999; Maxwell and Johnson, 2000; Snider et al., 2009, 2010; Valentini et al., 1995; Woo et al., 2008; Zhang et al., 2011). However, recent work by Snider et al. (2014) has indicated that primary photochemistry is relatively insensitive to water deficit sufficient to drastically limit net photosynthesis in the field. A more recently developed chlorophyll fluorescence method termed "OJIP" fluorescence analysis (O, J, I, and P are used to indicate steps in the chlorophyll fluorescence trace and are not abbreviations for other terms; Strasser et al., 2000), has been touted as more sensitive to drought and high temperature stress than traditional fluorescence methods (Boureima et al., 2012; Oukarroum et al., 2007, 2009; Tan et al., 2011), especially when the photosynthetic performance index (PI_{ABS}) is used as a bio-indicator. However, the utility of these novel methods for detecting drought stress has not been evaluated for field-grown cotton.

The current study was novel in that previous research has not been done in cotton examining Ψ_{PD} as irrigation triggers while also addressing the effect of tillage system on water use efficiency or in-season physiological status of the cotton crop. Therefore, it was hypothesized that a high biomass rye cover crop could maintain Ψ_{PD} at higher levels during the growing season, potentially increasing WUE over conventionally tilled plots, mitigating in-season stress and improving cotton yield and water use efficiency. Consequently, the objective of this study was to measure the physiological and agronomic responses of the cotton crop to multiple Ψ_{PD} irrigation thresholds in order to better define the water savings that can be achieved through the use of a high biomass rye cover crop.

Materials and methods

A field study was established to assess the growth, yield, and physiological response of cotton to a wide range of leaf water potential-based irrigation thresholds. At a site near Tifton, GA (USA) (31◦1648N, 84◦1729W), seeds of *G. hirsutum* cv. FM 1944 GLB2 (Bayer CropScience) were sown at a 2.5 cm depth on May 7, 2014 and May 11, 2015. A 0.91 m inter-row spacing and a target seeding rate of 13 seeds m^{-1} row were used. Plots were eight rows wide and 13.3 m long with 6.3 m bare-soil alleys. The experimental design was a randomized complete block design with one cultivar, two tillage strategies, and three irrigation treatments ($n = 6$). The soil type at the Tifton study site is a Tifton loamy sand (Fine-loamy, kaolinitic, thermic, Plinthic Kandiudults). Cereal rye (*Secale cereal* L.) was sown at a rate of 125.53 kg/ha on November 8, 2013 and November 12, 2014. Supplemental fertilization of 28 kg/ha for the rye cover crop was applied within 3 days of planting according to Georgia Cooperative Extension Service recommendations. The rye cover crop was simultaneously terminated and roller crimped on April 9, 2014 and April 11, 2015 according to Georgia Cooperative Extension Service recommendations. Rye biomass was characterized by cutting m^2 sections from each plot and drying each sample for 24 hours at 80C to determine dry matter per m^2. No significant differences were noted in dry mass between 2014 and 2015 with an average biomass observation of 393.20 g/m in 2014 and 349.52 g/m in 2015. All other seedbed preparation, fertilization, and pest management was conducted according to University of Georgia Cooperative Extension Service recommendations (Collins et al., 2014). Plots were not treated as a conservation tillage system as tillage was conducted by the farm manager during fallow periods. Uniform stand establishment and preemergent herbicide activation was obtained for all treatments by supplementing rainfall with sprinkler irrigation (2.54 cm applied within 7 days of planting both years). Plant stands averaged 12.6 plants m^{-1} row across all treatments, which is above the plant densities recommended to maximize yields (Collins et al., 2014).

Three different irrigation treatments were initiated on June 30, 2014 and July 3, 2015; each treatment is defined in Table 2.2. A brief description of treatments follows. T1: a very well-watered leaf water potential level of -0.4 MPa was used as the leaf water potential irrigation threshold. T2: plants were irrigated at a leaf water potential threshold of -0.5 MPa [previously shown to maximize WUE in cotton (Chastain et al., 2016)]. T3: plants were irrigated at a leaf water potential of -0.7 MPa. Treatments 1-3 were irrigated using leaf water potential thresholds after the first bloom growth stage. Irrigation management from emergence up to first bloom utilized UGA checkbook recommendations (Table 2.1). Plants were irrigated using a variable rate lateral irrigation system to allow for irrigation only in the plot area via manual shut off valves. Irrigation decisions were made twice weekly (Tuesday and Thursday) based on treatment average predawn leaf water potential (Ψ_{PD}) using an uppermost, fully expanded mainstem leaf (the fourth unfurled leaf node below the apical meristem). When a given treatment threshold was reached, the maximum application amount that could be applied was 1.78 cm.

The leaf was severed from three plants in each plot between 0400 and 0600 h and used for predawn water potential measurements. The petiole was sealed in a compression gasket, and the leaf blade was sealed in a Scholander pressure chamber (PMS Instrument CoMPany, Albany, OR) with a chamber pressurization rate of 0.1 MPa per second. Required pressure to bring the water column to the cut surface of the stem was recorded in MPa with less than 30 s elapsing from when the leaf was severed from the plant to the initial pressurization of the chamber. The same leaf was utilized in predawn measurements of Photosynthetic Performance Index (PI_{ABS}) and Maximum Quantum Yield of PSII (F_v/F_m) utilizing a FluorPen FP 100 (Photon Systems Instruments, spol. s r.o. Drasov 470 664 24 Drasov, Czech Republic). Irrigation was terminated at first open boll for the latest maturing plot.

Crop growth and development were assessed by measuring plant height, total number of mainstem nodes per plant, and the number of mainstem nodes above the first-position white flower (NAWF) every two weeks after irrigation treatments were initiated. Collection of this data was done by sampling five plants from the center two rows of each plot and obtaining average values for each plot prior to statistical analysis. In-season data collection was terminated at NAWF < 2 in the earliest maturing treatment. At 65% open boll in the latest maturing treatment, plot harvest aides were applied to promote defoliation and boll opening in order to facilitate timely harvest. Lint yield was determined at crop maturity by mechanically harvesting the 2 center rows with a John Deere 9930 cotton spindle picker. Harvested samples were weighted on site using a scale (Intercomp CS750, Intercomp, 3839 County Road 116 Medina, MN 55340-9342) positioned immediately adjacent to the field and taken to the University of Georgia Micro

Gin (Tifton, GA) to obtain a realistic lint percent for each sample. Lint yield was expressed as kg ha^{-1}, and a 454 g fiber sample was retained from each plot and taken to the local USDA classing office in Macon, GA to obtain HVI fiber quality measurements.

All statistical analyses were conducted using JMP Pro 12 (SAS Institute Inc., Cary, NC) and graphs were constructed using SigmaPlot 11.0 (Systat Software Inc., San Jose, CA). In all instances where comparative analyses were performed, $\alpha = 0.05$. Effect of irrigation treatment on end-of-season fiber yield, total plant nodes, plant heights, NAWF, WUE, chlorophyll fluorescence parameters, and fiber quality parameters were assessed using a mixed effects ANOVA according to a randomized complete block design. Blocks represented random effects, whereas irrigation treatment and tillage were fixed effects. Where significant main effects were observed, mean separation was performed using LSD post hoc analysis.

Results

Environmental data recorded in 2014 and 2015 at the field site near Tifton, GA indicated similar trends for T_{min} and T_{max} in both years; however, differences in rainfall were noted between the two growing seasons (Figure 2.1). For example, average T_{min} and T_{max} was 20.4 and 31.3°C and 20.5 and 31.6°C in 2014 and 2015, respectively. The highest recorded daily temperatures occurred on August 23, 2014 (36.4°C) and July 17, 2015 (36.4°C). In contrast to the ambient temperature conditions, the two growing seasons differed substantially in rainfall patterns and applied irrigation (Table 2.2 and Figure 2.1). For example, total rainfall was 40.1 cm in 2014 compared to 51.2 cm in 2015 (Table 2.2). The 2014 growing season had more extended episodic drought periods with the last 12 days of May 2014 having no measureable rainfall and severe water deficit conditions occurring between July 1 and 16, and August 1 and 12. In 2015, there were fewer episodic drought periods as compared to the 2014 season, with only one 7 day period without rainfall occurring the week of May 31 (Figure 2.1). Differences in water availability are illustrated further by extended periods of lower than -0.7 MPa leaf water potential (Ψ_{PD}) occurring in 2014 in T3 (Figure 2.2), whereas 2015 had only one period of leaf water potential lower than -0.7 MPa in T3 (Figure 2.2). The rye cover crop in T3 led to higher Ψ_{PD} readings late in the 2014 season (Figure 2.2); however, in the wetter 2015 growing season the T3 treatments responded similarly regardless of cover crop (Figure 2.2). T1 and T2 responded similarly regardless of cover crop in 2014 until late in the season with T1 and T2 with rye cover having slightly higher leaf water potential than the T1 and T2 treatments without cover crops (Figure 2.2). T1 and T2 responded similarly in 2015 regardless of cover crop (Figure 2.2). The longest period of decline in Ψ_{PD}; occurred from July 30, 2014 to cutout on August 11, 2014 with measurements in T3 Conventional below -0.8 MPa and nearly reaching -1.2 MPa, other treatments did not exhibit this severe drop in Ψ_{PD} (Figure 2.2). This severity of drought stress was not present in 2015, with both T3 treatments briefly dropping to -1.1 MPa on 8/3/2015 but recovering to greater than -0.8 MPa by August 10, 2015 (Figure 2.2). Rye treatments T1 and T2 were observed to have slightly higher Ψ_{PD} near the end of the 2014 growing season (7/30/2014-8/11/14) than T1 and T2 under conventional tillage (Figure 2.2). In 2015, Ψ_{PD} was similar for all treatments until August 3, 2015 with T3 treatments significantly lower for one week (Figure 2.2). Ψ_{PD} was maintained at a level above the thresholds more often in 2015 with values above -0.4 MPa in both T1 and T2 treatments regardless of cover crop occurring twice as often than the 2014 observations. In contrast, the lowest leaf water potentials in T1 and T2 were above -0.4 MPa only twice in 2014.

During the 2015 growing season, T1 and T2 irrigation treatments had the same amount of irrigation water applied (29.5 cm), with a 1.6 cm reduction in applied irrigation compared to T3 which was irrigated at a -0.7 MPa Ψ_{PD} threshold (Table 2.2). The 2014 growing season had reduced rainfall (40.1 cm vs. 51.2 cm). Irrigation events were reduced by 1 with the T2 treatment and by 2 in the T3 treatment compared to the T1 treatment, with irrigation amounts ranging from 25.1 cm for T1, 23.9 cm for T2, to 22.6 cm for T3 (Table 2.2).

Plant heights were not affected significantly by irrigation treatment or tillage in 2014, with T1-T3 having similar heights on all sample dates in 2014 (Figure 2.3). Tillage system did not significantly affect plant height in either year. However, tillage system significantly impacted final plant heights which were considerably higher in 2015 ranging from 140 cm for T3 to 160 cm for T2 compared to the 2014 range of 75 cm for T3 to 100 cm for T1 (Figure 2.2). Total mainstem nodes were similar between T1-T3 in 2014, regardless of tillage system (Figure 2.4). Total nodes in 2015 were similar for all irrigation treatments, as well averaging 19.5 mainstem nodes per plant during end of season measurements on August 16, 2015 (Figure 2.4). 2015 node counts were considerably higher than 2014 counts with end of season measurements averaging only 14 mainstem nodes per plant on August 8, 2014. No treatment differences were observed for NAWF in either year of the study. In contrast, cutout was hastened in 2014 by NAWF being highest 7/21/14 at first flower but then rapidly declining to average NAWF = 2 on August 6, 2014 (Figure 2.5). In 2015 cutout was reached considerably later with NAWF = 7 on July 12, 2015 and not reaching cutout until August 15, 2015 (NAWF =3) (Figure 2.5).

No significant irrigation treatment effects were observed in 2014 concerning lint yield or WUE (Figure 2.6a and 2.7a). There was also no significant tillage main effect in 2014. While there was not a significant tillage main effect in 2015 either, there was a significant irrigation treatment main effect for lint yield and WUE ($P < 0.05$; Figure 2.6b and 2.7b). For example, lint yields ranged from 1286 kg ha $^{-1}$ for T1 averaged across both tillage treatments to 1187 kg ha $^{-1}$

for T3 in 2014, with no significant differences observed between any treatments. In 2015, yields ranged from 2073 kg ha^{-1} (T1) to 2236 kg ha^{-1} (T3) (Figure 2.7b). Similar to yield trends, WUE was substantially different between years, averaging 18 kg ha^{-1} cm^{-1} and 27 kg ha^{-1} cm^{-1} for all irrigated treatments in 2014 and 2015, respectively (Figure 2.8). Average WUE response to irrigation, combined across tillage system, showed a similar trend to yield with no significant differences in 2014 (18 kg ha $^{-1}$ average). Significant differences in 2015 were observed in WUE between irrigation treatments with 32 kg ha $^{-1}$ cm^{-1} for T3 compared to 28 kg ha $^{-1}$ cm^{-1} for T1 (Figure 2.7b). While there was no significant interaction between irrigation treatment and tillage in any year of the study, the mean yields and WUE for each irrigation treatment × tillage combination are shown in Figures 2.8 and 2.9 to provide readers additional information.

Throughout both growing seasons, PI_{ABS} ranged from 1.08 to 5.91 in 2014 and 1.36 to 6.68 in 2015 and varied greatly depending on sample date with no consistent association with irrigation treatments or rye cover (Figure 2.10). Similar observations were noted for Maximum Quantum Yield of PSII (F_v/F_m) in 2014 and 2015 (Figure 2.11). For example, the ranking of each treatment varied greatly, depending upon sample date. Importantly, no clear association with plant water status was observed for chlorophyll α florescence measurements (data not shown). In fact, where large differences in Ψ_{PD} were observed (August 14, 2014), the lowest Ψ_{PD} treatment produced the highest F_v/F_m value (Figure 2.11). Season average PI_{ABS} was similar in both 2014 and 2015, where T2 produced with conventional tillage had the highest PI_{ABS} in both 2014 and 2015 (Figure 2.12). Season average F_v/F_m was similar for all treatments regardless of irrigation or tillage in both 2014 and 2015 (Figure 2.13).

Discussion

The observations from two years of field trials in Tifton, Georgia demonstrated that the high biomass rye cover crop system impacted plant water status but there was no improvement in WUE or yield, indicating no short term agronomic benefits. This study hypothesized that rye treatments would maintain Ψ_{PD} thresholds better than conventionally tillage treatments which could lead to increased WUE over conventionally tilled treatments; however, WUE did not differ statistically between any of our irrigated treatments (the exception being WUE in 2015 when combined across tillage), which does not support this hypothesis. Importantly, even though WUE was not affected by tillage, no significant yield loss (Figure 2.6) was detected from utilizing any of the Ψ_{PD} thresholds. Furthermore, season-long irrigation water savings of 1.5 to 2.5 cm less applied irrigation were observed for the -0.7 MPa triggers. Therefore, these results verify that lower Ψ_{PD} thresholds of -0.7 MPa could be used to conserve irrigation application while still providing a suitable environment for optimum yields (Figure 2.6). For example, Figure 2.6 illustrates similar yields for all 3 irrigation treatments in 2014, even with 11.1 cm less rainfall in 2014 than 2015. In contrast, substantial yield differences and declines in WUE are seen for T1 relative to T3 in 2015, illustrating the importance of applying irrigation appropriately in cotton production in the southeastern U.S., and highlighting the possibility of negative impacts of excessive irrigation during periods of adequate rainfall (Figure 2.6, 2.9). Cetin and Bigel (2002) noted that providing excess irrigation tends to lead to reduced yield due increases in fruit shed. These observations also suggest that -0.4 MPa Ψ_{PD} thresholds are not realistic for cotton production in the southeastern US. High yields in 2015 led to increased WUE observations in 2015, especially with increased rainfall during the bloom period as compared to 2014. Based on the data presented herein, it appears that predawn leaf potential irrigation thresholds between

-0.5 MPa and -0.7 MPa may be feasible in the southeastern U.S. to help maximize water use efficiency and limit yield losses resulting from excess irrigation. However, it should be noted that Chastain el al. (2016) reported maximum yields at Ψ_{PD} = -0.5 MPa and yield losses when utilizing season-long Ψ_{PD} irrigation thresholds ≤ -0.7 MPa. This is likely because that study was conducted under much drier conditions than the 2015 growing season, and drip irrigation allowed for more frequent irrigation events relative to the overhead irrigation system used in the current study, thereby allowing for greater yield separation between treatments. Similar to the current study, WUE was maximal whether using Ψ_{PD} = -0.5 or -0.7 MPa. Chastain et al. (2016) also noted that -0.5 MPa Ψ_{PD} irrigation thresholds produced similar yields to the well-watered "checkbook" method recommended by the University of Georgia Cooperative Extension Service (Collins et al., 2014) while increasing WUE, demonstrating the potential to increase WUE with this type of irrigation strategy without reducing yields below optimum levels.

It is important to note that using a particular tillage system in the short term does not necessarily mean that cover crops do not increase WUE. For example, season ending Ψ_{PD} suggests that given enough time, tillage system can impact plant water status (Figure 2.2). Previous work done by Sullivan et al. (2007) has indicated that long term use of a rye cover crop (10 years) can lead to substantial water savings up to 14%. Using the fluorescence-based bio-indicators, PI_{ABS} and F_v/F_m, measurements season long indicated no consistent differences between irrigation or tillage treatments, reinforcing recent work (Chastain et al., 2014; Snider et al., 2014) that indicated that primary photochemistry is relatively insensitive to water deficit sufficient to drastically limit net photosynthesis in the field. Relatively new chlorophyll fluorescence methods termed OJIP fluorescence have been touted as more sensitive to drought and high temperature stress than traditional fluorescence methods (Boureima et al., 2012;

Oukarroum et al., 2007, 2009; Tan et al., 2011) especially utilizing PI_{ABS} as a bio-indicator. However, this method was no more sensitive than F_v/F_m for detecting drought stress in field-grown cotton in a plant based irrigation scheduling system, where PI_{ABS} was not correlated with Ψ_{PD} in either year or across years (data not shown).

It has been demonstrated that drought stress occurring prebloom could result in shorter plants with fewer nodes than well-watered plants, but despite the decrease in plant height, the cotton crop could achieve comparable end of season lint yields (Bauer et al., 2012; Snowden et al., 2014). However, in this study, comparable yields were not observed when comparing the yields of the two years (Figure 2.6, 2.8). In this study, reduced total water in 2014 led to reduced plant heights (Figure 2.3), indicating physiological limitations to cellular expansion processes. Growth has long been regarded as the most sensitive physiological process to the onset of water deficit (Hsiao, 1973). Crop maturity, as measured by mainstem nodes above white flower (NAWF), was hastened in 2014; T1-T3 all had comparable NAWF throughout the season, indicating a cessation of new vegetative growth and fruiting site development. Observations in 2015 noted crop maturity that was not hastened with longer periods of NAWF >5. This effect was noted by Pettigrew et al. (2004) as well, with irrigated plants maintaining vegetative growth longer after reproductive growth was undertaken by the plants. Additional nodes on the plants allowed for flowering to be sustained and for the production of more fruiting sites relative to stressed plants, leading to substantially higher yields in 2015 (Figure 2.4, 2.6, 2.7).

Figure 2.1 illustrates the season long environmental conditions encountered in 2014 and 2015 with similar minimum and maximum temperature trends noted in both 2014 and 2015. However, precipitations patterns were substantially different, with extended drought periods in 2014 during the second half of the growing season. Rainfall events occurring in 2015 were more frequent and intense than 2014, with rainfall amounts at times reaching ~6 cm per event. Rainfall amounts during the 2015 growing season were in excess of that needed to maximize yield according to previous work conducted by Bednarz et al. (2002). Field conditions in 2014 were not optimal in terms of irrigation due to the limitations of the lateral irrigation system and its inability to supply higher amounts irrigation. Despite attempts to irrigate according to predefined thresholds, it should be noted that Ψ_{PD} for most treatments was below target thresholds for much of the 2014 growing season. This indicates that irrigated cotton may often experience yield-limiting water deficit stress despite using the best available practices due to irrigation system time requirements between successive irrigation events.

Conclusions

There are three major conclusions that can be derived from this study. First, when using the leaf water potential monitoring system and methods defined herein, these results suggest that pre-bloom irrigation thresholds between -0.5 and –0.7 MPa can be used to provide adequate irrigation for optimum yields and WUE. Yield data in 2015 especially reinforces this conclusion with yields above 2000 kg ha^{-1}. Second, excessive irrigation as noted in 2015 at -0.4 MPa thresholds, limit yield through processes that may include excess vegetative plant growth and increased boll rot. Lastly, despite the fact that the high biomass rye cover crop approaches did not increase WUE in a drier year (2014) or wetter year (2015), other studies such as Raper et al., (2016) have noted increased WUE; therefore, further studies are needed to better define the utility of high biomass rye cover crops in cotton production. However, this study did document higher Ψ_{PD} in rye plots versus conventional tillage plots at some points during the growing indicating that rye cover can increase plant water potential.

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Table 2.1. Typical checkbook schedule (UGA Extension Recommendation) for cotton irrigation in Georgia (Collins et al., 2014).

Growth Stage	cm per week
Pre-Bloom	1.91 to 2.54
1st Bloom (week 1)	2.54
2nd week after 1st bloom	3.81
3rd week after 1st bloom	5.08
4th week after 1st bloom	5.08
5th week after 1st bloom	3.81
6th week after 1st bloom	3.81
≥ 7th week after 1st bloom	2.54

Table 2.2 Rainfall, irrigation, and total water received (in cm) by the cotton crop in irrigation treatments 1 (T1) through 3 (T3) during the 2014 and 2015 growing seasons near Tifton, GA.

Year	Treatment	Irrigation Threshold (MPa)	Irrigation (cm)	Rainfall (cm)	Total (cm)
2014	T1	-0.4 MPa	25.1	40.1	65.2
	T2	-0.5 MPa	23.9	40.1	64.0
	T3	-0.7 MPa	22.6	40.1	62.7
2015	T1	-0.4 MPa	29.5	51.2	80.7
	T2	-0.5 MPa	29.5	51.2	80.7
	T3	-0.7 MPa	27.9	51.2	79.1

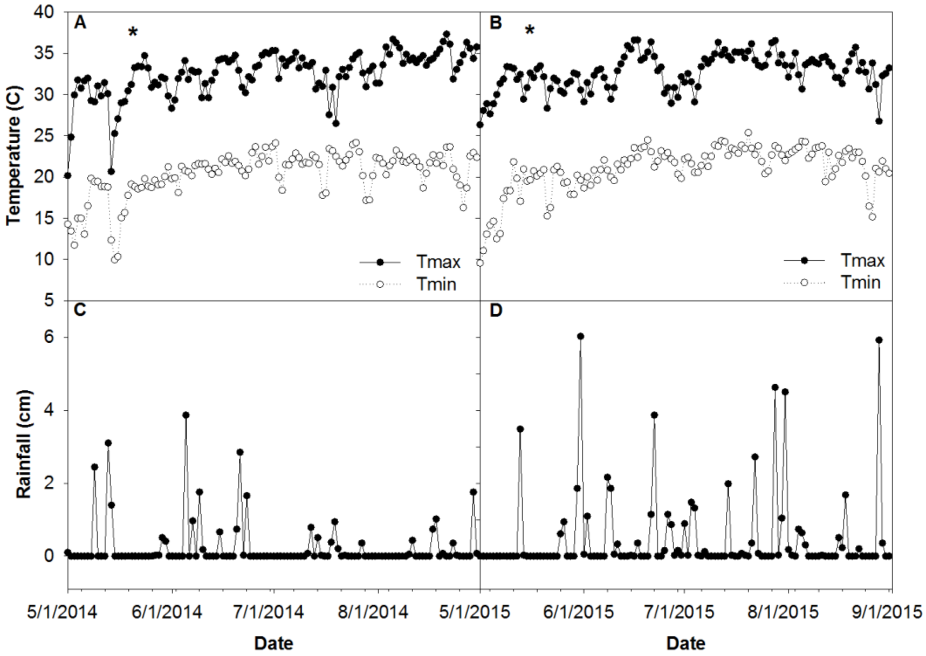

Figure 2.1**.** Environmental data for the 2014 and 2015 growing seasons near Tifton, GA in 2014 and 2015. Data collected include maximum (T_{max}) and minimum (T_{min}) daily temperatures in 2014 (A) and 2015 (B) and rainfall events in 2014 (C) and 2015 (D). Asterisks in A and B indicate date of planting.

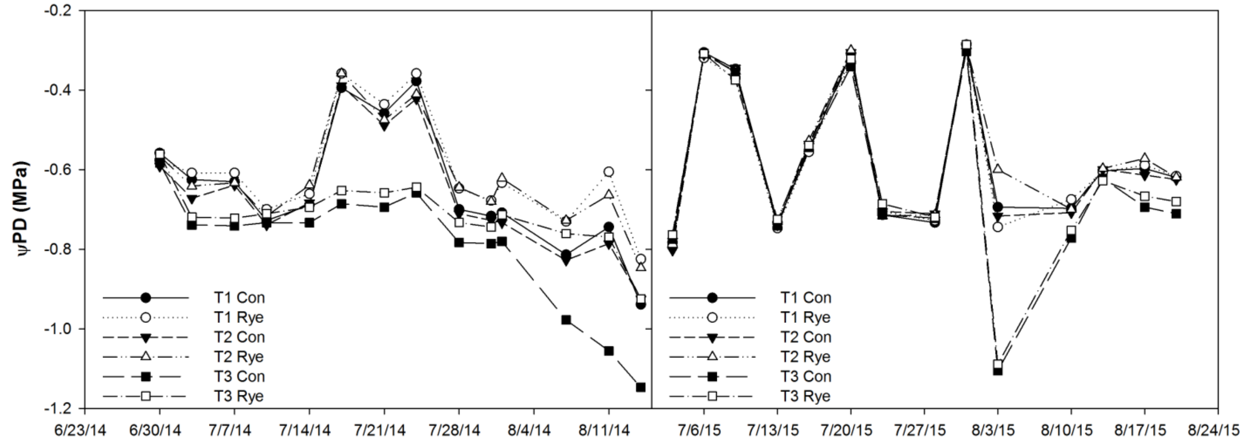

Figure 2.2**.** Predawn leaf water potential readings (Ψ_{PD}) for cotton grown under irrigation regimes T1-T3 and planted into either conventionally tilled beds (Con) or a heavy rye cover crop residue (Rye) during the 2014 and 2015 growing season near Tifton, GA. There were six replicate plots per treatment, and 3 Ψ_{PD} readings were averaged for each plot prior to analysis.

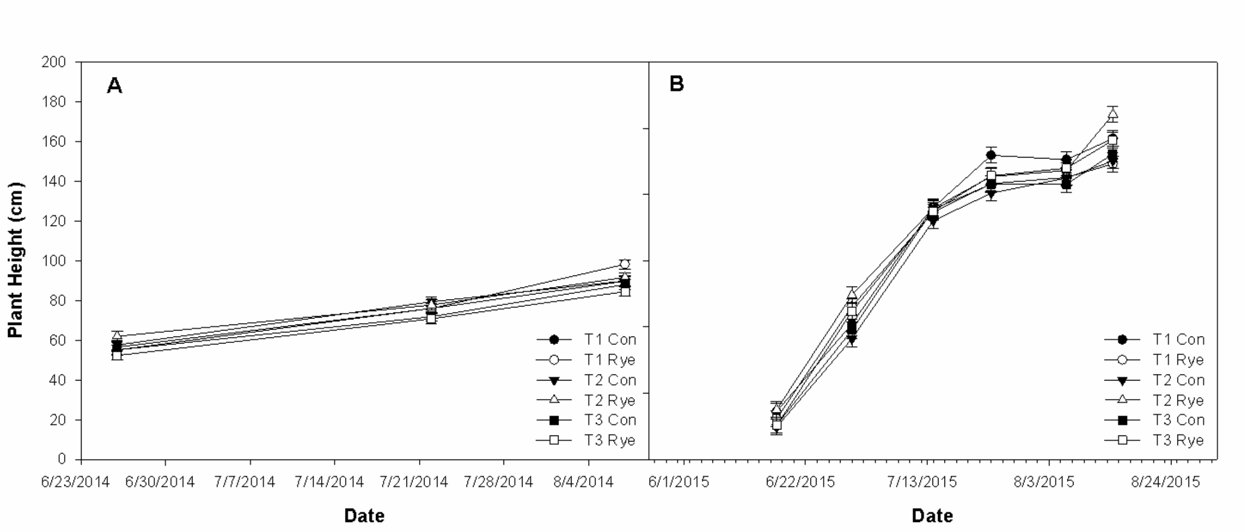

Figure 2.3**.** Plant heights for cotton grown under irrigation regimes T1-T3 and planted into either conventionally tilled beds (Con) or a heavy rye cover crop residue (Rye) during the 2014 (A) and 2015 (B) growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6).

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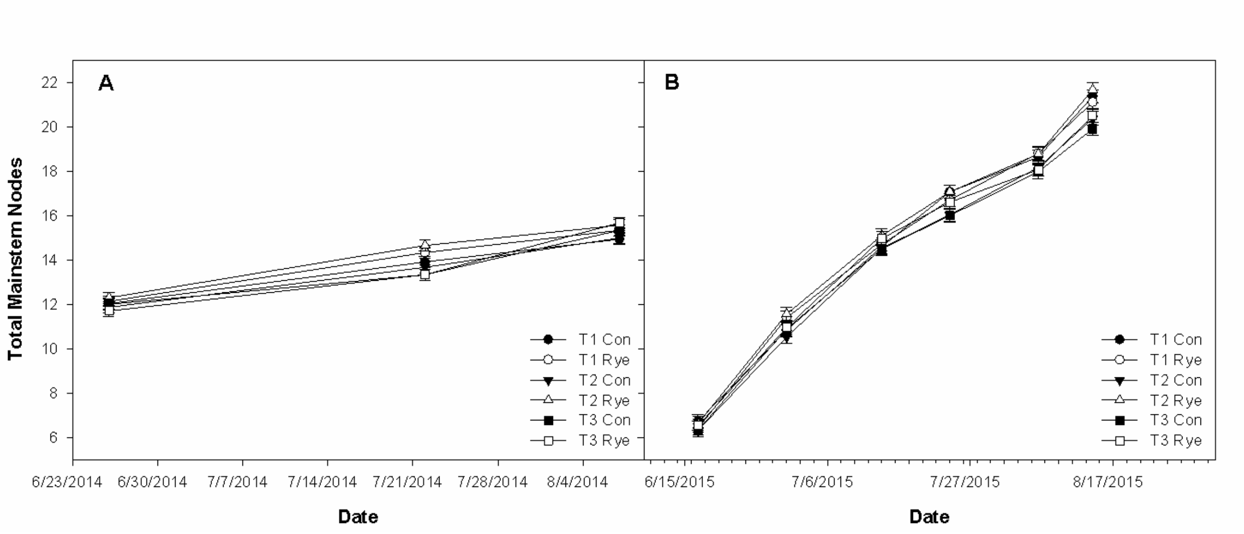

Figure 2.4**.** Total mainstem nodes for cotton grown under irrigation regimes T1-T3 and planted into either conventionally tilled beds (Con) or a heavy rye cover crop residue (Rye) during the 2014 (A) and 2015 (B) growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6).

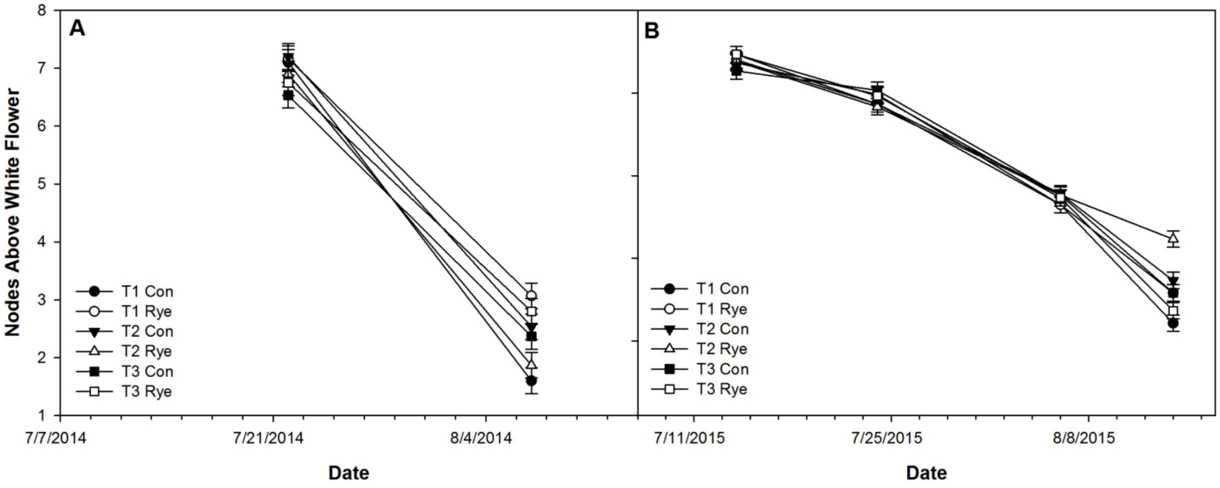

Figure 2.5**.** Mainstem nodes above the first position white flower for cotton grown under irrigation regimes T1-T3 and planted into either conventionally tilled beds (Con) or a heavy rye cover crop residue (Rye)during the 2014 (A) and 2015 (B) growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6).

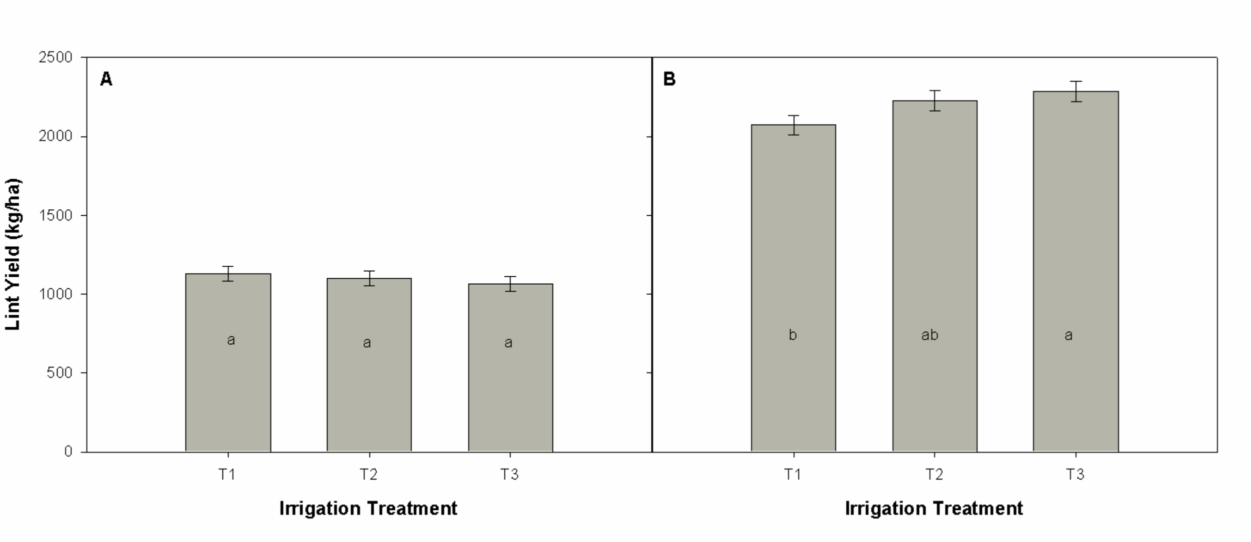

Figure 2.6**.** Lint yield in the 2014 (A) and 2015 (B) growing seasons (kg/ha) for under irrigation regimes T1-T3 during the 2014 (A) and 2015 (B) growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6) and bars not sharing a common letter within a given year are significantly different ($P < 0.05$).

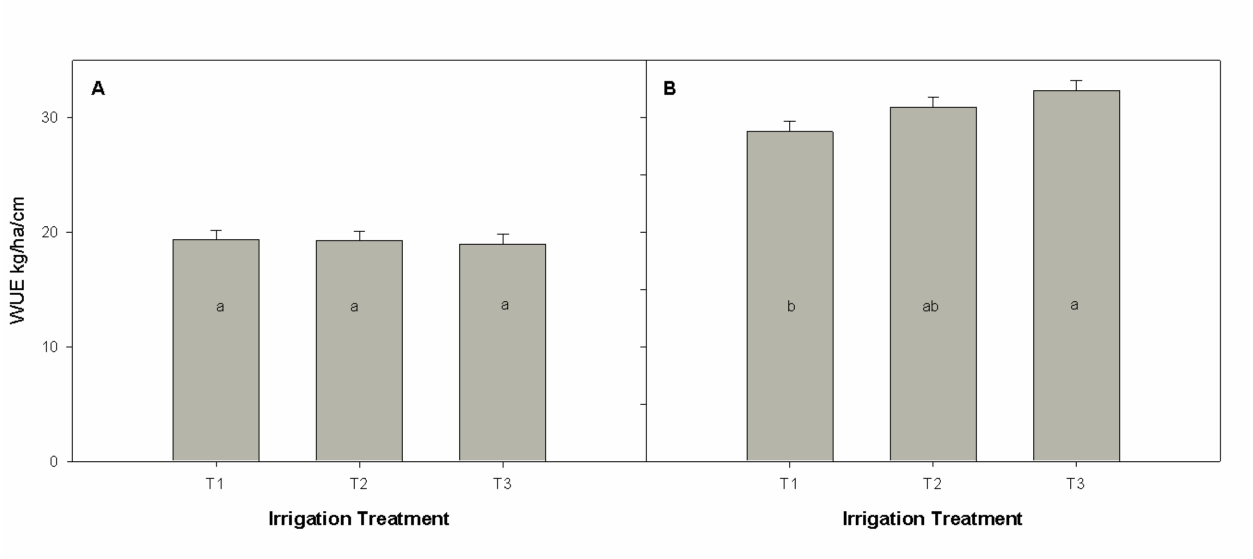

Figure 2.7. Water use efficiency (WUE) in the 2014 (A) and 2015 (B) growing seasons (kg/ha/cm) under irrigation regimes T1-T3 during the 2014 (A) and 2015 (B) growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6), and bars not sharing a common letter within a given year are significantly different ($P < 0.05$).

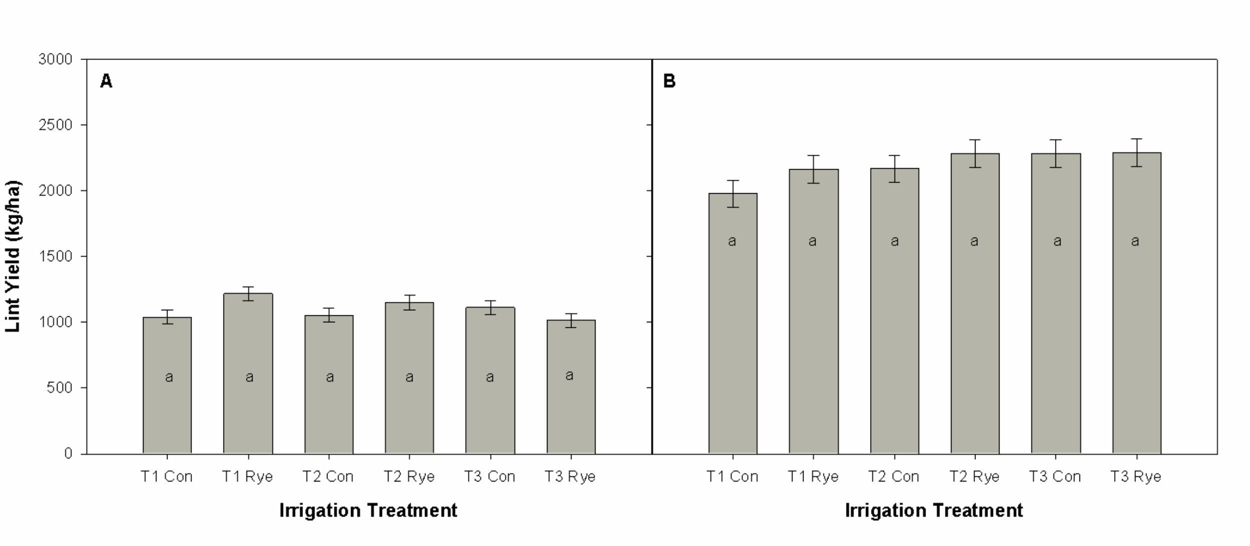

Figure 2.8**.** Lint yield in the 2014 (A) and 2015 (B) growing seasons (kg/ha) for under irrigation regimes T1-T3 and planted into either conventionally tilled beds (Con) or a heavy rye cover crop residue (Rye)during the 2014 (A) and 2015 (B) growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6) and bars not sharing a common letter within a given year are significantly different ($P < 0.05$).

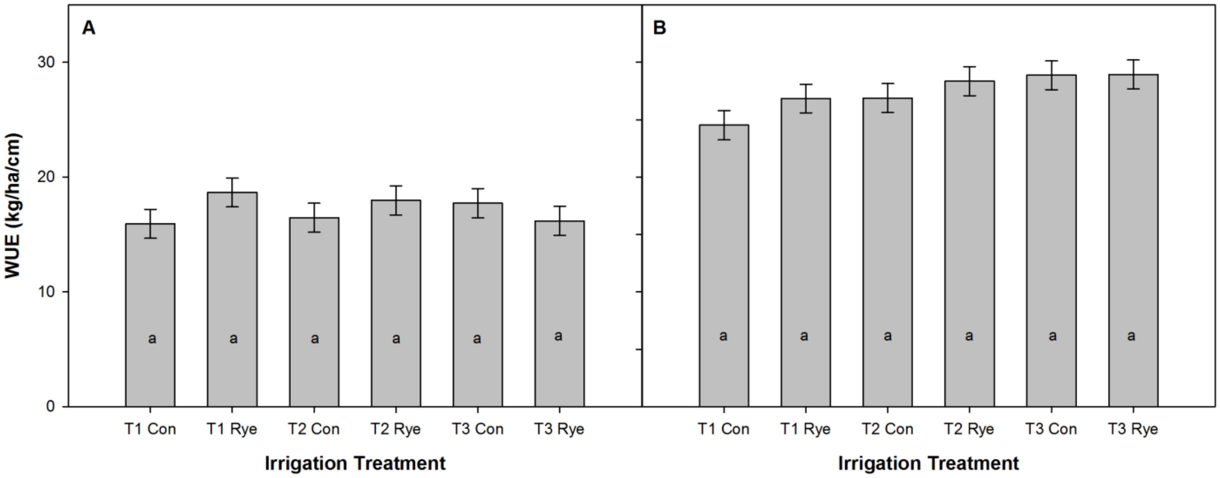

Figure 2.9**.** Water use efficiency (WUE) in the 2014 (A) and 2015 (B) growing seasons (kg/ha/cm) under irrigation regimes T1-T3 and planted into either conventionally tilled beds (Con) or a heavy rye cover crop residue (Rye)during the 2014 (A) and 2015 (B) growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6), and bars not sharing a common letter within a given year are significantly different ($P < 0.05$).

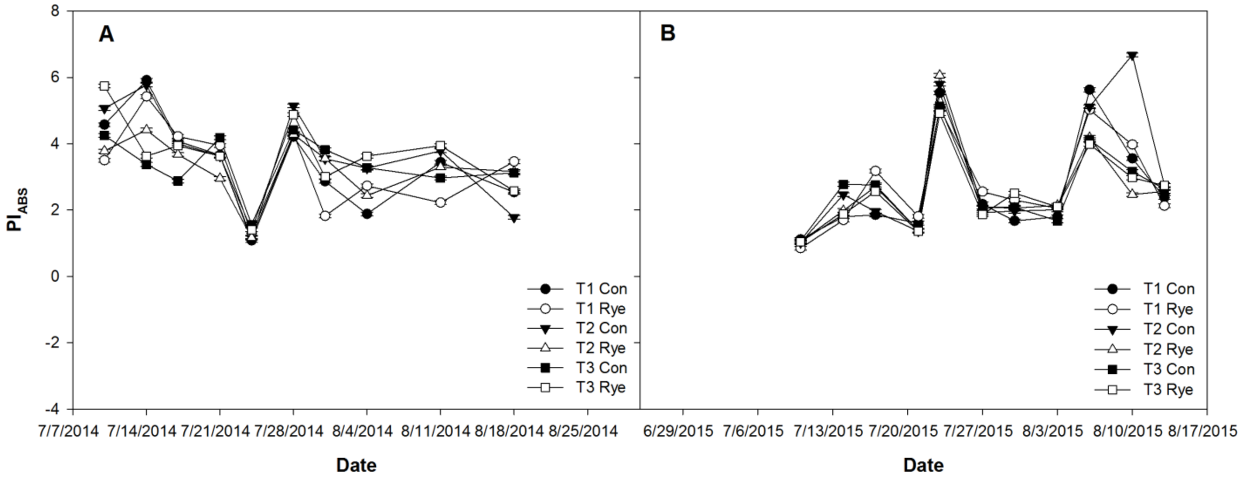

Figure 2.10**.** Photosynthetic Performance Index (PI_{ABS}) for the 2014(A) and 2015 (B) cotton crop grown under irrigation regimes T1-T3 and planted into either conventionally tilled beds (Con) or a heavy rye cover crop residue (Rye)during the 2014 (A) and 2015 (B) growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6).

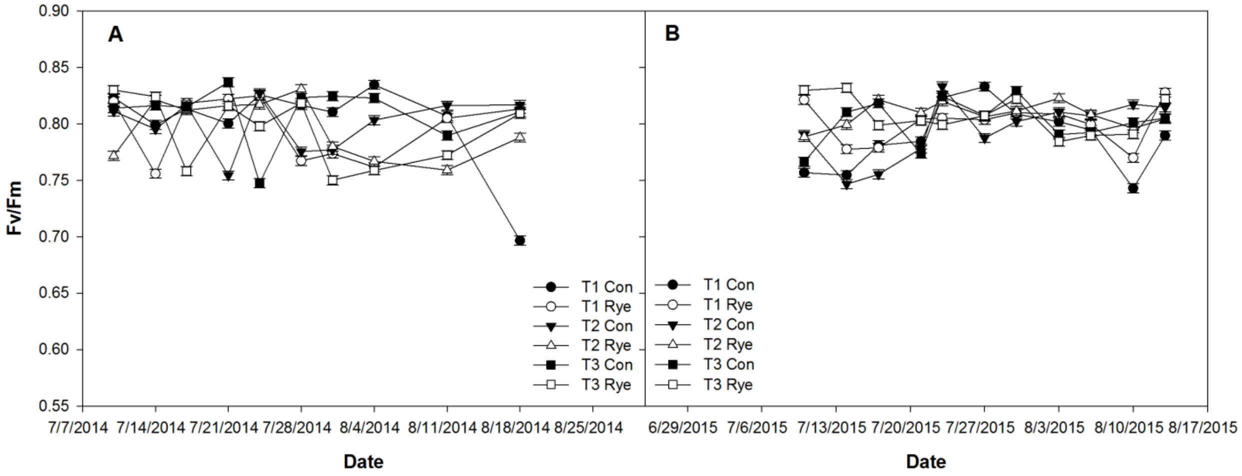

Figure 2.11**.** Maximum Quantum Yield of PSII (F_v/F_m) for the 2014(A) and 2015 (B) cotton crop grown under irrigation regimes T1-T3 and planted into either conventionally tilled beds (Con) or a heavy rye cover crop residue (Rye)during the 2014 (A) and 2015 (B) growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6).

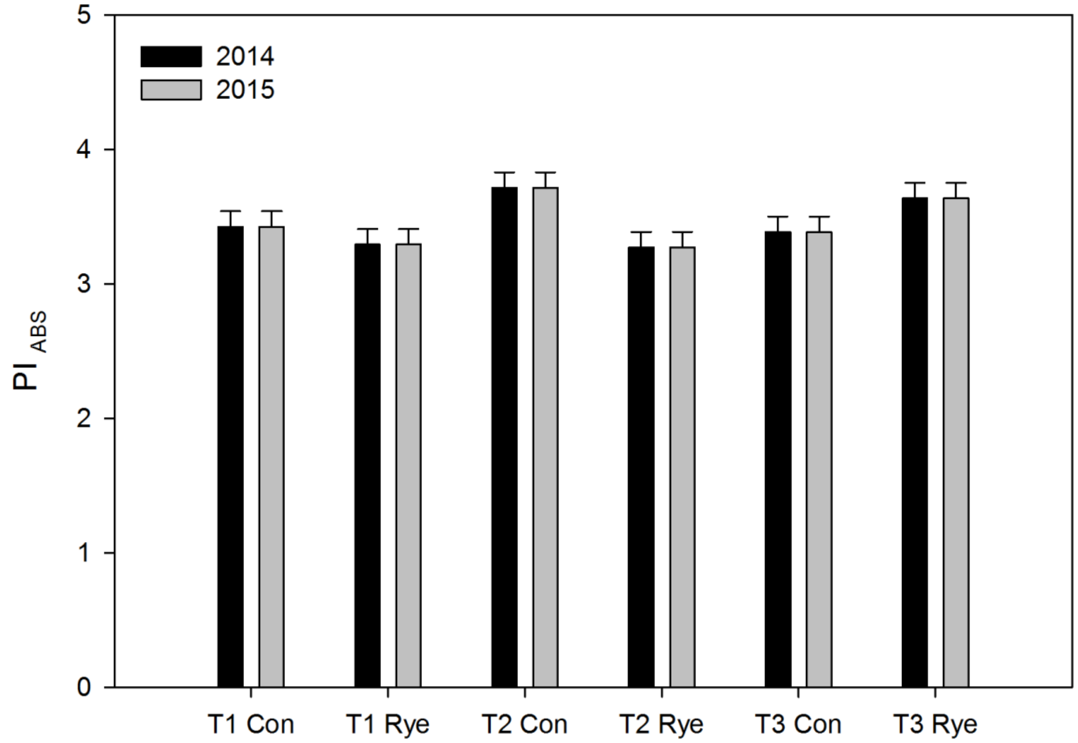

Figure 2.12. Photosynthetic Performance Index (PI_{ABS}) for the 2014 and 2015 cotton crop grown under irrigation regimes T1-T3 and planted into either conventionally tilled beds (Con) or a heavy rye cover crop residue (Rye) during the 2014 and 2015 growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6).

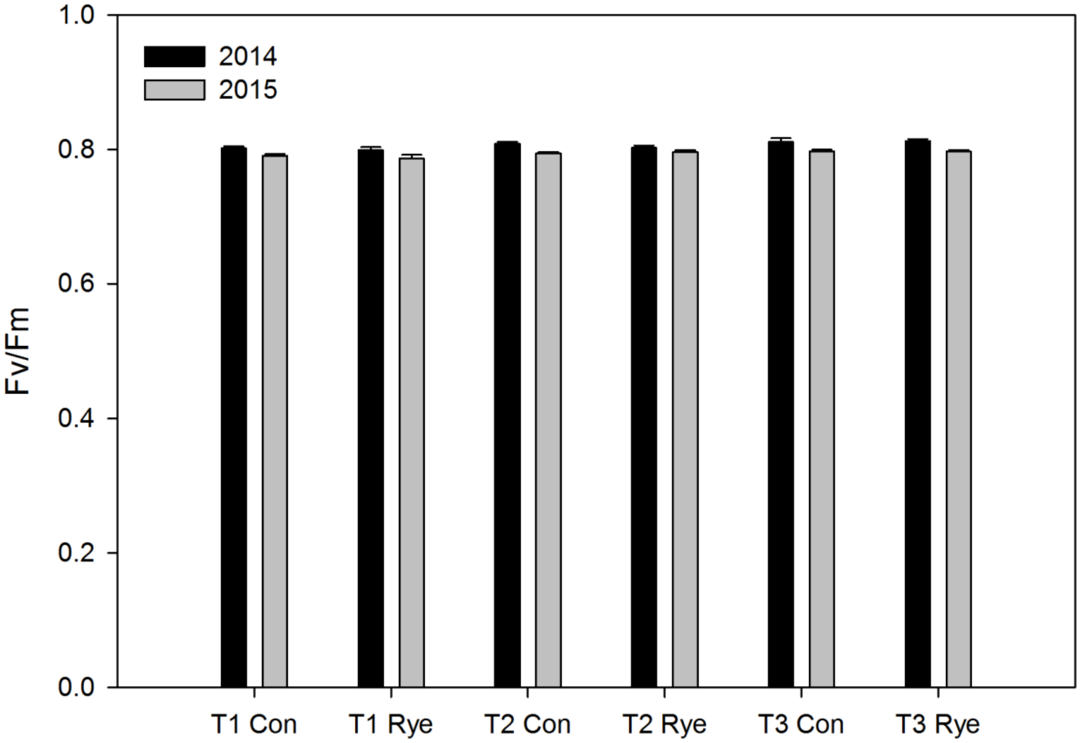

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Figure 2.13. Maximum Quantum Yield of PSII (F_v/F_m)for the 2014 and 2015 cotton crop grown under irrigation regimes T1-T3 and planted into either conventionally tilled beds (Con) or a heavy rye cover crop residue (Rye) during the 2014 and 2015 growing seasons at a field site near Tifton, GA. Values are means ± standard error (n = 6).

CHAPTER 3

QUANTIFYING COTTON RESPONSE TO EARLY SEASON WATER DEFICIT USING A MULTI-FACETED APPROACH[3]

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[3] Meeks,. C.D., J.L. Snider, M. Babb-Hartmann, and T. Barnes. To be submitted to *Crop Science*.

Abstract

This study addressed the potential of cotton plants to recover from early season drought stress occurring soon after planting. To address this, a study was conducted near Athens, Georgia and near Tifton, Georgia in University of Georgia greenhouse facilities and imposed varying irrigation scheduling treatments during the pre-bloom stage of development. Early season thresholds were a well-watered check (Treatment 1), 21 days to first irrigation (DFI) (Treatment 2), 28 DFI (Treatment 3), 35 DFI (Treatment 4), and 42 DFI (Treatment 5). Reductions in leaf area were noted of up to 73% for heavily drought stressed plants compared to well-watered plants. In some instances, photosynthesis and ETR were increased in the presence of drought stress; however, generally these parameters were significantly reduced compared to well-watered plants. Extreme reductions in plant biomass and reproductive structures were noted for drought stressed treatments, in some cases greater than fivefold when compared to well-watered plants. The results of this study conclude that early season irrigation is necessary to maintain plant growth and fruiting sites, whereas episodic drought coinciding with early season crop development represents a major threat to cotton production.

Introduction

Bednarz et al. (2002) found that cotton grown in Southern Georgia requires a minimum of 46 cm of water per growing season for maximum yields to be achieved, which is below the amount of rainfall received during a typical growing season in the southeastern US. However, rainfall is not always distributed in the amounts needed for specific growth stages; episodic drought and the coarse-textured, sandy soils that have poor water retention occur in the majority of cultivated land in Georgia (Chesworth et al., 2008). This poor water retention means that sufficient moisture may be present at planting to cause germination and emergence, but moisture may not be present in sufficient quantities after emergence if additional rainfall has not occurred. Water ranges from 70 to 90 percent of total plant fresh weight and is essential for nutrient transport, chemical reactions, cell enlargement, and transpiration (Gardner et al., 1984). Previous research in multiple crop species, including cotton, has indicated that the vegetative stage of crop development may be less sensitive to water deficit than early reproductive stages (Rowland et al., 2012; Snowden et al., 2014). However, yield limitations can occur in cotton if the early season stress level is severe enough (Cook and El-Zik, 1992).

Total above ground carbon assimilation has been shown to be dependent upon leaf area and photosynthetic efficiency (Gardner et al. 1985; Kreig and Sung, 1986; Turner et al. 1986). It is well-established that photosynthetic efficiency of drought stressed individual leaves decreases compared to well-watered plants (Pettigrew 2004; Ennahli and Earl, 2005; Snider et al. 2014; Chastain et al., 2014). Massacci et al (2008) observed daily declines in stomatal conductance that occurred at significantly greater rates for cotton leaves that were stressed as compared to leaves from well-watered cotton plants. Because the availability of water to a plant has a significant impact on a large number of physiological processes, all plants can be negatively affected by water deficit which leads to inhibited plant growth and development, hindered cell expansion, altered enzyme activities, and eventually decreased photosynthesis, and assimilate translocation (Loka et al., 2010). Similarly, Lokhande and Reddy (2014) determined that water deficient cotton had low photosythetic rates which stemmed from stomatal reductions. However, individual leaf photosynthesis has been observed to be less sensitive to both soil and leaf water deficits than leaf area development (Turner et al., 1986). Increasing leaf area has been indicated to lead to more productive plants in general (Hirose et al., 1997), and other authors have reported that canopy-level carbon assimilation (total source strength) is primarily limited under drought due to decreased total leaf area which causes reduced light interception by photosynthetic surfaces (Wells and Stewart, 2010; Kreig and Sung, 1986; Turner et al. 1986). Early season drought stress can result in abscission of young squares (Loka et al., 2011, Loka and Oosterhuis, 2012). These water deficit periods also cause vegetative growth to slow which in turn causes plant height/terminal growth to occur at a slower rate as compared to well-watered conditions, leading to reduced mainstem node development (Ritchie et al., 2009), and limiting upward development of effective fruiting sites. Crop maturity, as measured by nodes above the first square and nodes above the uppermost first-position white flower is hastened under drought due to reduced upward growth with premature cutout limiting the number of fruiting sites per plant (Bourland et al., 1992; Bourland et al., 2001; Brown and Oosterhuis, 1992, Meeks et al., 2017). Drought has been shown to decrease stem height, stem dry weight, leaf area, leaf dry weight, and total number of main stem nodes in cotton as well (Pace et al. , 1999, Ritchie et al. 2007). Growth is the most sensitive physiological process to drought stress due to declines in cell turgor pressure which limits cell expansion (Hsiao, 1973, Ball et al., 1994). Leaf expansion has been observed in the past to be more sensitive to water deficits than the root expansion (Ball et al., 1994). However, this response can increase the ratio of root growth compared to above ground shoot growth such that boll abscission increases and harvestable lint yield is reduced for dryland cotton (Cook and El-Zik, 1992). Thus, the results of the aforementioned studies provide abundant reason to avoid drought stress in order to maximize yield and profitability. Leaf expansion limitations from drought stress were also observed by a number of authors (Matsuda and Riazi, 1981; Masle and Passioura, 1987; Cutler et al., 1977). This is especially important due to the fact that leaf expansion declines have been observed in as little as 2 days of drought stress (Ball et al., 1994). Ball et al., (1994) noted as well that a rebound in leaf expansion was observed

5 days after drought stress was alleviated; however, water deficit treatments had significant reductions in leaf area index (LAI) at season's end.

The current study was novel in that a multi-faceted assessment of early season physiological response to drought duration has not been done recently in cotton utilizing modern cultivars. Previous studies also were not undertaken to only examine early season drought and did not examine the ability of cotton to rebound from early season stress prior to flowering. Therefore, it was hypothesized that early season drought stress would have negative impacts on photosynthetic processes and plant growth, but that plants would rebound from early season stress, in a manner dependent upon the duration of the drought stress and recovery periods. Consequently, the objective of this study was to measure individual-leaf and whole-plant physiological and agronomic responses of the cotton crop to multiple drought stress timings in order to better the cotton crop's response to early season drought stress.

Materials and methods

Two greenhouse studies were established to assess the growth and physiological response of cotton to a range of early season drought durations. Experiment 1 was conducted at a greenhouse in Athens, GA (USA) (33.930173, -83.363619), seeds of G. hirsutum cv. FM 1944 GLB2, (Bayer CropScience), PHY499 WRF (Dow Agroscience), and Deltapine 1050 B2RF (Monsanto) were sown at a 2.5 cm depth on March 3, 2015. The experimental design was a randomized design with three cultivars and three irrigation treatments (n = 5). Experiment 2 was conducted at a greenhouse in Tifton, GA (USA) (31.474869, -83.524631), seeds of G. hirsutum cv. FM 1944 GLB2, FM 1740 B2F, (Bayer CropScience), PHY499 WRF (Dow Agroscience), and Deltapine 1050 B2RF (Monsanto Co) were sown at a 2.5 cm depth on April 11, 2016. The experimental design was a randomized complete block design with four cultivars and five irrigation treatments (n =20). Due to greenhouse system limitations, the 2015 study was reduced in size as compared to the 2016 study. All seeds were planted into 5.6 L pots containing Promix BX (Premier Tech Horticulture) commercial nursery production medium to ensure uniform soil conditions. Initially, three seeds were sown per pot. All plants were fertilized uniformly by incorporating a complete nursery fertilizer with micronutrients into the potting medium according to manufacturer recommendations to prevent nutrient limitations (Harrells 12-6-6 Nursery Special fertilizer incorporated at 3.1 kg/cu m^{-3}).Uniform emergence was ensured by planting seeds into the soil at water holding capacity. Plant stands were thinned to a single plant per pot after emergence.

Irrigation treatments were initiated immediately after planting in both experiments. For Experiment 1, the treatments were implemented as follows: T1 (control), soil moisture kept at field capacity throughout the experiment; T2, 21 days until first irrigation (DFI) and maintained at field capacity thereafter until termination of the study; T3, 28 DFI and maintained at field capacity thereafter until termination of the study. Experiment 2 included the aforementioned treatments plus the following treatments: T4, 35 DFI then maintained at field capacity until study termination; T5, 42 DFI then maintained at field capacity until study termination. Treatments are depicted in Table 3.1, and in both experiments, the study was terminated following a week of recovery for the treatment exposed to drought for the longest period of time: 42 DAP for Experiment 1 and 56 DAP for Experiment 2. When plants were irrigated, a drip irrigation system with an automated timer was programed to apply 2.5L of water once daily at 12:00 PM.

Plant growth and development were assessed dynamically over the entire study period by measuring plant height and total number of mainstem nodes per plant for all treatments at weekly intervals during Experiment 1 and at least every 3 days in Experiment 2. Destructive harvest of all plants in the greenhouse was undertaken at the termination of the study (at 7 days of recovery for the treatment receiving the longest exposure to early season drought). Plants were separated into leaves, stems, and squares for final growth analysis. Leaf area per plant was determined using an LI-3100 table-top leaf area meter (LI-COR: Lincoln, NE), and the number of squares per plant was determined. Subsequently, plant parts were dried in a forced-air oven at 80°C for 48 h to determine total dry weight, and dry weights for each component plant part as well.

In both experiments, gas exchange measurements were conducted at midday (1100 to 1400 h) on the uppermost fully expanded leaf on each plant (fourth mainstem node below the plant terminal) using the portable photosynthesis systems available at each site. In Experiment 1, the CIRAS-1 (PP Systems) with a transparent top chamber was utilized to measure net photosynthesis (A_N) and stomatal conductance (g_s) when plants were placed under an external LED light source at photosynthetically active radiation (PAR) = 1517 ± 22 µmol m^{-2} s^{-1} incident at the leaf surface. In Experiment 2, and LI-6400 XT (LI-COR: Lincoln, NE) portable photosynthesis system with a built-in LED light source and an integrated leaf chamber fluorometer were used to measure gas exchange and fluorescence under constant PAR (1500 µmol m^{-2} s^{-1}). In addition to steady state A_N and g_s, the integrated fluorometer allowed for simultaneous measurement of photosynthetic electron transport rates (ETR) through photosystem II using the multi-phase flash method described elsewhere (Earl and Ennahli, 2004). Reference CO2 concentration was ~400 µL L-1 and chamber block temperature was equal to ambient temperature. Steady state values for all parameters of interest were obtained within 120 seconds of enclosing the leaf in the chamber.

ATP content was determined according to methods modified from Snider et al. (2009). Briefly, five 6 mm diameter leaf discs were taken from the uppermost fully expanded leaf on each sample date and extracted by boiling them in a 3 ml solution of 50 mM TRIS buffer for 10 minutes and then allowing the samples to cool to room temperature. Subsequently, 100 µL of each sample was added to 100 µL of ATP Bioluminescent Assay Reagent (ATP Bioluminescent Assay Kit FLAA, Sigma-Aldrich, St. Lousi MO)) and luminescence was recorded using a Glomax 20/20 luminometer (Promega Corporation, Madison, WI). Luminescence from each sample was compared with ATP standard solutions ranging from 0.04 to 0.00001 µg ml^{-1} and sample ATP concentrations were calculated according to the standard curve.

Total chlorophyll content was determined by placing 4, 6 mm leaf discs from the uppermost expanded leaf and extracting them in an amber vial containing 5 mL of reagent grade ethanol at 4°C for 14 days. After extraction, 300 µl of each sample was placed into a 96 well microplate and absorbance read with a Spectramax 250 microplate reader (Molecular Devices, Sunnyvale CA). Absorbance at 649 and 665 nm were used to calculate chlorophyll A and B according to the equations given in Lichtenthaler and Wellburn, (1983). Chlorophyll A and B were summed to obtain total chlorophyll content.

Statistical analysis was conducted using JMP Pro 12 (SAS Institute Inc., Cary, NC) and graphs were constructed using SigmaPlot 11.0 (Systat Software Inc., San Jose, CA). In all instances where comparative analyses were performed, $\alpha = 0.05$. The effect of irrigation treatment and cultivar on all parameters of interest was assessed using a full factorial two-way analysis of variance (ANOVA) where irrigation treatment and cultivar were fixed effects. Where significant main effects were observed, mean separation was performed using LSD post hoc analysis. Due to logistical constraints, gas exchange, fluorescence, and biochemical measurements (ATP and total chlorophyll) were done only on the last day of the stress period for a given treatment of interest (i.e. T2 measured at 21 days, T3 measured at 28 days, etc.), which means that plants were at different ages and different drought stress durations. Thus, measured values were converted to a percent of the well-watered control (average value for the well-watered control across all cultivars measured on the same day as the treatment of interest) prior to performing comparative analysis. Because cultivar main effects and cultivar x irrigation interactions were rarely and inconsistently observed, data presentation in the current study will focus on irrigation treatment main effects for all parameters of interest.

Results

Plant heights and nodes were not affected significantly by irrigation treatment early in the 2015 study until 28 days after planting (DAP), with significant differences noted in plant height, and total mainstem nodes on the 28, 35, and 42 DAP sample dates in 2016 (Table 3.2 and Figure 3.1). End of study height measurements demonstrated significant differences between T1 and the drought stressed treatments (T2 andT3) with reduced plant height occurring under drought stress (Figure 3.1), where T1 measured 27 cm as compared to 20 cm and 18 cm for T2 and T3, respectfully. A similar trend is noted for total mainstem nodes as well in 2015 (Figure 3.1). In 2016, a similar trend in plant height is noted with up to a 30 cm reduction in plant height when compared to T1 (Figure 3.1). For example, in this study significant irrigation effects were observed a week earlier than in the 2015 study, for discussion purposes, this indicates that measurable stress was observed more rapidly in 2016 than 2015. Total mainstem nodes were significantly affected by irrigation treatment in 2016 on all sample dates throughout the study (Table 3.3). Total mainstem nodes followed a similar trend as compared to plant height with T1 observed to have the greatest number of mainstem nodes (9), T2 observed was reduced the least (7) and T3-T5 were reduced the most (6-5) (Figure 3.1).

In 2015, a significant irrigation effect was observed for net photosynthesis, stomatal conductance (g_s), and total chlorophyll content, but not adenosine triphosphate content (ATP) (Table 3.4; Figure 3.2). For example, A_N was similar between T1 and T2; however, significant differences between T1 and T3 were noted, with T3 being only 20% of the control (Figure 3.2). Stomatal conductance differed significantly between all treatments, with 56% reductions in gs, relative to the control for T2 and 19% for T3 in 2015 (Figure 3.2). Total chlorophyll content increased with duration of drought stress, where chlorophyll content was 119% of the control for T2 and 202% of the control for T3 (Figure 3.2).

In 2016 A_N, g_s, and ETR were impacted by irrigation with similar trends (Figure 3.3). For example, T4 values for g_s and A_N in 2016 were 141% and 191%, respectively, of the control; T2, T3, and T5 were similar in the observed response, varying from 47%-61% of the control (A_N) and 57%-63% (g_s) of the control (Figure 3.3). ETR followed a similar trend, with T4 being 147% of the control and T2, T3, and T5 ranging from 56%-64% of the control (Figure 3.3). ATP in 2016 was noted to be higher in the more heavily drought stressed T4 (246% of the control, but was not significantly different from T2 at 140% or the control) and T5 (170% of the control) treatments with T4 demonstrating the highest ATP content relative to the control, T3 was observed to be similar at 115% of the control; however, T2 was similar to T5 at 140% of the control (Figure 3.3). Treatment 4 at the time of the data collection was observed to appear to be more vigorous than previous with new leaves being added, possibly undergoing remobilization to tolerate the drought conditions.

In 2015, drought duration significantly affected all end-of-season growth parameters (Table 3.5). For example, T1 treatments demonstrated an average leaf area of 1263 cm^2/plant compared to the 583 cm^2/plant leaf area of the next treatment (T2) (Figure 3.4). Leaf dry weight (DW) followed a similar trend with T1 demonstrating an average leaf dry weight of 6.3 g $plant^{-1}$ compared to 3.2 g $plant^{-1}$ for the next treatment (T2) (Figure 3.4). Stem DW followed similar trends with drought stressed treatments T2-T3 (2.1 to 1.4 g $plant^{-1}$) demonstrating reduced dry weight when compared to T1 (5 g $plant^{-1}$) (Figure 3.4). Square counts per plant were noted to be significantly greater in the control (4.3) as compared to T2-T3 as well (2.3-1.8), and square DW followed a similar trend (Figure 3.4). For total plant dry weight, similar trends were observed as well, with well-water plots weighing 11.5 g versus 5.4 to 3.6 g for T2-T3 in 2015 (Figure 3.4).

As in 2015, early season drought in the 2016 study had a pronounced effect on growth parameters (Table 3.5; Figure 3.5). For example, T1 treatments demonstrated an average leaf area of 5127 cm^2/plant compared to the 2674 cm^2/plant leaf area of the next treatment (T2) (Figure 3.5). T2 had significantly greater leaf area than T4-T5 (Figure 3.5). Leaf dry weight followed a similar trend, with the T1 treatment having an average leaf dry weight of 38.6 g/plant compared to the of 13.4 g/plant of the next treatment (T2) (Figure 3.5). Dry weights of plant stems followed similar trends with drought stressed treatments T2-T5 demonstrating reduced dry weight when compared to the T1 treatment (Figure 3.5). Square counts were considerably greater in the control (42 squares per plant) as compared to T2-T5 as well (11-8 squares per plant) (Figure 5). Reproductive dry weights also followed this trend with treatments T2-T5 demonstrating reduced dry weights when compared to T1. Similarly, for total plant dry weight for well-watered control plants averaged 87.6 g versus 23.5-7.68 g for T2-T5 (Figure 3.5).

Discussion

The observations from two years of greenhouse trials in Athens, Georgia and Tifton, Georgia demonstrated the need for an adequate early-season irrigation strategy to avoid periods of episodic drought. This study hypothesized that drought stressed treatments would lead to stunted plants that could possibly rebound after irrigation was undertaken. Photosynthetically the plants did indeed rebound, which does support this hypothesis (data not shown). However, even though internal plant processes recovered, significant square loss (Figure 3.4, 3.5) was detected from all drought stressed treatments, ranging from 21 to 49 days of withholding irrigation after planting (T2-T5). Furthermore, plants under these treatments were observed to be considerably less vigorous and had less leaf area (Figure 3.2-3.5). Therefore, these results verify that adequate soil moisture must be maintained to ensure adequate early season growth and reproductive development. For example, Figure 3.5 illustrates similar reproductive dry weight for all 4 drought-stressed treatments in 2016, whether water was withheld for 3 weeks (followed by a 7 week recovery) or 6 weeks (followed by a week recovery). In contrast, substantial reproductive DW gains (2.6 g vs 1.2 g) are noted with well-watered plants (T1), illustrating the importance of supplemental irrigation during the early season to minimize drought risk and highlighting the possibility of negative impacts of drought stress during the prebloom period (Figure 3.5). Therefore, even if the plants were drought stressed earlier in the season, if severe enough, yield loss could still occur if plants didn’t have sufficient time to recover. Overall, these observations are similar to those of Loka et al. (2011) and Loka and Oosterhuis (2012) in which early season drought stress led to abscission of young squares.

It is important to note that using a particular cultivar does not necessarily mean that drought stress will be mitigated. For example, Phytogen 499 in 2016 was observed to be greater in height and have more mainstem nodes (data not shown); however, this did not translate into more reproductive structures or greater reproductive dry weight under water deficit at the end of the experiment when compared with any other cultivar (Table 3.5). Thus, while early season water deficit periods may have less of an effect on final yield than stress during reproductive periods (Snowden et al., 2014), early season irrigation management should be based on actual measures of crop water status, such as soil moisture (Meeks et al., 2017) to prevent the negative consequences of early season drought noted in the current study. Future work should take the plants to yield following each of these stress periods because it has been demonstrated that early season drought stress could result in shorter plants with fewer nodes than well-watered plants, but despite the decrease in plant height, comparable end of season lint yields can be obtained (Bauer et al., 2012; Snowden et al., 2014).

As noted in the introduction, the capacity for plant growth is dependent upon leaf area and average photosynthetic efficiency of leaves. The declines in whole plant growth noted in the current study under early-season drought were likely the result of inhibition of both of these processes. Numerous authors (Chastain et al., 2014; Kitao and Lei, 2007; Snider et al., 2014; Zhang et al., 2011) demonstrated in field-grown cotton plants that drought stress can lead to reduced net photosynthesis and stomatal conductance, whereas ETR and actual quantum yield of photosystem II (ΦPSII) were not significantly reduced by a wide range of water deficit conditions. In this study, net photosynthesis was reduced at the end of the drought period in all but one treatment in 2016 (T4; 35 DFI). In this instance, T4 had significantly higher photosynthetic rates than the well-watered T1 (Figure 2, 3), and a similar response was observed for g_s. In all instances where drought stress limited A_N, significant declines in ETR were observed, which is contrary to the aforementioned reports on cotton. However, it should be noted that those studies were conducted at later stages of plant development and under field conditions. The limited rooting volume in potted plant experiments typically causes plants to experience drought stress more rapidly than in the field, which is apparent when considering that irrigation treatments differed in growth responses very early in the experimental period (Figure 3.1). Thus, it appears that under these extreme early season stress conditions, metabolic impairment to photosynthesis (non-stomatal limitation) does occur. Interestingly, photosynthetic limitations do not appear to be associated with reduced ATP content as described elsewhere for other species (Tezara et al., 1999, 2008; Lawlor and Tezara, 2009) because the ATP content of cotton leaves showed a generally increasing trend as duration of drought stress increased (Figure 3.3).

Regardless, plant growth has been demonstrated to be the most sensitive physiological process to the onset of water deficit (Hsiao, 1973). As expected, leaf area was reduced across T2-T5 treatments compared to T1 treatments (Figure 3.4, 3.5). Final plant biomass and square dry weights followed nearly an identical trend to that of whole plant leaf area, indicating that leaf area development largely governed whole-plant and reproductive growth response to early season drought (Figure 3.4, 3.5). The findings of the current study illustrate the importance of the timing of rainfall or irrigation events occurring during early season growth. Squares were retained at a greater rate under well-watered conditions and plants were more vigorous. Thus, it is possible that end of season yield losses might have occurred for treatments T2-T5. However, longer term studies should be undertaken to confirm this due to the cotton plant’s ability to compensate for early season stresses by retaining bolls higher in the plant if more favorable growing conditions occur later in the growing season.

Conclusions

Episodic drought during prebloom substantially limits reproductive growth through processes that may include: fruit abscission or a reduction in the total number of available fruiting sites due to reductions in overall plant growth and decreased node development, decreased whole-plant photosynthesis resulting from low single leaf photosynthetic rates and whole-plant leaf area. Lastly, well-watered plants were considerably more vigorous and had significantly more squares, where even the earliest stress period with the longest recovery time had significantly reduced plant growth and square retention, illustrating the need for adequate irrigation regardless of plant growth stage. Full season studies in the field would also help determine what periods of stress could be tolerated and recovered from given a full growing season.

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Table 3.1. Description of irrigation treatments 1 (T1) through 5 (T5) during the 2015 experiment at a greenhouse in Athens, GA and 2016 experiment in at a greenhouse in Tifton, GA..

Year	Treatment	Description
2015	T1	Well watered
	T2	21*
	T3	28*
2016	T1	Well watered
	T2	21*
	T3	28*
	T4	35*
	T5	42*

*Indicates the number of days without irrigation after initially sowing seeds into potting medium at field capacity soil moisture conditions.

Table 3.2. Analysis of variance results for plant height (cm) and number of mainstem nodes per plant for three cotton cultivars under three irrigation regimes planted March 3, 2015. Measurements were conducted weekly beginning at 7 days after planting (DAP) and concluding at 42 DAP.

Sample Date	**Error Source**	**P Value**	
		Height	**Node**
7 DAP	**Irrigation**	0.2415	0.5977
	Cultivar	0.1181	0.5039
	Irrigation x Cultivar	0.8181	0.8711
14 DAP	**Irrigation**	0.6830	0.1601
	Cultivar	0.4533	0.1462
	Irrigation x Cultivar	0.8232	0.9812
21 DAP	**Irrigation**	0.0309	0.2871
	Cultivar	0.6225	0.6425
	Irrigation x Cultivar	0.8653	0.8592
28 DAP	**Irrigation**	**< 0.001**	**0.0005**
	Cultivar	0.7576	0.5428
	Irrigation x Cultivar	0.6142	0.8107
35 DAP	**Irrigation**	**< 0.001**	**< 0.001**
	Cultivar	0.5756	0.6433
	Irrigation x Cultivar	0.1492	0.3365
42 DAP	**Irrigation**	**< 0.001**	**< 0.001**
	Cultivar	0.7737	0.4170
	Irrigation x Cultivar	0.2997	0.4442

Table 3.3. Analysis of variance results for plant height (cm) and number of mainstem nodes per plant for four cotton cultivars under three irrigation regimes planted April 11, 2016. Measurements were conducted twice weekly beginning at 7 days after planting (DAP) and concluding at 56 DAP. For brevity, only ANOVA results for weekly measurements beginning at 7 DAP are shown in Table 3.3.

Sample Date	Error Source	P Value	
		Height	Node
7 DAP	**Irrigation**	**0.0014**	**0.0071**
	Cultivar	< **0.001**	**0.0002**
	Irrigation x Cultivar	0.1169	0.6928
14 DAP	**Irrigation**	0.2455	**0.0134**
	Cultivar	< **0.001**	**0.0003**
	Irrigation x Cultivar	0.4901	0.6604
21 DAP	**Irrigation**	< **0.001**	< **0.001**
	Cultivar	< **0.001**	0.0178
	Irrigation x Cultivar	0.7300	0.8832
28 DAP	**Irrigation**	< **0.001**	< **0.001**
	Cultivar	< **0.001**	**0.0194**
	Irrigation x Cultivar	0.5999	0.5985
35 DAP	**Irrigation**	< **0.001**	< **0.001**
	Cultivar	< **0.001**	0.0873
	Irrigation x Cultivar	0.6268	0.8037
42 DAP	**Irrigation**	< **0.001**	< **0.001**
	Cultivar	0.0985	0.0362
	Irrigation x Cultivar	0.7849	0.8548
49 DAP	**Irrigation**	< **0.001**	< **0.001**
	Cultivar	0.3821	0.1997
	Irrigation x Cultivar	0.7315	0.9201
56 DAP	**Irrigation**	< **0.001**	< **0.001**
	Cultivar	0.1503	0.0290
	Irrigation x Cultivar	0.6794	0.5415

Table 3.4. Analysis of variance results for photosynthetic and biochemical measurements for three cotton cultivars under three irrigation regimes planted March 3, 2015 and four cotton cultivars under five irrigation regimes planted April 11, 2016. Data for electron transport rates (ETR) was not available in 2015 and Chlorophyll measurements were not available in 2016.

Study Year	**Error Source**	**P Value**				
		A_N	**g_s**	**Total Chlorophyll**	**ATP Content**	**ETR**
2015	**Irrigation**	**< 0.001**	**< 0.001**	**< 0.001**	0.1660	
	Cultivar	0.8922	0.8254	**0.0420**	0.4754	
	Irrigation x Cultivar	0.7181	0.7758	0.2515	0.4224	
2016	**Irrigation**	**< 0.001**	**< 0.001**		**0.0099**	**< 0.001**
	Cultivar	**0.0015**	0.4337		0.1102	0.7965
	Irrigation x Cultivar	0.1074	0.9537		0.0100	0.6338

Table 3.5**.** Analysis of variance results for leaf area, square counts, and plant component dry weights (DW) for three cotton cultivars under three irrigation regimes planted March 3, 2015 and four cotton cultivars under five irrigation regimes planted April 11, 2016. Destructive harvest was conducted 35 DAP in 2015 and 56 DAP in 2016.

Study Year	**Error Source**	**P Value**				
		Leaf Area	**Square counts**	**Leaf DW**	**Stem DW**	**Square DW**
2015	**Irrigation**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.0081**
	Cultivar	0.1198	0.4457	0.0723	0.1154	0.4303
	Irrigation x Cultivar	0.0210	0.1465	0.0202	0.0328	0.1754
2016	**Irrigation**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
	Cultivar	**0.0324**	0.6226	0.0828	0.0767	0.1379
	Irrigation x Cultivar	0.8059	0.4738	0.7727	0.6478	0.4135

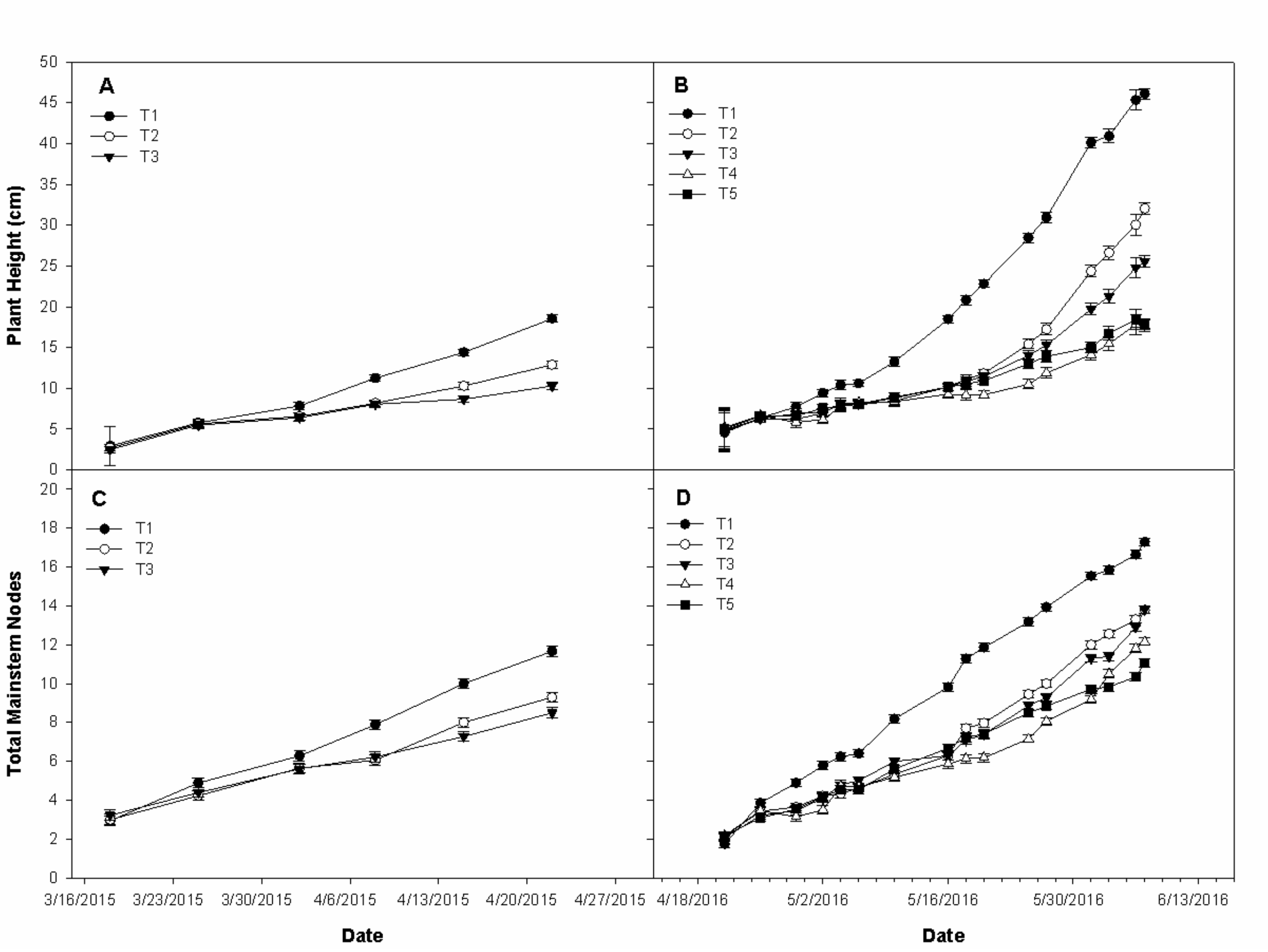

Figure 3.1**.** Plant heights and total mainsten nodes for cotton grown in irrigation regimes T1-T3 during the 2015 experiment (A, C) and T1-T5 during the 2016 experiment (B, D). Data in 2015 was collected weekly and 2016 was collected biweekly. Values are means ± standard error (n = 15 for 2015 and n=24 for 2016).

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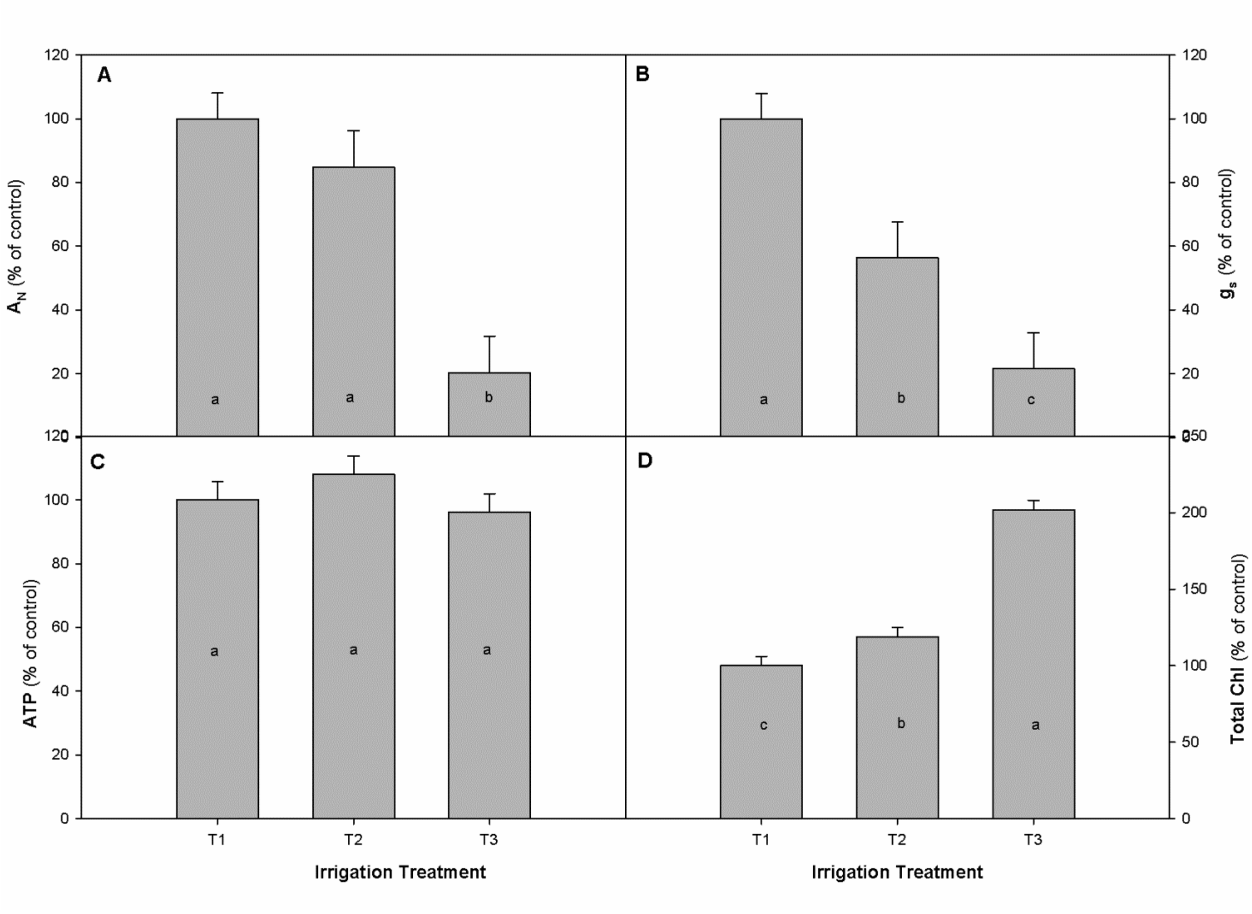

Figure 3.2. Net photosynthesis (A_N), (A), stomatal conductance (g_s) (B), Adenosine 5'-triphosphate (ATP) content (C), and total chlorophyll (Chl) (D) for cotton grown in irrigation regimes T1-T3 during the 2015 experiment in Athens, GA. Values are means ± standard error (n = 12 represented as a percent of the control and bars not sharing a common letter are significantly different ($P < 0.05$).

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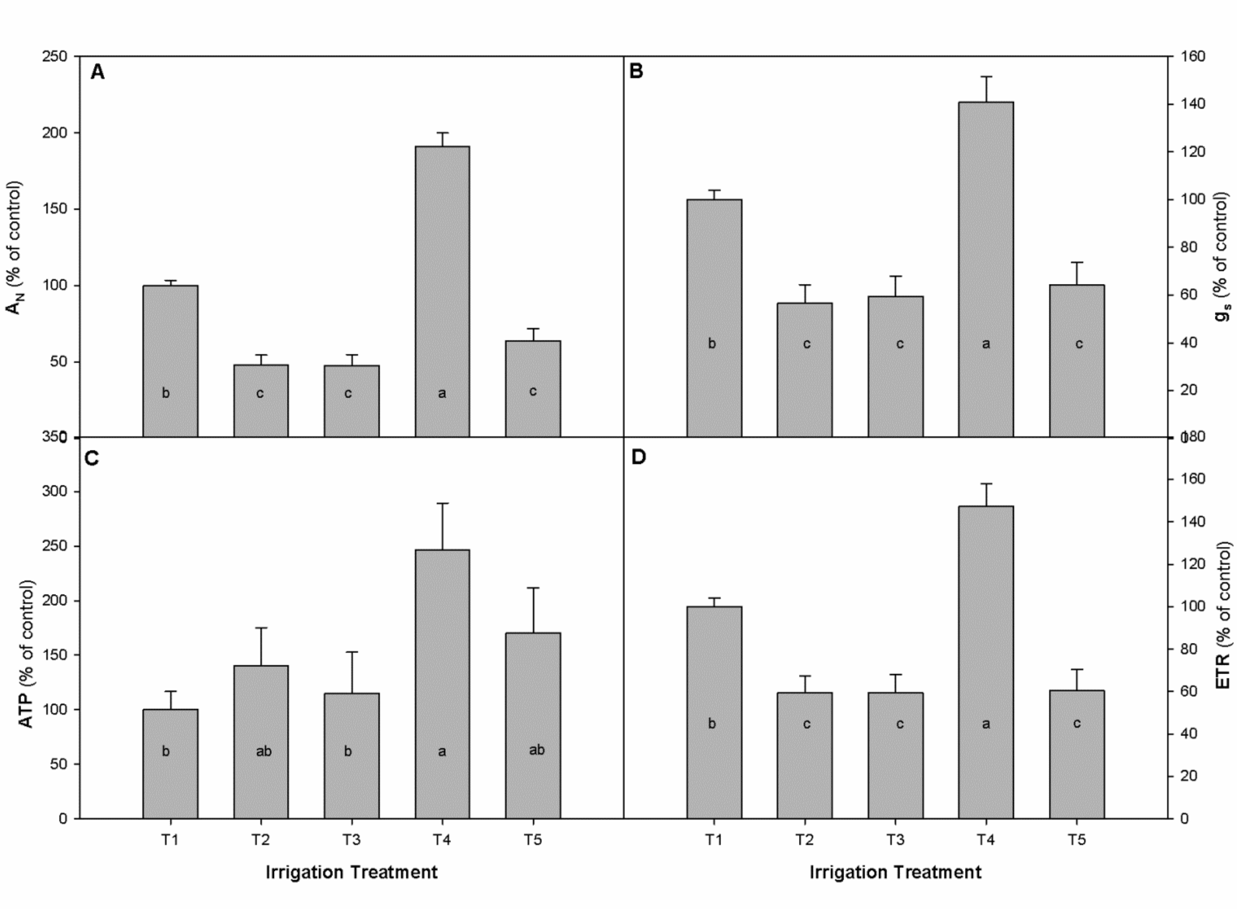

Figure 3.3. Net photosynthesis (A_N), (A), stomatal conductance (g_s) (B), Adenosine 5'-triphosphate (ATP) content (C), and electron transport rate (ETR) (D) for cotton grown in irrigation regimes T1-T5 during the 2016 experiment at a greenhouse near Tifton, GA. Values are means ± standard error (n = 16) represented as a percent of the control and bars not sharing a common letter within a given year are significantly different ($P < 0.05$).

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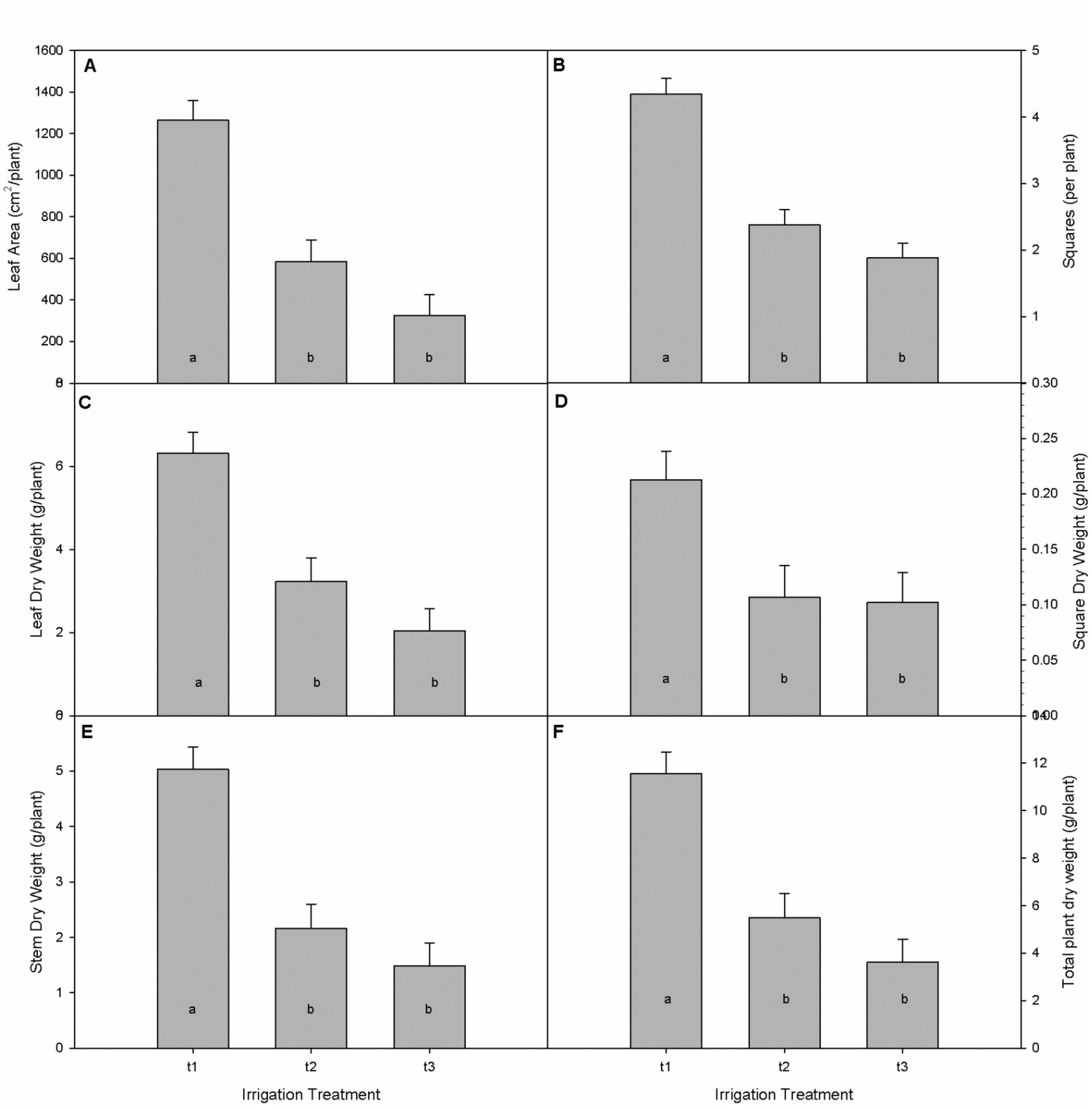

Figure 3.4. Leaf area per plant (A), square counts per plant (B), Leaf dry weights (DW) (C), Square DW (D), Stem DW (E), and total plant DW (F) for cotton grown in irrigation regimes T1-T3 during the 2015 experiment at a greenhouse site near Athens, GA. Values are means ± standard error (n = 15) and bars not sharing a common letter within a given year are significantly different ($P < 0.05$).

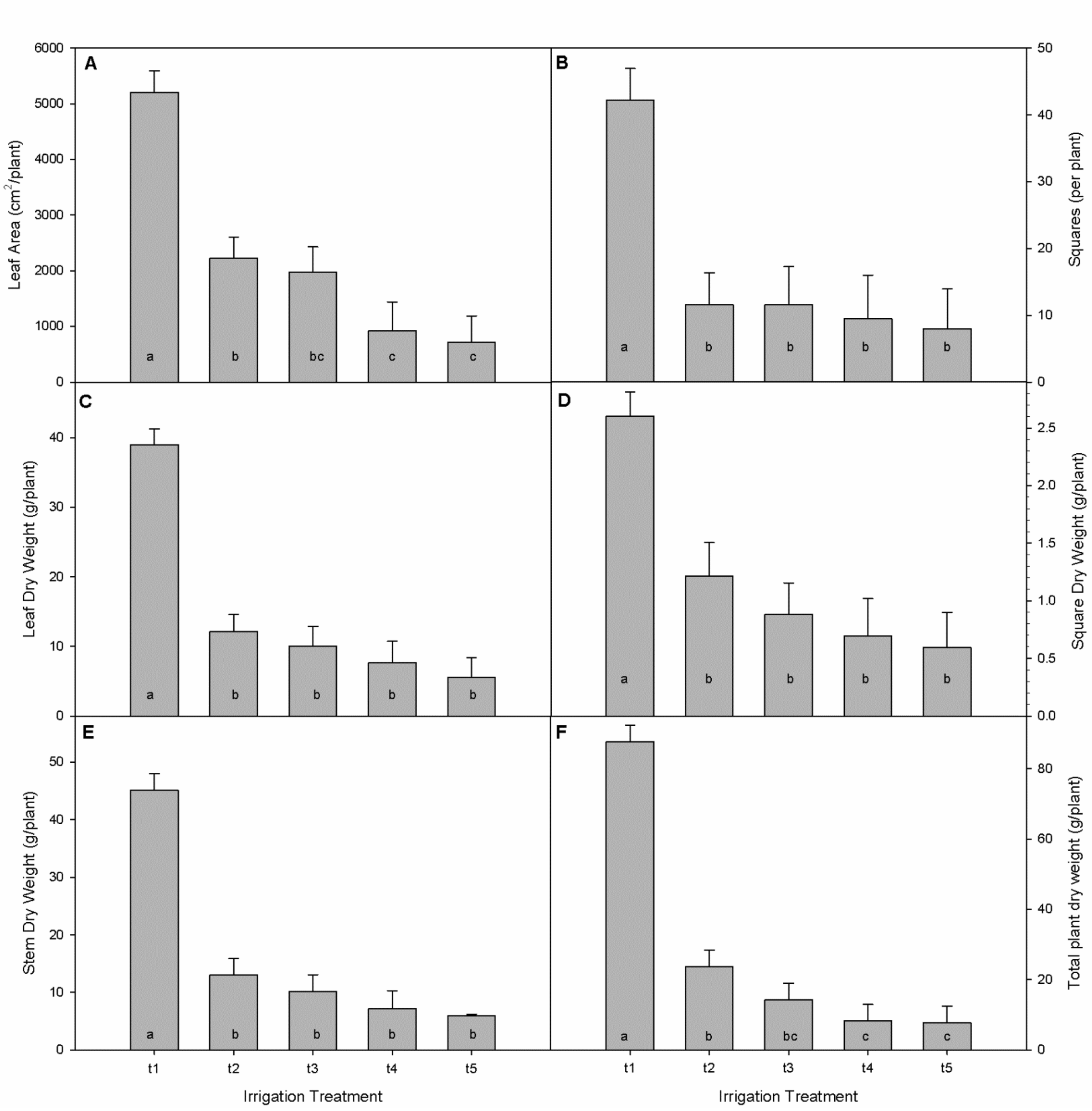

Figure 3.5. Leaf area per plant (A), square counts per plant (B), Leaf DW (C), Square DW (D), Stem DW (E), and total plant DW (F) for cotton grown in irrigation regimes T1-T5 during the 2016 experiment at a greenhouse near Tifton, GA. Values are means ± standard error (n = 24) and bars not sharing a common letter within a given year are significantly different ($P < 0.05$).

CHAPTER 4

CONCLUSIONS

There are three major conclusions that can be derived from the primed acclimation study in Chapter 1. When utilizing soil moisture monitoring systems and methods defined herein, these results suggest that prebloom irrigation thresholds between −70 and −100 kPa can be used to reduce the number of prebloom irrigation events without penalizing yield relative to well-watered treatments using −20 or −40 kPa irrigation thresholds prior to flowering. Plant mapping data from this experiment also reinforces the utility of using the lower −70 or −100 kPa triggers because of no pronounced differences in boll distribution between any of the four different prebloom irrigation thresholds. Episodic drought during flowering substantially limits yield as well. This was noted due to reduced total bolls per plant through processes that may include the following: fruit abscission, a reduction in the total number of available fruiting sites, reductions in overall plant growth, decreased node development, and hastening of cutout. Lastly, while sensor-based approaches had higher water use efficiency (WUE) in a dry year (2014), WUE was substantially higher in rainfed plots during the 2015 season (a high rainfall year) than in plots irrigated using any of the sensor-based approaches. This observation highlights the need for further studies to better define growth-stage-specific, sensor-based irrigation thresholds at all developmental stages, including prebloom, of the crop to maximize WUE irrespective of year-to-year variation in rainfall patterns.

There are three major conclusions that can be derived from the high biomass rye study. Utilizing the leaf water potential monitoring system and methods defined herein, these results suggest that pre-bloom irrigation thresholds between -0.5 and –0.7 MPa can be used to provide adequate irrigation for optimum yields and WUE. Yield data in 2015 especially reinforces this conclusion with yields above 2000 kg ha^{-1}. Excessive irrigation as noted in 2015 at -0.4 MPa thresholds, limit yield through processes that may include excess vegetative plant growth and increased boll rot. Despite the fact that the high biomass rye cover crop approaches did not increase WUE in a drier year (2014) or wetter year (2015), other studies have noted increased WUE. This highlights the need for further studies are needed to better define the utility of high biomass rye cover crops in cotton production. Observations in this study did document higher Ψ_{PD} in rye plots versus conventional tillage plots at some points during the growing indicating that rye cover can increase plant water potential further reinforcing the need for further studies.

Two conclusions were derived from the greenhouse studies. Episodic drought during prebloom substantially limits reproductive growth through processes that may include: fruit abscission or a reduction in the total number of available fruiting sites due to reductions in overall plant growth and decreased node development, decreased whole-plant photosynthesis resulting from low single leaf photosynthetic rates and whole-plant leaf area. Lastly, well-watered plants were considerably more vigorous and had significantly more squares, where even the earliest stress period with the longest recovery time had significantly reduced plant growth and square retention, illustrating the need for adequate irrigation regardless of plant growth stage.