DEFINING PHYSIOLOGICAL CONTRIBUTIONS TO YIELD LOSS IN RESPONSE TO IRRIGATION IN COTTON

by

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(Under the Direction of John L. Snider)

ABSTRACT

The objective of this research was to quantify the relative yield loss attributable to Intercepted Photosynthetically Active Radiation (IPAR), Radiation Use Efficiency (RUE) and Harvest Index (HI) for cotton grown under three distinct irrigation treatments in 2018 and 2019. The results showed that Ψ_{PD} remained relatively high in both seasons and was rarely affected by irrigation treatment. A significant reduction in yield of 318 kg ha^{-1} was observed for over-irrigated treatments (which were comparable to the control) relative to the dryland treatment, despite irrigated plots producing higher biomass. Any positive effects of IPAR and RUE on lint yield due to excess irrigation were substantially offset by large declines in HI in irrigated treatments relative to the dryland. We conclude that HI was the dominant driver of yield loss due to excess irrigation, and our observations illustrate a need to refine irrigation management practices to maximize productivity and water use efficiency.

INDEX WORDS: cotton physiology, yield contribution, water stress, intercepted photosynthetically active radiation (IPAR), radiation use efficiency (RUE), harvest index (HI), boll retention

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Water stress is a frequent obstacle that farmers in the southeastern United States have to face and overcome to achieve a sustainable production and remunerative yield. Throughout the whole growing season cotton needs nearly 18” to achieve maximum production in Georgia but the rainfall pattern is not always sufficient to cover demand at key phenological stages. Drought is known to negatively impact yield and fiber quality thus reducing the farmer’s income. At the same time, water excesses can negatively affect cotton productivity; therefore, it is important for farmers to know when the most critical time is to irrigate and how much to irrigate. A better understanding of the water requirements of cotton can lead to improved Water Use Efficiency (WUE) which in turn will allow agricultural production to have a less disruptive ecological footprint on the surrounding environment and especially on the ever more precious freshwater resources.

Some efforts have been undertaken by scholars to understand the underlying factors contributing to yield changes linked to abiotic stresses such as water stress. Importantly, Monteith (1972) proposed a quantifiable relationship between energy input (via solar radiation) into a given ecosystem and its yield. In subsequent work, the relationship proposed by Monteith has been simplified to:

$$Yield = IPAR * RUE * HI$$

In this formula, **Yield** is a function of intercepted photosynthetically active radiation (IPAR) that represents the total amount of PAR absorbed by the canopy during the growing season, Radiation Use Efficiency (RUE) that represents the amount biomass produced per unit of light energy absorbed by the canopy, and Harvest Index (HI) that represents the fraction of total biomass accounted for by the commercial product (for cotton this is lint).

A study by Earl and Davis (2003), evaluated maize response to drought and quantified the relative contributions of each of the components listed above to the final yield. This paper provides a good example of the approach I will pursue in my MS research. Experiments attributing specific irrigation-induced yield losses to IPAR, RUE, and HI are limited for cotton.

Broad Implications of Drought

Drought is detrimental for crop productivity and the well-being and stability of society. Periods of drought will unfortunately be more frequent in the future. A recent analysis (Wang et al. 2014) shows that since 1949, drought events have become 41.09% more frequent and the area affected by drought events has increased by 16.19%. Europe, South America, and eastern Asia are the regions where most of the chronically drought-prone areas are located. This is especially problematic given the importance that these regions have on the global agricultural market. Another report (Li et al. 2009) indicated that drought disaster frequency (the risk of drought disaster can be defined as “the combination of both the probability (frequency) of drought event occurrence and the degree of damage caused by drought event”) will increase; furthermore, future global warming will increase the area affected by drought disaster events from 15.4% to 44%. Africa is expected to be the most negatively affected region in terms of percentage of cultivated land affected by drought events.

A report from Van Zyl et al. (1987), shows that drought reduces the gross income from field crops extensively. Specifically, during the period 1982-85, a period in which the studied areas were affected by extensive droughts compared to the years of the precedent decade, the value of field crop production was on average 45.3% per annum lower than predicted by the long-term trend, even though deviations in horticultural and animal production were smaller than 8% per annum.

Another report (Mc William, 1986), explains how in many scenarios, drought is the cause of extensive yield losses of grain crops in Africa and North America, even under current climatic conditions. The most vulnerable areas are the rainfed agricultural regions: even when total rainfall is seemingly in excess of water demands, yield can still be water-limited, suggesting a need to improve and expand irrigation practices around the world.

Drought is still poorly understood even though it impacts more people than any other natural hazard; its impact can last for months or even years, and its effects on society, economy and environment are difficult to fully quantify because they result from a complex interaction of different factors. To better mitigate these negative effects, scientists must assess in detail the characteristics of each particular drought event (Wilhite, 1993).

An extensive and recent report by Iowa State University (Walthall et al., 2013) about the challenges that agriculture in the United States will be facing explains how climate change will affect surface-water resources, which account for 58% of water withdrawals for irrigated production nationally. This same report shows that rising temperatures and shifting precipitation patterns will alter crop water requirements, crop water availability, crop productivity, and costs of water access across the agricultural landscape even though the cost for the agricultural sector to adapt to these changes is difficult to estimate because of a lack of agreement between politicians, scientists and farmers on which strategies to implement to better face each threat to crop yield.

Whole-Crop Responses to Drought in Cotton

Introduction

Cotton is the most important fiber crop grown in the world and it was produced on 5.9 million planted hectares during the 2011 growing season in the United States of America alone. Its impact on the economy is also very important: Upland cotton production contributed approximately $6.6 billion to the U.S. farm economy while Pima (extra-long staple) cotton production contributed approximately $670 million (NASS 2011).

Cotton is a very important crop which evolved in tropical and subtropical regions of the world (most of the now cultivated cotton originated in Mesoamerica and the other important species are from the area of the middle-east that are generally characterized by arid or semi-arid conditions (Australian Government Office of the Gene technology Regulator, 2008). Therefore, it is a plant that is considered more drought tolerant than many other row crop species. Despite cotton's reported drought tolerance, drought has been shown to affect cotton growth and development and by extension, its fiber yield and quality. To give an example of the total yield and economic reduction due to drought in cotton, a study compared five irrigation treatments (no irrigation after establishment, checkbook irrigation treatment, and three treatments in which irrigation was applied when predawn leaf water potential fell below -0.5, -0.7 or -0.9MPa) during two growing seasons in southern Georgia (Chastain et al., 2016; Shurley et al., 2016). In a wet year (2013; 66.93 cm of rainfall during the growing season) there were no significant differences between any of the irrigation treatments and yield averaged 1602.14kg ha^{-1}. In contrast, 2014 was a very dry season, so the yield of the two most well-watered treatments was significantly higher than the three driest treatments; the average yield ranged from a maximum of 1996.24kg ha^{-1} to

818kg ha^{-1} with a difference of 1178kg ha^{-1}. The research considered also the cost of the irrigation treatments and the price of lint for each year (with adjustments for fiber quality). The net revenue for the two years ranged from 2399.38$/ha (for the checkbook treatment) to $2789.81/ha (for the -0.7MPa treatment) in 2013 and from $1902.70/ha (for the non-irrigated treatment) and $2599.54/ha (for the -0.5MPa treatment) in 2014. Given the environmental conditions in which this study was conducted there was no statistically significant relationships in the first year between irrigation and the fiber quality or gross yield, and the only significant differences in quality parameters could be attributed solely to cultivar differences, while in the second year, the most well-irrigated treatments had significantly higher yields compared to the drier treatments, and overall fiber quality was reduced by drought due to increases in fiber micronaire and length (Hu et al. 2018).

To better understand the effect of drought on cotton yield it is necessary to distinguish the responses of the various parts of the plant to water deficit stress.

Plant Growth (Roots and Shoots)

As noted previously, cotton is known to tolerate a certain level of drought stress but even this plant species can face growth impairment due to water limitations. In the study by Pace et al. (1999), cotton plants raised in pots were exposed to a 13 day stress period and a subsequent 10 day recovery period, and there were many significant differences between the experimental group and the control for a number of growth parameters such as height, leaf area, number of nodes and the dry weight of leaves and stems. An interesting discovery was that the drought treated plants had taproots that were deeper than the control, but the weight was not significantly different. This suggests that a common strategy for cotton to adapt to drought could be the development of deeper and thinner roots. Additionally, the drought-treated plants had a lower shoot: root ratio. Basal et al. (2005) reports that another source of drought resistance in cotton could be an increase in lateral root number which is largely genotype dependent although its expression is triggered by water deficit conditions.

A common adaptation mechanism seen in plants that suffer from water stress is osmotic adjustment (OA); to preserve the turgor of a tissue, plants try to lower their water potential through the accumulation of solutes. As the paper by Hsiao et al., (1976) explains, water potential is defined by the equation $\Psi = \Psi_p + \Psi_s + \Psi_m + \Psi_g$ where Ψ_p is the pressure potential, Ψ_s is the osmotic potential, Ψ_m is the matric potential and Ψ_g is the gravitational potential which in crop plants is usually considered negligible (Jones, 2006). When there is water stress the plant mitigates Ψ_p changes by lowering osmotic potential through the accumulation of compatible solutes. The theory about the osmotic potential is confirmed by the scientific literature; a study by Wang et al. (2016) reports that during drought, carbon metabolite concentration was generally higher in drought stressed plants even though photosynthesis was strongly inhibited. The same study reveals also that osmotic adjustment (OA) was observable in most of the sampling dates during the drought period. K+ was the main contributor during the first part of the stress period to OA at 10 and 24 DPA (days post anthesis) while amino acids became the most important factor at 38 and 50 DPA. It is plausible to conclude that a production of molecules destined for OA would reduce the amount of photosynthate available for growth.

Canopy growth is influenced by many factors, including nutrient availability, temperature, light, position of the plant, plant density, planting date, pests, and soil water content, among other factors (Wullschleger and Oosterhuis, 2008; Roussopoulos et al., 1998; Constable, 1986; Sadras, 1996; Denmead and Shaw, 1962) and each of these factors has a different impact on canopy development. The main effect of drought on canopy development is the impairment of leaf development and expansion which in turn limits total leaf area. Carmo-Silva et al. (2012) studied various Pima cotton cultivars and reported a significant difference in specific leaf area (leaf area/dry weight) correlated to water treatment, but their data did not show any statistical difference between the cultivars. Another study by Noreen et.al. (2013) reported differences in LAI (leaf area index) between well-watered and water-stressed cotton plants. The difference was first noted at squaring and it reached its maximum at peak flowering, where well-watered plants had LAI = 3.5 and water-stressed plants had a LAI = 3. The gap between treatments became smaller and at maturity, well-watered plants had LAI = 1 and water-stressed had LAI = 0.75. A paper from Rosenthal et al. (1987) reports a complete arrest of leaf expansion when plant available water falls below 50% . The extent of the leaf area reduction caused by drought is further explained in the study by Pace et al. (1999) which reports that water-stressed plants' leaf area was a third of the leaf area of the non-stressed plants (sampled at 49 DAP after a 13 days drought period), and even after a period of recovery, the difference was still significant.

Overall cotton growth is negatively affected by water stress. According to the review by Başal and Ünay (2006) leaf expansion is one of the most sensitive processes to the onset of drought, even before appreciable changes in net photosynthesis of individual leaves are observed. A study by Pettigrew (2004) revealed that drought stress reduced plant height and caused a 35% leaf area index (LAI) reduction, which in turn resulted in an 8% reduction in solar radiation interception. This is very important because LAI development and solar radiation interception, along with photosynthetic efficiency, form the foundation of crop yield as described in the biophysical model developed by Monteith (1972). This will be the focus of the subsequent section.

Light Interception, Radiation Use Efficiency, Harvest Index

As previously mentioned, growth can be influenced significantly by drought, but to what extent does drought alter light interception and the efficiency with which the crop utilizes the solar radiation absorbed? The absorbed radiation is influenced by various crop factors among which leaf area is the most important. Radiation use efficiency is a self-explanatory term used to determine how efficiently the absorbed radiation is converted into energy available for plant metabolism. There are various ways to quantify it: quantum yield of CO_2 uptake, which defines how efficiently the absorbed radiation is used for carbon assimilation, another way is by measuring the fluorescence emitted by chlorophyll under particular light wavelengths.

A common way to analyze the quantum yield of CO_2 uptake is by using an infrared gas analyzer in which a section of a photosynthetically active leaf is enclosed in a sealed chamber that has a light emitting PAR (photosynthetically active radiation) source, then air with a set concentration of CO_2 is made to circulate in and then out of this chamber. After determining the difference in CO_2 concentration between the input air and the output air, it is possible to determine the actual amount of CO_2 absorbed per unit of light absorbed i.e. the quantum yield of CO_2 uptake.

Another way to analyze RUE is by analyzing chlorophyll fluorescence. According to Peñuelas et al., 1995 Radiation Use Efficiency (RUE) can be determined as $(F_m' - F) / F_m' = \Delta F / F_m'$ where F represents the leaf fluorescence under ambient light and F_m' represents leaf fluorescence under saturating light. Here, RUE is a measure of the quantum yield of photosystem II (PSII). From this equation it is commonly understood that when ambient light is high, RUE decreases and this means that PSII is at or above light saturation. In this condition, a little increase in radiation intensity would overload the photosynthetic machinery leading to an increased risk of generation of dangerous free radicals, thus RUE can be used as a tool to determine the effect of drought stresses on the activity of PSII.

The most common way to calculate RUE and the most readily utilized in the Monteith yield equation (Monteith, 1972) is by collecting total plant dry matter data and IPAR (total interception PAR for a given time period). This efficiency is estimated as dry matter accumulated per unit of photosynthetically active radiation intercepted by the crop canopy over a specific period of crop growth. Drought is known to affect RUE. In a study by Earl and Davis (2003), maize yield was shown to be affected by drought, and the aim of the researcher was to quantify the relative contributions of each of the component processes noted below to drought-induced yield loss:

$$Yield = IPAR * RUE * HI$$

IPAR is intercepted photosynthetically active radiation (MJ), RUE is radiation use efficiency (g MJ^{-1}) and HI is harvest index. The researchers utilized a simplified path model to attribute specific yield reductions to each of these components, and their results indicated that the impact of reduced IPAR was limited (between 2.0% and 16.9% compared to the control) while the reduction in RUE and HI (between 8.7% and 37.7% and between 2.0 and 32.7%, respectively compared to control) contributed similarly to yield loss under drought.

Even in cotton drought negatively affects these components. A study by Lacape and Wery (1998) compared 5 cotton genotypes by applying drought stress near flowering and they showed a reduced RUE (defined as “the slope of the linear relationship between the above-ground biomass production and the accumulated radiation absorbed by the canopy at the same date”) mainly because of a reduction of stomatal conductance and changes in the efficiency of the photosynthetic machinery. Overall, all the stressed cultivars showed similar RUE and radiation interception because of the similar values of LAI among them. The difference in RUE between the irrigated

(1.4 g MJ^{-1}) and non-irrigated (0.9 g MJ^{-1}) plots were significantly different. At the same time Radiation Absorption Efficiency was similar between the various irrigation treatments although the individual leaf size among cultivars was different. Total biomass is also reduced under drought not only because of the reduced RUE but also because water deficit shortens the duration of the vegetative cycle and thus the total amount of absorbed radiation intercepted in a given growing season.

HI has also been reduced by water deficit in some situations specifically, a study by Gerik et al. (1996) reported a small difference in HI between water-stressed and well-watered plants of about 0.04 (where the well-watered HI was higher) although the more important factor determining HI variation was genotype, and the drought effect was relatively small. A study by Kimball and Mauney (1993) reported no significant difference in HI with different levels of irrigation.

The claims of the previous studies about the effect of water stress are confirmed by a study by Hussein et al. (2011) who, by using both the FAO AquaCrop model to run a simulation and a field trial, reported no significant difference between HI in cotton grown with 4 different levels of irrigation.

Opposite results were seen in the study conducted by Pettigrew (2004) who reported a 30% higher HI in water-stressed plants compared to well-watered which is explained by a similar weight of the seed cotton and a reduced canopy mass in the stressed plants. Similar results have been reported by Ünlü et al. (2010) who reported a higher HI in dryland (0.32 ± 0.052) compared to the non-stressed plants (0.26 ± 0.054).

Single-Leaf Responses of Cotton to Drought

As noted elsewhere in this review, drought is known to impair canopy growth and limit a number of yield components (especially boll density), thereby limiting the quantity and quality of fiber produced. Importantly, reduced yield is a consequence of the effect that drought has on the synthesis of molecules in the plant and their translocation throughout the plant. While studies on the effects of drought on root or canopy growth have been important for advancing our understanding of drought stress, leaves are the main centers for photosynthetic activities and the efficiency with which they function can influence whole-canopy radiation use efficiency since they are the primary organs for carbon uptake by the plant. The paper by Baker et al. (2007) evaluated drought severity via whole canopy (temperature) and single-leaf measurements (temperature, gas exchange, etc.). An important conclusion they realized, was that single-leaf measurements were better indicators of drought than some widely accepted whole-canopy assessments. Specifically they analyzed single leaf parameters to correlate them to plant water status and photosynthetic rate, and the leaf to air temperature differential (T_L - T_a) and leaf to air vapor pressure deficit (VPD) were better predictors of plant water status and photosynthetic rate than other types of data, specifically whole-canopy temperature. This study shows that it is preferable to analyze single leaves because of the reliability of the data collected and also because of the feasibility of conducting this type of analysis compared to whole-canopy ones. As explained in the paper by Zelitch, (1982), net photosynthesis can be positively correlated to yield in various crops. In cotton specifically, a study by Chastain et al. (2014) showed a lint yield decrease of 35% for drought stressed plots, relative to well-watered plots, and net photosynthesis was between 14% and 54% lower for drought stressed treatments, depending on the date of the measurement.

Subsequent sections of this review will attempt to provide an overview of the current scientific literature concerning single leaf characteristics in connection with water stress in cotton.

Photosynthesis (A_N)

In the scientific literature, net photosynthesis is defined as the total amount of fixed carbon minus the carbon oxidized in the respiration reactions. One of the main processes affected by drought, the reduction of internal cell turgor, limits leaf expansion and consequently, the total photosynthetic area of a single leaf but this also impacts the metabolic processes of photosynthesis. According to Deeba et al. (2011) drought limits photosynthesis through stomatal closure at a low drought stress level, while during more severe stress, even chloroplast carbon fixation reactions can be affected. Zhang et al. (2011) explained how, during drought, the quantum efficiency of the photosynthetic processes overall is reduced because part of this energy, instead of being directed to carbon assimilation, is directed to two main photoprotective mechanisms, photorespiration and thermal dissipation. Water stress in the plant and consequent osmotic potential in plant cells have a strong effect on photosynthetic rate. Boyer (1964) reports that at -8.5 bar of osmotic potential in the cotton plant there was a 25% reduction in the photosynthetic rate. Drought is a stress obviously affecting water content in the plant and since the stomata are the organs through which most of the water losses (transpiration) and CO_2 uptake are carried out, researchers divide the mechanisms limiting net photosynthesis under drought into two main groups: stomatal limitations (important under mild to moderate drought) and non-stomatal limitations (also called metabolic limitations) which can become an important factor during severe stresses.

Stomatal Limitations

One of the first reactions of plants during water stress is to close the stomata to maintain an adequate water content. Therefore, in order to estimate the degree of the water stress it is important to assess stomatal conductance to water vapor. This conductance is correlated with leaf age, hormone concentrations, air temperature, water vapor content in the air and plant water potential. Thimmanaik et al. (2002) shows a direct link between reduced g_s and reduced concentration of photosynthesis-related enzymes like RuBP kinase, NAD- and NADP-glyceraldehyde-3-phosphate dehydrogenases and 3-phosphoglycerate kinase even though many studies report no significant effect on enzymes or photosynthetic intermediate molecule concentration due to reduced gs for gs values above 0.1 mol H_2O m^{-2} s^{-1} (Sharkey and Seemann, 1989; Sánchez-Rodríguez et al., 1997). In water stressed cotton plants a reaction that has been reported is the premature closing of stomata in the presence of high abscisic acid (ABA) levels produced by the root during water stress and transported to the leaves even though water tension in the plant was not at levels that should have caused stomatal closure (Wilkinson and Davies, 2002). The closing of stomata can limit total yield because it strongly reduces the diffusion of CO_2 into the leaf. According to Cornic (2000) stomatal closure and consequent increase in stomatal resistance to diffusion of CO_2 is most likely the major factor reducing photosynthesis during mild water stress. This typically causes a reduction in substomatal CO2 concentration (C_i). Multiple papers report stomatal limitation to photosynthesis under drought. For example, Chastain et al. (2014) explain that drought limits net photosynthesis mainly because of reduced stomatal conductance (from 58% and 72% reduction along with a concomitant decline in C_i). A paper by Chastain et al. (2016a) reported a relationship between predawn water potential measurements and lint yield; the maximum yields were observed at a season-long average predawn leaf water potential of -0.5MPa and declined at values lower than this. A companion study (Chastain et al., 2016b) showed similar trends for uppermost fully expanded leaves, where net photosynthesis was positively associated with leaf water potential and stomatal conductance. In the same study, drought did not have a substantial impact on thylakoid processes. Another study by Snider et al., 2014 showed a strong relationship between predawn leaf water potential and stomatal conductance to water vapor and between predawn leaf water potential and net photosynthesis. Despite substantial water-induced variability in net photosynthesis it appeared that that electron transport rate (ETR) and quantum efficiency of PSII were not correlated to predawn leaf water potential. Kitao and Lei, 2006 reported reduced stomatal conductance to water vapor in water stressed cotton plants, but they found evidence of an increased ETR. These observations imply that thylakoid reactions were relatively insensitive to drought, even at drought levels known to substantially limit net photosynthesis.

Even though stomata closure intuitively is known to block diffusion of gases, cuticular diffusion during water stress can still maintain some flow of water and CO_2 between plant and environment and should not to be overlooked Ennahli and Earl (2005) .

Non-Stomatal Limitations

Non-stomatal limitations are the limitations that are not dependent on diffusion of CO_2 into plant tissues through the stoma. These are usually disruption of normal enzymatic activity linked to photosynthesis or impairment of electron flow in the electron transport chain. A paper by Loka et al. (2011) reported extensively on the various elements of non-stomatal limitations. Some of the current scientific literature reported that water stress limited the activity of rubisco and in turn reduced the regeneration rates of ribulose 1,5-bisphosphate (RuBP) while other researchers pointed out that with the onset of drought, ATP-synthase activity can be severely reduced. An interesting behavior observed by some researchers is that after the drought is relieved by rehydration, cotton plants seemed to have a higher PSII quantum efficiency, probably due to higher chlorophyll per leaf area unit (some scholars reported a positive correlation between PSII quantum efficiency and quantum efficiency of CO_2 fixation). Some studies reported a decreased PSII quantum efficiency with the onset of drought. Ennhali et Earl., 2005 reported a reduction of carboxylation rate and CO_2 concentration at the carboxylation site during drought and a prolonged lag time (more than 48h) between re-watering and the initial recovery of photosynthesis. It is likely that drought stress induces lasting damage to chloroplast structures, thus it is unclear what time is required for full recovery or at what level of drought severity, photosynthetic inhibition becomes irreversible. Genty et al., 1987 reported no effect on electron flow through PSII and a slight reduction of electron flow through PSI due to drought stress. Osmotic adjustment is known to maintain water turgor in cells as an acclimation response to drought and according to Osmond et al., 1987 it seems to mitigate the effects of non-stomatal limitations of photosynthesis.

Photorespiration

Photorespiration is the name given to CO_2 evolution in the light due to the oxygenation reaction carried out by rubisco. This process releases a molecule of CO_2 for every two oxygenation events and accounts for a substantial reduction (around 25%) in photosynthetic efficiency for C3 plants (Peterhansel et al., 2010). As reported in the previous sections, various studies have been conducted under field conditions to assess the behavior of the various components of the photosynthetic apparatus. The study by Chastain et al. (2014) reported large reductions in carbon assimilation (An) (between 14% and 54% in dryland) while ETR remained statistically consistent. The researchers explained the difference in response between these two parameters by showing that the electron flux not used for carbon assimilation is actually exhausted by carrying out photorespiration reactions. A study by Snider et al., 2014 showed a strong direct correlation between predawn leaf water potential and net photosynthesis and it was also reported that Electron Transport Rate (ETR) and quantum efficiency of PSII were not correlated to predawn leaf water potential. Kitao and Lei, 2006 found evidence of an increased ETR. Massacci et al., 2008 reported, in cotton, higher rates of photorespiration as the light intensity got higher because of an increased total electron flux through PSII. Ennahli and Earl, (2005) also reported increased photorespiration during drought, but their study specifies that at mild water stress, the carboxylation efficiency remains the same while at severe water stress it reduces mainly because of a reduction in CO_2 concentration at the carboxylation site. Zhang et al., 2011 contested the method of Massacci (2008) and with a different type of analysis concluded that photorespiration is reduced during drought and that the electron flow through PSII is likely consumed by nitrogen assimilation.

Dark respiration (R_D)

Between 30 and 80% of the CO_2 taken up by photosynthesis (P) each day is subsequently consumed through respiration (Atkin et al., 1996). Similarly to how photosynthetic rate reacted Boyer, 1964 reports that at -8.5bar of osmotic potential in the plant there was a 25% reduction of the dark respiration rate in cotton plants.

Dark respiration is also affected by drought: the impaired growth reduces the amount of tissues performing the respiratory processes, mainly the leaves Başal and Ünay, (2006). A review by Atkin and Macherel, 2009 shows that while respiration tends to decrease in roots and shoots during water stress, the same cannot be said for single leaves: most of the studies up to date (around two thirds) showed a decrease in total dark respiration due to water stress, while the rest reported no change in respiration rates and very few of the total showed even a slight increase in total dark respiration coincidently with the water stress. A paper by Snider et al., 2015 tried to explain why all these strange results were reported: the reason is because dark respiration has a biphasic response to drought stress, initially decreasing under mild water stress and finally increasing at a most serious level of plant water deficit. This same paper explains how the respiration rate is highly correlated with final lint yield therefore making it a powerful performance indicator and at the same time drought always increases respiration rates as a percentage of total gross photosynthesis.

Drought Effects on Yield Components in Cotton

According to Coyle and Smith, 1997 the elements composing yield are: the number of bolls per unit land area, the number of seeds per boll and total fiber weight per seed, which is influenced by fiber number per seed, mean fiber length, and weight per unit of fiber length. To sum up and simplify these combined effects on cotton production the final yield can be explained as:

$$\frac{Number\ of\ bolls}{m^2} * \frac{Number\ of\ seeds}{boll} * \frac{Lint}{seed}$$

Each of these components can be influenced by genotype, management and environment.

An intuitive way to classify cotton yield components is to divide them into intra-boll (N° of seeds per boll, lint per seed, etc.) and extra-boll (also known as whole-crop) yield components (N° of bolls per square meter). Breeding efforts have increased cotton yield by acting on these factors, mainly increasing lint percentage with a reduction in seed size according to Groves et al. (2016).

Extra-Boll

As noted elsewhere in this review, multiple drought studies (Chastain et al., 2016; Grimes and Yamada, 1982; Meeks et al., 2017; Pace et al., 2000) have reported an inhibition of mainstem growth for plants exposed to water deficit conditions. This ultimately produces shorter plants with a reduced number of mainstem nodes, and this is an important factor because stunted growth reduces canopy growth needed for photosynthetic input and a stunted canopy will often have fewer sympodial branches and fruiting positions along a sympodial branch. Another scenario is one in which a well-developed canopy is present during flowering and boll formation, but drought stress during reproduction substantially limits retention of bolls at existing fruiting sites. The overall result is a general decline in the total number of bolls retained per plant and boll density per unit land area under drought. For example, a number of recent reports have documented reductions in the total number of retained bolls in experiments where drought stress limited yield (McMichael et al., 1973; Hu et al., 2018; Lokhande and Reddy, 2014; Meeks et al., 2017; Snider et al., 2019)

reported a linear correlation between pre-dawn leaf water potential and boll shedding, ranging from 30% abscission at -1 MPa to almost 90% at -2.6 MPa. The majority of the abscission occurred within the first few days after plants were allowed to recover following the aforementioned stress level. Another observation made was that older leaves were the most sensitive to abscission, yet for bolls younger fruit were the first to shed. Once bolls were at least 14 days past anthesis, they were retained by the plant even in very severe water stress conditions. Gerik et al., 1996 also report a total boll reduction in water stressed plants which in turn resulted in a lower harvest index for the stressed plants; another interesting observation was that boll shedding was mainly affecting the lower branches of the canopy. In experiments where drought-induced yield loss has been attributable to individual yield components has been quantified, declines in boll density per unit land area account for the majority of yield loss (Hu et al., 2018; Sharma et al., 2015; Snider et al., 2019).

Intra-Boll

As noted previously, a number of important yield component parameters such as fiber density (numbers per unit seed coat area) and individual fiber mass, can be derived by combining fiber quality estimates like fiber length and micronaire with more traditional yield component estimates like boll number, boll mass, lint percent, and seed and lint index (total weight of seed or lint obtained from 100 seed). For a complete list of yield component parameters and their calculation, readers are referred to (Groves et al., 2016). The previously noted, detailed yield component assessments have only been utilized in a limited number of breeding programs

(Clement et al., 2014; Groves et al., 2016). However, they provide a unique opportunity to evaluate how intra-boll processes respond to water availability.

Some studies have reported a reduction in boll weight in severe water stress conditions. For example, Gerik et al. (1996) reported a reduction in boll weight between 19% and 36%, depending on water stress severity, with the smaller bolls limited to the higher nodes. A study by Sarwar et al., 2006 further confirmed this hypothesis: among a wide range of cultivars the reduction of boll weight under drought was a consistent behavior. Sharma et al. (2015) also documented a small but consistent contribution of decreased boll weight to drought induced yield loss (around 10% decline in boll weight).

Furthermore, Hu et al., 2018 reported a reduction in the number of fibers per seed in water stressed plants; however, the individual fiber weight responded positively to drought stress, which produced higher lint percent and lint index as drought severity increased.

Wang et al. (2016) reported no effect of drought on lint percentage. Pettigrew 2004 reported slightly higher lint percentage in water stressed plants, while Grimes et al. 1969 reported lower lint percentage in water stressed plants. The inconsistency is likely because lint percentage is a factor influenced more by genotype than by water treatment. Beyond the report by Hu et al. (2018), the data concerning lint index responses to drought are limited. However, Pettigrew (2004) reported a 13% increase in lint index in irrigated plants compared to water stressed plants mainly because of an increase in seed surface that can accommodate more fibers. The paucity of data concerning intra-boll yield component responses to irrigation illustrates a need for further research in this area.

Fiber Quality

Fiber length: This parameter is very important for the processing of cotton into yarn Cotton incorporated (2019). The scientific community largely agrees that a reduction in fiber length is to be expected when plants are drought stressed. Hu et al. (2018) have seen a reduction of average fiber length from more than 3 cm to around 2.8cm. Zheng et al. (2014) also reported a fiber length reduction due to water stress (from 2.96cm to 2.59cm). Lokhande and Reddy (2014) reported that in severe water stress, irrigation can exert a negative influence on fiber length.

Fiber strength: This parameter is expressed as g/tex, which indicates the force in g to break a bundle of fiber one tex in size (a tex is equal to the weight in grams of 1000 m of fiber) (source: Cotton incorporated (2019). Strength is mainly influenced by cultivar, but water availability has an important impact. Hu et al. (2018) reported a small increase in strength of the fibers produced in water stressed plants: this is mainly explained by the fact that these fibers grew thicker compared to the non-stressed ones. Snowden et al., (2014) instead reports thicker (therefore stronger) fibers in plants that were well watered or that were deprived of water just for the period between squaring and the beginning of flowering.

Micronaire: This is a parameter that measures the fineness of the fibers and is defined as a measure of the air permeability of compressed cotton fibers Cotton incorporated (2019).There is not a consensus on the behavior of micronaire under drought: Wang et al. (2016) and Kim et al., (2013) reported a reduction of micronaire correlated with water deficit, while studies like Dag˘delen et al. (2009) and Hu et al. (2018) reported an increase. It’s likely that the inconsistency is due to an interaction of cultivar * level of water stress that, according to the variation of each, produces different results Wang et al. (2016), Snowden et al., (2013).

Uniformity index: This is an index used to determine the variability in the length of the fibers in a particular lint sample. Pettigrew 2004 reported no statistically significant effect on fiber length uniformity in drought stressed cotton. Similarly Hu et al., 2018 reported no significant difference in uniformity and the only differences are likely to be attributed to cultivar differences and not water treatment. According to Snowden et al., (2014) who evaluated the Maturity Ratio of fiber in cotton plants differentially stressed this parameter is most negatively affected when cotton suffer water deficit from peak blooming to the season's end.

Assessing Overall Fiber Quality: Some researchers have also attempted to develop some way to provide an overall index for assessing fiber quality by normalizing and providing different weights to cotton fiber quality parameters. Bourland et al., 2010 developed an important index called the Q-score that helps to easily compare different lint samples by giving a score that is calculated giving a relative importance (percentage) to the final quality to different factors: fiber length (50%), micronaire (25%), length uniformity index (15%) and strength (10%). Overall, it seems that drought events induce a reduction of fiber quality depending on the timing of the stress. The study by Snowden et al., (2014) reported a reduction of fiber quality in all the water stressed plots except when the stress was induced from squaring to flowering in which case the quality characteristics analyzed (upper quartile length (UQL), mean fiber length by number, fineness, and maturity ratio) were comparable or even slightly improved compared to the fully irrigated plants. In this experiment the biggest contributor to the reduction of fiber quality that can be attributed to irrigation is Maturity Ratio which is a parameter linked to fiber uniformity.

Rationale

As noted elsewhere in the proposal, water stress (caused either by excess or deficit) reduces yield and fiber quality via yield component alterations or impairment of other physiological contributors to yield. While the effects of drought at the whole canopy, organ, and cellular scale have been investigated extensively, future research will need to focus on quantification of the relative contributions of the different component factors to final cotton yield. This will help identify the weak link in cotton production under water stress and will create a basis from which breeders can create resistant varieties by strengthening these weaknesses and for future scholars to develop better agronomic and technological approaches to cope with this issue.

Objectives

1. To determine the effect of irrigation regime on yield, water use efficiency and fiber quality in cotton.
2. To define the contributions of component processes and/or characteristics on yield response to irrigation.

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CHAPTER 2

DEFINING PHYSIOLOGICAL CONTRIBUTIONS TO YIELD LOSS IN RESPONSE TO IRRIGATION IN COTTON

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ABSTRACT

Excessive irrigation can sometimes reduce cotton yield, but studies that assess the relative contribution of underlying physiological processes to the final lint yield are limited. The objective of this experiment was to quantify the relative yield loss attributable to Intercepted Photosynthetically Active Radiation (IPAR), Radiation Use Efficiency (RUE) and Harvest Index (HI) for three distinct irrigation treatments: well-watered (100% of ETc), over-irrigated (125% of ETc), and Dryland during the 2018 and 2019 growing seasons. The data collection included biweekly measurements of predawn leaf water potential (Ψ_{PD}) and light interception along with end-of-season measurements of biomass, lint yield, fiber quality, and harvest index. Irrigation effects on yield were only observed during the 2019 season, and the results showed that Ψ_{PD} remained relatively high in both seasons and was rarely affected by irrigation treatment. A significant reduction in yield of 318 kg ha^{-1} was observed for over-irrigated treatments (which were comparable to the control) relative to the dryland treatment, despite irrigated treatments producing higher biomass. Any positive effects of IPAR and RUE on lint yield due to excess irrigation were substantially offset by large declines in HI for irrigated treatments relative to the dryland. We conclude that HI was the dominant driver of yield loss due to excess irrigation, and our observations illustrate a need to refine irrigation management practices to maximize productivity and water use efficiency.

INDEX WORDS: cotton physiology, yield contribution, water stress, intercepted photosynthetically active radiation (IPAR), radiation use efficiency (RUE), harvest index (HI), boll retention, biomass

Introduction

Water deficit in cotton substantially limits crop yield and profitability by inhibiting growth and development (Pace et al., 1999). Even in the humid southeastern United States, (Chastain et al., 2016; Shurley et al., 2016), yield losses as large as 1178kg ha^{-1} and losses in net revenue of $697 ha^{-1} have been observed due to drought stress. Overall fiber quality was also reduced by drought due to increases in fiber micronaire and reductions in length (Hu et al. 2018). However, excessive irrigation should also be avoided because 1) the costs associated with pumping ground water when it is not needed can decrease economic productivity, 2) unnecessary irrigation events deplete groundwater resources and can exacerbate nutrient leaching concerns, and 3) cotton yield can respond negatively to over-irrigation (Cholpankulov et al., 2005 ; Willis et al, 1997, Pereira et al., 2009; Jackson and Tilt, 1968; Grimes et al., 1968). For example, Cetin and Bilgel, 2002 reported that an excess of irrigation can induce a reduction of seedcotton yield, number of bolls per plant, and it can increase boll shedding. Given the importance of water in determining cotton yield, a better understanding of the underlying processes that determine yield response to irrigation is needed.

Yield is the product of cumulative photosynthetically active radiation intercepted by the crop canopy during the growing season (IPAR), the efficiency with which the crop converts that radiation into dry matter (Radiation Use Efficiency), and the fraction of total dry matter allocated to the economically important part of the crop (Harvest Index) Monteith (1972).

$$Y = IPAR \ x \ RUE \ x \ HI$$

Water can strongly influence all three elements. For example, water stress can influence total intercepted photosynthetically active radiation (IPAR). According to the review by Başal and Ünay (2006) leaf expansion is one of the most sensitive processes to the onset of drought (specifically because drought reduces internal cell turgor, limiting leaf expansion and consequently the total photosynthetic area of a single leaf), even before appreciable changes in net photosynthesis of individual leaves are observed. A study by Pettigrew (2004) revealed that drought stress reduced plant height and caused a 35% leaf area index (LAI) reduction, which in turn resulted in an 8% reduction in solar radiation interception. This is very important because LAI development and solar radiation interception, along with photosynthetic efficiency, form the foundation of crop yield as described in the biophysical model developed by Monteith (1972). A report by Bange et al., (2003) reported a slight reduction in light interception due to water logging induced by excess irrigation, but overall it seems that light interception is not the most affected factor when yield is limited by excessive irrigation.

Water can also affect Radiation Use Efficiency (RUE) which is properly described as the slope of the linear relationship between above-ground biomass production and the accumulated radiation absorbed by the canopy at the same date (Plénet et al.,2000). In cotton, drought negatively affects RUE. A study by Lacape and Wery (1998) compared 5 cotton genotypes by applying drought stress near flowering, and they showed a reduced RUE mainly because of a reduction of stomatal conductance and changes in the efficiency of the photosynthetic machinery. Overall, all the stressed cultivars showed similar RUE and radiation interception because of the similar values of LAI among them. The difference in RUE between the irrigated (1.4 g MJ^{-1}) and non-irrigated (0.9 g MJ^{-1}) plots were significant. At the same time, Radiation Absorption Efficiency (defined as the fraction of incident light absorbed by the canopy) was similar between the various irrigation treatments. Total biomass is also reduced under drought not only because of the reduced RUE but also because water deficit shortens the duration of the vegetative cycle and thus the total amount of absorbed radiation intercepted in a given growing season. Regarding excessive irrigation, the study by Bange et al., (2003) showed a reduction in RUE associated with excessive irrigation (waterlogging) of about 35%. Overall, it seems that very little material concerning excessive, non-waterlogging stress in cotton is present in the literature for RUE.

Drought has been reported to affect Harvest Index. Specifically, HI was reduced by water deficit in a study by Gerik et al. (1996), which reported a small non-significant difference in HI between water-stressed and well-watered plants of about 0.04 (where the well-watered HI was higher). In their experiment, the more important factor determining HI variation was genotype, and the drought effect was relatively small. A study by Kimball and Mauney (1993) reported no significant difference in HI with different levels of irrigation, and a study by Hussein et al. (2011) reported no significant difference in HI for cotton grown with four different levels of irrigation. In contrast, Pettigrew (2004) reported a 30% higher HI in drought-stressed plants compared to well-watered which is explained by a similar weight of the seedcotton and reduced canopy biomass in the stressed plants. Similar results have been reported by Ünlü et al. (2010) who documented a higher HI in dryland (0.32 ± 0.052) compared to the non-stressed plants (0.26 ± 0.054). The impact of over-irrigation on harvest index is much less studied, but because cotton is an indeterminate perennial plant, it will respond to an over-abundance of water or nutrients with rank vegetative growth. This has the effect of shading lower leaves in the canopy and limiting fruit retention at lower mainstem nodes of fruiting branch attachment (Stockton et al, 1907; Earn, 1980)

Work conducted by Earl and Davis (2003) illustrated that yield loss under water deficit tress in corn was primarily determined by a comparable reduction of RUE and HI (between 8.7% and 37.7% and between 2.0% and 37.2% respectively) while the reduction of IPAR was of less importance (between 2.0% and 16.9%). As noted in previous sections, researchers have extensively characterized crop physiological responses to water deficit, but studies quantifying the relative yield loss attributable to each parameter under water excess are non-existent in cotton. The current studies characterized cotton physiological response to irrigation during the 2018 and 2019 growing seasons in the south eastern United States. The 2019 season was unique in that the highest yielding treatment was the rainfed treatment and successive increases in water application suppressed yield. This provided a rare opportunity to address our objective to quantify the relative importance of IPAR, RUE, and HI in driving over irrigation-induced yield loss.

Materials and Methods

Study Site Details and Uniformly Applied Management Practices

A two-year study was conducted during the 2018 and 2019 growing seasons at the Stripling Irrigation Research Park located in Camilla, Georgia (31°16'43"N 84°17'41"W). The soil at the Camilla study site is classified as Lucy loamy sand (loamy, kaolinitic, thermic Arenic Kandiudults). Maximum and minimum temperature, precipitation, and total solar radiation data for the study site were obtained from an on-site weather station at the Stripling Irrigation Research Park, which is part of the state-wide Georgia Weather Network (http://www.georgiaweather.net). Weather data are provided in Table 1. Seeds of the cotton cultivar *Gossypium hirsutum* cv. ST 6182 GLT (Stoneville®; BASF United States) were planted on May 5, 2019 at a rate of 9.84 seed m^{-1} row length, and the inter-row spacing was 0.91 m. Planting depth was 2.5cm, and plant density (9 plants per m of row length) assessed at two weeks after planting was above recommendations for preventing stand-associated reductions in yield (Whitaker et al., 2018). Agronomic practices, including fertilization, plant growth regulator applications, arthropod pest management, and weed control were conducted for all plots in the experimental area according to University of Georgia Cooperative Extension Service recommendations (Whitaker et al., 2018). To ensure that stand establishment was not a confounding factor in our experiment, all plots received blanket applications of sprinkler irrigation of 3.3cm in 2018 and 6.1cm in 2019. Differential irrigation treatments were initiated when the first floral buds were visible (the “squaring” stage).

Irrigation Treatments and Experimental Design

Three different irrigation treatments were imposed in the current study. The first was a **Dryland** treatment, receiving no supplemental irrigation past squaring. The second treatment was the well-watered control treatment receiving supplemental irrigation to meet 100% of crop evapotranspiration demands after accounting for rainfall (**100% ETc**). The third treatment was an over-irrigated treatment in which supplemental irrigation was applied to meet 125% of crop evapotranspiration after accounting for rainfall (**125% ETc**). Crop evapotranspiration was estimated using an algorithm defined in Vellidis et al. (2014) which calculates daily ETc by estimating reference ET from daily minimum and maximum temperature, total solar radiation, and then quantifies ETc by multiplying reference ET by a growth stage-specific crop coefficient based on heat unit accumulation. This constituted the 100% ETc treatment. Daily water demand for the 125% ETc treatment was estimated by multiplying the ETc obtained using the Vellidis (2014) approach by 1.25. Irrigation was applied using overhead sprinkler irrigation from a linear move system, and irrigation events were triggered whenever the deficit between ETc and effective rainfall was 1.63 cm for a particular treatment [This was the maximum amount of irrigation water that could practically be supplied by the irrigation system]. Thus, differences in irrigation amounts between treatments are primarily the result of differences in the frequency of irrigation events. The experimental design for the current study was a randomized complete block design with three irrigation treatments nested and randomized within a given block. There was a total of three replicate plots per treatment, and each plot was 8 rows (12.19 m) wide, with a minimum of 12.19 m buffer between adjacent plots (8 rows of buffer).

Leaf Water Potential Measurements

Predawn leaf water potential (Ψ_{PD}) data was collected between 0400 and 0600 h in approximately two-week intervals during the irrigation treatment period (June 4, 14, 24, July 16, 31 and August 13). To measure Ψ_{PD}, a Scholander pressure chamber (PMS Instrument Company, Albany, OR) was used, and two uppermost, fully expanded mainstem leaves (usually the fourth leaf node below the terminal) were severed near the axillary base of the petiole. Immediately afterward, the petiole was sealed in the compression gasket while the leaf blade was enclosed in the pressure chamber. After the chamber was sealed, the leaf was pressurized at a rate of 0.05 MPa s^{-1}, and the pressure necessary to force water to emerge at the cut surface of the petiole was documented. Water potential is reported in negative MPa and seasonal trends for 2018 and 2019 are provided in Figure 1.

In-Season Light Interception Measurements

Light interception measurements were performed between 1000 and 1400 h on the same dates and in the same plots that Ψ_{PD} data were taken. Specifically, two measurements of light interception were collected per plot using an AccuPAR LP-80 Ceptometer (METER Environment, Pullman, WA). This instrument consists of a central data logger attached to two different types of probes. One is a line quantum sensor 0.84 m long that contains multiple, integrated quantum sensors used for below-canopy photosynthetically active radiation (PAR_{below}) measurements and the second one is a point quantum sensor attached to the data logger by a 5 m cable, which is used for simultaneous measurements of above-canopy irradiance (PAR_{above}). One of the below-canopy measurements in each plot was conducted with the line sensor positioned perpendicular to the row (across the row) and the other measurement was done with the line sensor parallel to the row in the row middle. The above-canopy sensor was mounted on a camera tripod to maintain the sensor at a 1.5 m height above the canopy and to keep the sensor level. The fraction of incident PAR intercepted by the canopy ($IPAR_f$) was calculated as $[(PAR_{above} - PAR_{below})/PAR_{above}]$. $IPAR_f$ was plotted versus days after planting, and a sigmoidal function fit to the resulting data for each plot (Figure 2).

The sigmoidal function was used to estimate total PAR intercepted by the canopy during the growing season ($IPAR_{total}$) by multiplying total daily solar radiation by 0.45 (assumes PAR represents 45% of total daily insolation; Kiniry et al., 1989) by $IPAR_f$ and then summing all daily values from planting until crop maturity. $IPAR_{total}$ is reported in MJ m^{-2}.

End of Season Measurements

At crop maturity for each treatment (~60% open boll), defoliants were applied to facilitate leaf drop and stimulate boll opening for the mature bolls remaining unopened on the plant. Importantly, defoliation occurred on 12/09/2019 for the rainfed treatment and 18/09/2019 for the irrigated treatments due to differences in days to reach crop maturity. To assess lint yield from each plot, 2 rows from the center of each plot were mechanically harvested using a two-row spindle picker (John Deere 9930 Two-Row Cotton Picker). The machine-harvested samples were weighed on-site and the seedcotton was sent to the University of Georgia MicroGin located in Tifton, GA. Samples were ginned to obtain a realistic estimate of gin turnout and fiber samples were sent to the USDA classing office in Macon, Georgia to obtain HVI measures of fiber quality, including fiber length, strength, micronaire, and uniformity (%). Immediately prior to defoliation, a 1 m length of row from each plot was destructively harvested, and then the samples were dried in a forced air oven at 80°C for 72 h to estimate total above-ground biomass in kg ha^{-1}. Harvest index (HI) values were calculated for each plot by dividing lint yield in kg ha^{-1} by total above-ground dry biomass. Radiation use efficiency (RUE) was determined by dividing crop biomass (g m^{-2}) by $IPAR_{total}$ (MJ) to express RUE values in g MJ^{-1}.

Statistical Analysis

Yield losses attributable to IPAR, RUE, and HI were calculated according to a simplified path model, wherein yield loss due to IPAR is calculated first as follows.

$$L(IPAR) = Yc * (1 - \frac{IPARs}{IPARc})$$

Where Y_C is the yield of the control treatment (the treatment used was the Rainfed due to its higher yield) and $IPAR_S$ and $IPAR_C$ are the total seasonal IPAR for the stress and control plots, respectively. Successively the yield losses due to RUE where calculated as:

$$L(RUE) = (Yc - L(IPAR)) * (1 - \frac{RUEs}{RUEc})$$

Where RUE_S and RUE_C are the whole-season radiation use efficiencies for the stress and control plots, respectively. Lastly, the yield losses caused by HI where calculated as:

$$L(HI) = (Yc - L(IPAR) - L(RUE)) * (1 - \frac{HIs}{HIc})$$

Where HI_S and HI_C are the harvest indexes for the stress and control plots, respectively.

Treatment effects were assessed for each parameter of interest using a mixed-effects analysis of variance (ANOVA). Specifically, block was considered a random effect and irrigation treatment was considered a fixed effect with three irrigation levels and three replicates of each level. Post hoc analysis to test for differences between treatment means was conducted using Fisher's protected least significant difference test. For all comparative analysis, $P < 0.05$ was indicative of a significant irrigation effect or significant difference between means. All curve fitting and comparative statistical analyses were conducted using JMP® Pro 14.3.0, and graphs were built using SigmaPlot 14.0.

Results

Weather conditions, irrigation, and predawn leaf water potential

Cumulative rainfall, irrigation, total water received by the crop along with total incoming solar radiation for the 2018 and 2020 growing seasons for the three irrigation treatments used in the current study are provided in Table 1.

The values show that the crop received much more rainfall in the 2018 season than the 2019 season. Specifically, 81.3 cm were received in 2018 and 54.7 cm of rainfall was received in 2019. As noted previously in the Materials and Methods, the irrigation amount for the Dryland treatment was not zero (3.3 cm in 2018 and 6.1cm in 2019) because blanket applications of water were made to all treatments to facilitate uniform emergence. Nonetheless, irrigated treatments received either 18 cm (100% ETc) or 19 cm (125% ETc) more irrigation than the dryland in 2018 and either 21.9 (100% ETc) or 26.6 cm (125% ETc) more irrigation than the dryland in 2019. In 2018, all the treatments received the same amount of total incident solar radiation (2621 MJ m^{-2}), whereas in 2019, there was a difference between the Dryland and the irrigated treatments (2804 MJ m^{-2} and 2977 MJ m^{-2} respectively) because the Dryland treatment exhibited early maturation so that the growing season ended approximately two weeks prior to irrigated treatments. All the treatments in 2019 received more cumulative total solar radiation compared to all the 2018 treatments.

To describe seasonal trends in crop water status, we performed biweekly measurements of predawn leaf water potential (Ψ_{PD}). As shown in Figure 1, there was no significant differentiation between the irrigation treatments at any point during the growing season in either year of the experiment except for the second last measurement taken on the 31 July 2019 where the Dryland Ψ_{PD} was -0.375Mpa while the 100%ETc and the 125% ETc where -0.5Mpa and -0.483Mpa respectively. For 2018, the lowest value of Ψ_{PD} was recorded in the Dryland on 21 June 2018 at -0.467 MPa and the maximum value was recorded in the Dryland on 07 June 2018, when the measurements first began, and it was equal to -0.175Mpa. For 2019, the lowest value of Ψ_{PD} was recorded in the 125% ETc on 16 July 2019 and it was equal to -0.725Mpa and the maximum value was recorded in the 125% ETc on 14 June 2019, when the measurements started, and it was equal to -0.367Mpa.

Lint yield and biomass

Table 2 provides analysis of variance results for the effect of irrigation on lint yield and fiber quality parameters during the 2018 and 2019 seasons. For 2018 there was no significant effect of irrigation on lint yield or any of the HVI fiber quality parameters ($P < 0.05$), and in 2019 there was only a significant effect of irrigation on lint yield. As a result, the remainder of our results will focus entirely on component processes affecting yield during the 2019 season. Lint yield decreased as the amount of water provided through irrigation increased (Figure 3). The Dryland treatment yielded the highest (1559 kg ha^{-1}), and the 125% ETc treatment yielded the lowest (1241 kg ha^{-1}). Statistically, the 100% ETc treatment and the 125%ETc treatment were equivalent. When the average yield of the two irrigated treatments is compared with the yield of the Dryland treatment, supplying irrigation during the 2019 season suppressed yield by 267 kg ha^{-1}. Conversely, biomass was approximately 30% higher in the irrigated plots (averaging 12,270 kg ha^{-1}) than the Dryland plots (9,459 kg ha^{-1}). Both the 100% ETc and the 125% ETc treatments produced statistically equivalent biomass.

Intercepted Photosynthetically Active Radiation (IPAR), Radiation Use Efficiency (RUE) and Harvest Index (HI)

As shown in Figure 2 the data collected for $IPAR_f$ followed a sigmoidal response to day of the year for each individual plot. Due to some plot-to-plot variability within a treatment, $IPAR_f$ reached 95% solar radiation interception between 72 and 117 DAP (days after planting) in the Dryland treatment, between 78 and 84 DAP in the 100%ETc treatment, and between 74 and 78 DAP in the 125% ETc treatment. Figure 4 provides information on cumulative intercepted photosynthetically active radiation (IPAR), radiation use efficiency (RUE), and harvest index (HI) responses to irrigation. IPAR was statistically the same among all treatments although numerically the highest value was recorded in the 100%ETc treatment. The treatments had, respectively. 812.13MJ for the Dryland, 939.54MJ for the 100%ETc, and 900.90MJ for the 125% ETc. Radiation Use Efficiency (RUE) increased numerically with an increase in water applied but statistically, there were no differences between treatments, where mean RUE ranged from 1.18 g MJ^{-1} for the Dryland to 1.40 g MJ^{-1} for the 125% ETc. Harvest Index (HI) was statistically the highest in the Dryland plots (approximately 16%), while both the irrigated treatments had statistically equivalent HI values that averaged approximately 10.5%. When the average HI of the two irrigated treatments is compared to the average HI of the Dryland, irrigation during the 2019 season lowered HI by 35%.

Yield Loss Contributions

Figure 5 describes the irrigation induced yield loss contributions for the three physiological parameters of interest (IPAR, RUE, and HI) expressed in kg ha^{-1} for the three irrigation treatments. For the 100%ETc and 125% ETc treatments IPAR positively contributed to yield, where the yield contribution for each of these two treatments was 240.49 kg ha^{-1} and 167.58 Kg ha^{-1}, respectively.

Similarly, RUE had a positive contribution to yield for the 100%ETc and 125% ETc. In these cases, yield contribution attributed to RUE was 162.28 kg ha^{-1} and 259.45 kg ha^{-1} for the 100% ETc and 125% ETc treatments, respectively. Conversely, HI had a much more substantial and negative contribution to the yield of the 100% ETc and 125% ETc treatments. Specifically, the yield loss attributable to this factor was 644.43 kg ha^{-1} and 769.80 kg ha^{-1} for the 100% ETc and 125% ETc, respectively. Thus, the negative impacts of excess irrigation on HI offset any positive effects of irrigation on IPAR or RUE, resulting in substantial total yield losses relative to the Dryland. Overall, the total yield loss relative to the Dryland was of 208.88 kg ha^{-1} for the 100%ETc and 312.60 Kg ha^{-1} for the 125%ETc.

Discussion

It is well-established that drought can drastically limit lint yield and economic productivity in cotton by negatively impacting multiple physiological processes (Meeks et al., 2017; Chastain et al., 2014; Chastain et al., 2016; Hu et al., 2018). However, excess irrigation is known to negatively impact water use efficiency and economic productivity, largely due to the cost associated with pumping more irrigation water than is actually needed to maximize lint yield (Perry et al., 2012). In some instances, excess irrigation can also limit lint yield, but the importance of key physiological processes in driving yield loss due to excess irrigation have received only minimal attention. The current experiment was designed to quantify the relative contributions of cumulative Intercepted Photosynthetically Active Radiation (IPAR), Radiation Use Efficiency (RUE) and Harvest Index (HI) to yield loss in response to irrigation. While the current experiment included a dryland treatment, a well-watered control designed to provide ETc requirements as described in Vellidis et al. (2014), and an over-irrigated treatment, there was no significant irrigation treatment effect on lint yield or fiber quality during the 2018 season. By comparison, irrigation treatment had a pronounce effect on lint yield during the 2019 season, where the amount of water applied was negatively associated with yield. This provided a unique opportunity to evaluate the physiological contributors to yield loss in response to excess irrigation.

Firstly, the Dryland treatment had the highest yield with 1559 kg ha^{-1} while the 125% ETc treatment yielded the lowest at 1241 kg ha^{-1} and the 100% ETc treatment's yield was statistically similar to the 125%Etc treatment (Figure 3). While drought has been shown to drastically limit cotton yields in numerous studies previously (Chastain et al., 2014; Chastain et al., 2016; Hu et al., 2018; Snowden et al., 2014), experiments assessing yield loss due to excess irrigation are limited, and where published research is available, they do little to address the cause of yield reduction. For example, Wanjura et al., 2002 compared various irrigation volumes and regimes in a 12 year-long study and in the whole study the treatments that received the highest amount of water suffered a reduction of yield during the first 8 years. During this period the differences of total water received between the wettest treatment and the highest yielding treatment ranged from 0.8cm to 47.7cm while the yearly yields for the wettest treatments were from 5% to 37% less than the highest yielding treatments. Karam et al., 2006 reports a reduction of yield with increased irrigation, where total irrigation ranged from 57.8cm and 47.4cm the first year and between 60.2cm and 48.3cm in the second year, and yield was 653.4 kg ha^{-1} in the driest treatment compared to the wet control yield of 423.3kg ha^{-1} in the first year, while the second year dry treatment yielded 623.9kg ha^{-1} and the control yield was 490.6kg ha^{-1}. This finding of yield reduction due to excessive irrigation is confirmed by other studies (Grimes et. al, 1968, Letey and Dinar, 1986, Jackson and Tilt, 1968).

An important result from this study is the increase of biomass associated with over-irrigation (Figure 3): Dryland biomass was 9,459 kg ha^{-1} while 125%ETc (that is statistically equivalent to 100%ETc) was 12,270 kg ha^{-1}. The literature reports similar results (Grimes et al., 1968, Letey and Dinar, 1986, Karam et al., 2006, Wang et al.,2016), confirming that this is a plausible adaptation of the cotton plant to over-irrigation. By comparison drought reduces total biomass production in cotton (Zhang et al., 2017).

Also, in 2019, component parameters contributing to yield were differentially affected. Specifically, during the 2019 season, there was not a significant effect of irrigation treatment on RUE or IPAR although numerically, the mean values for each the aforementioned parameters were highest in the over-irrigated treatment. This is notable since biomass was 30% higher in irrigated treatments than in dryland treatments, and biomass production would presumably be the product of RUE or IPAR (Monteith, 1972), even if the individual effects were not significant.

In assessing yield loss contributions attributable to each parameter, it is apparent that IPAR was calculated to have a positive impact on yield, where IPAR in the 100%ETc and 125% ETc treatments would have contributed 240 kg ha^{-1} and 168 kg ha^{-1} respectively. The study by Zhi et al. (2014) reports a linear relationship between IPAR and Leaf Area Index, and this behavior, even in other species, is confirmed in the studies by Tharakan et al (2008) and Hipps (1983). These studies suggest that increased vegetative growth allows the plant to absorb a larger fraction of incoming light for conversion into biomass.

Mean RUE values increased with an increase in irrigation amount, though not statistically (Figure 4). Similar to IPAR, RUE had a positive contribution to yield for the 100%ETc and 125% ETc. Here, yield contribution due to RUE was 162 kg ha^{-1} for the 100% ETc and 259 kg ha^{-1} for the 125% ETc treatments, respectively. Rosenthal and Gerik, 1991 reported values of RUE between 1.3 g MJ^{-1} and 1.5g MJ^{-1} in non-stressed cotton plants. These values are close to the values reported in Figure 4. Mild drought stress can cause stomatal closure and reduce photosynthetic rates at certain times during the season without negatively impacting yield (Chastain et al., 2014) because processes that are dependent on turgor maintenance (growth, stomatal movements) are among the first to be affected by drought (Hsiao, 1973). Furthermore, water deficit conditions have been shown to negatively impact RUE previously in cotton (Ahmad et al., 2015; Maqsood et al., 2006). Thus, it is reasonable to assume that non-waterlogging, water-replete conditions would have a positive impact on RUE. However, there is a paucity of data in the literature concerning the impacts of water excess on RUE.

Finally, HI was significantly higher in the non-irrigated treatment. Dryland HI was 0.16 while the 100%ETc HI was 0.11 and the 125%ETc was 0.10 (Figure 4). In contrast with the previous two physiological parameters, HI had a much larger and negative effect on final yield of the 100% ETc and 125% ETc treatments. In fact, the yield loss attributable to this factor was 644 kg ha^{-1} and 770 kg ha^{-1} for the 100% ETc and 125% ETc treatments, relative to the dryland treatment. Thus, the negative impacts of excess irrigation on HI substantially offset any positive effects of IPAR or RUE on yield, resulting in substantial total yield losses relative to the Dryland. Overall, the total yield loss compared to the Dryland was of 209 kg ha^{-1} for the 100%ETc and 313 kg ha^{-1} for the 125%Etc. In a study with maize under drought, Earl and Davis (2003), reported that reduced HI was the largest component responsible for yield reduction in mild water deficit stress treatments. Heuer and Nadler, (2000) and Alvarez-Reyna, (1991) instead report in cotton an increase in HI in water-limited conditions, similar to our observations for the dryland treatment. While studies assigning yield loss contributions to HI in cotton due to over-irrigation are sparse in the literature, it is plausible to say that more vigorous vegetative growth may have led to reduced boll retention because the upper branches in the irrigated plants may have shaded the lower branches and their subtending leaves which account for the majority of the carbohydrate requirements for a developing boll (Mauney, 1986). Furthermore, the fruiting branches on lower nodes account for the highest percentage of total yield (Liu et al.,2015, Jenkins at al., 1990). Most reports have focused on the impacts of water deficit on yield components, with a reduction in total boll numbers due to drought-induced abscission being the greatest contributor to yield loss (Onder et al., 2009; Pettigrew, 2004; Stockton et al., 1961; Wang et al.,2016). In our experiment, based on visual observations, Rainfed plants, despite being substantially shorter than irrigated plants, had conspicuously higher boll retention. Given the boll retention of our experiment (inferred from the HI data and from visual observation), data reported in the literature, and leaf water potential (Ψ_{PD}) observations (explained subsequently), it is reasonable to say that our dryland plants received growth limiting levels of water deficit but not sufficient stress to cause increased boll abscission as reported in the previously mentioned papers.

As stated in the materials and methods, the irrigation scheduling approach utilized in the current study made use of an ETc modelling approach described elsewhere (Vellidis et al., 2014). These approaches are valuable in that they utilize readily available weather data to estimate reference ET and then adjust crop water requirements using a crop and developmental stage-specific crop coefficient. However, these approaches do not provide a measure of crop water status, which would be important for determining if the crop actually requires irrigation to prevent yield limiting stress. A reliable measure of plant water status is Predawn Leaf Water Potential (Ψ_{PD}) (Snider et al., 2016, Shurley et al., 2015). For example, Chastain et al. (2016) evaluated multiple Ψ_{PD} thresholds for irrigation scheduling in comparison with an established water balance approach and found that water use efficiency was maximized using Ψ_{PD} = -0.5 MPa as an irrigation threshold for the entire season, and yields were only slightly reduced at a Ψ_{PD} threshold of -0.7 MPa for the entire growing season. McMichael, (1972) indicated that drought-induced boll abscission just begins to increase at Ψ_{PD} values less than -0.8MPa for a short period of time. As a reference, the data from figure 2 are reported here. In 2018, the lowest value of Ψ_{PD} for any treatment was -0.467 MPa and the maximum value was -0.175MPa. The lowest value of Ψ_{PD} recorded for the Dryland treatment in the entire experiment was -0.65MPa and only occurred on one of the sample days during the seasons. Thus, plant-based measures of water status indicated that the Dryland crop was rarely, if ever, under yield limiting drought stress during this experiment and would not have required irrigation. Thus, the results described herein, reiterate the need to either refine existing irrigation scheduling approaches or to incorporate plant-based measures of water stress into irrigation management decisions.

To conclude, this study shows how excess irrigation can suppress yield without suppressing biomass production. For example, the highest yield was observed in the Dryland treatment, which produced the lowest total biomass. Secondly, data show that the three physiological parameters assessed (IPAR, RUE and HI) differed substantially in their response to water availability and contribution to yield loss. For example, any positive effects of IPAR and RUE on lint yield due to excess irrigation were substantially offset by large declines in HI in irrigated treatments relative to the dryland. Therefore, HI was the dominant driver of yield loss due to excess irrigation. These efforts also emphasize the importance of research aimed at refining irrigation management practices to maximize productivity and water use efficiency.

Figures Captions

Figure 1. Example sigmoidal response of interception of photosynthetically active radiation ($IPAR_f$) to day of the year for a single plot of cotton measured throughout the 2019 growing season at a field site near Camilla, GA.

Figure 2. Predawn leaf water potential (Ψ_{PD}) for field grown cotton. for three different irrigation treatments during the 2018 (A) and 2019 (B) growing seasons for a field site near Camilla, GA. Values are means ± standard error (n = 6 for 2018, n = 3 for 2019).

Figure 3. Total Lint Yield (A) and Biomass (B) expressed in Kg ha^{-1} for field grown cotton for three different irrigation treatments during the 2019 growing season for a field site near Camilla, GA. Values are means ± standard error (n = 3).

Figure 4. Total Intercepted Photosynthetically Active Radiation (A) expressed as MJ m^{-2}, Radiation Use Efficiency (B) expressed in g MJ^{-1} and Harvest Index (C) for field grown cotton for three different irrigation treatments during the 2019 growing season for a field site near Camilla, GA. Values are means ± standard error (n = 3).

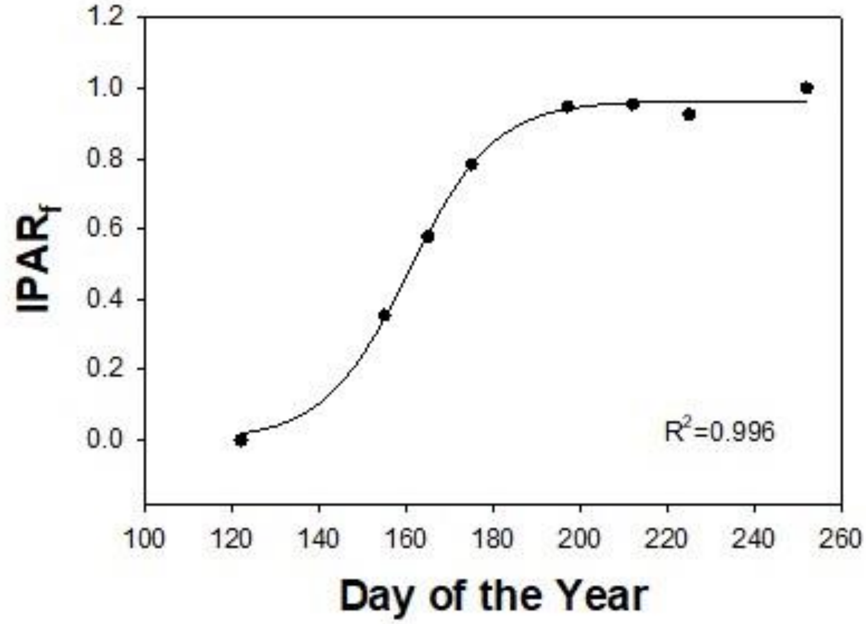
Figure 5. Yield losses contribution of Intercepted Photosynthetically Active Radiation (IPAR), Radiation Use Efficiency (RUE) and Harvest Index (HI) expressed as kg ha^{-1} for field grown cotton for three irrigation treatments during the 2019 growing season for a field site near Camilla, GA. Values are means ± standard error (n = 3).

Table 1. Irrigation, rainfall, total water received from rainfall plus irrigation, and total solar radiation for three different irrigation treatments during the 2018 and 2019 growing seasons for a field site near Camilla, GA.

Year	**Treatment**	**Irrigation (cm)**	**Rainfall (cm)**	**Total water (cm)**	**Total Solar Radiation (MJ m^{-2})**
2018	**Dryland**	3.3	81.3	84.6	2621
	100%	21.3	81.3	102.6	2621
	125%	22.3	81.3	103.6	2621
2019	**Dryland**	6.1	54.7	60.7	2804
	100%	27.0	54.7	80.9	2977
	125%	32.7	54.7	86.6	2977

Table 2. Analysis of variance results for the effect of irrigation on lint yield and HVI fiber quality parameters for the 2018 and 2019 season.

Parameter	Irrigation Effect (P Value)	
	2018	2019
Lint Yield	0.393	**0.012**
Length	0.990	0.428
Strength	0.892	0.613
Micronaire	0.463	0.301
Uniformity	0.926	0.352



IPAR$_f$
1.2
1.0
0.8
0.6
0.4
0.2
0.0
R^2=0.996
100
120
140
160
180
200
220
240
260
Day of the Year

Figure 1

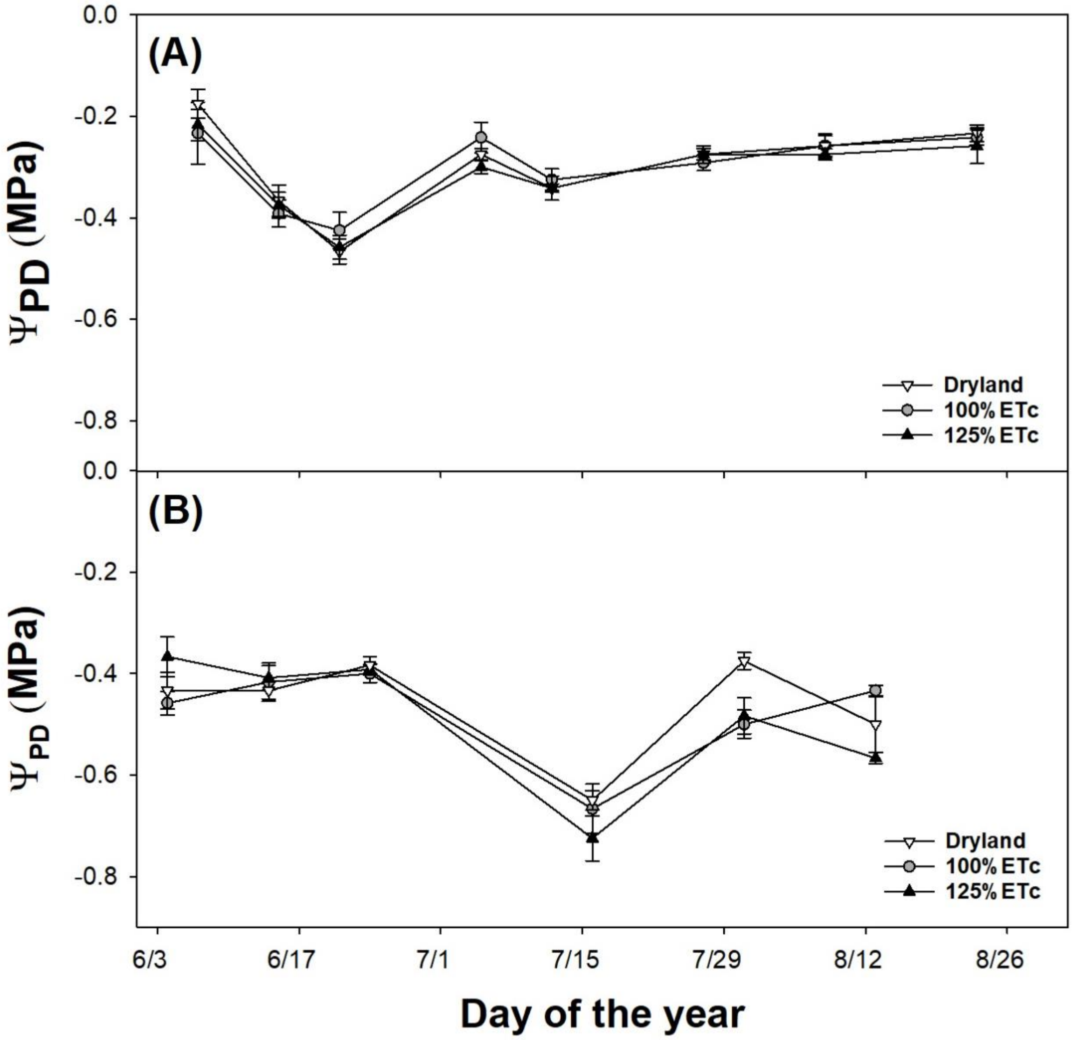

(A)
(B)
Ψ_{PD} (MPa)
0.0
-0.2
-0.4
-0.6
-0.8
Dryland
100% ETc
125% ETc
6/3
6/17
7/1
7/15
7/29
8/12
8/26
Day of the year

Figure 2

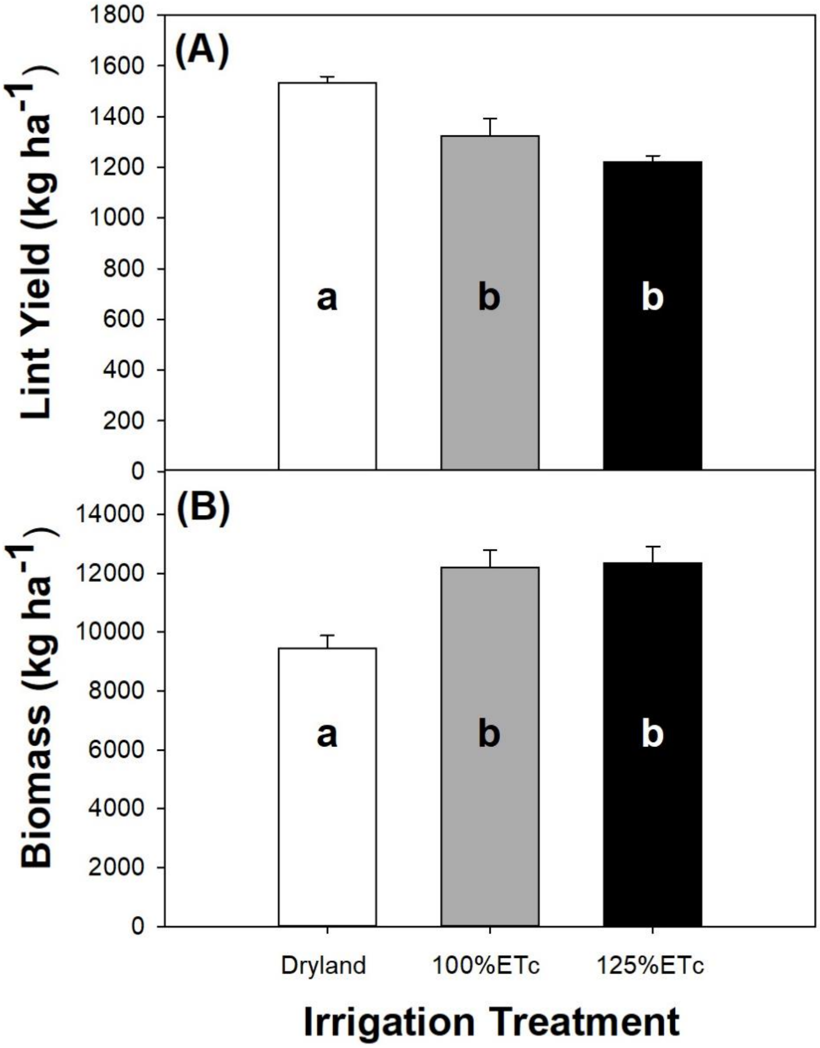

(A)
Lint Yield (kg ha^{-1})
1800
1600
1400
1200
1000
800
600
400
200
0
a
b
b
(B)
Biomass (kg ha^{-1})
14000
12000
10000
8000
6000
4000
2000
0
a
b
b
Dryland
100%ETc
125%ETc
Irrigation Treatment

Figure 3

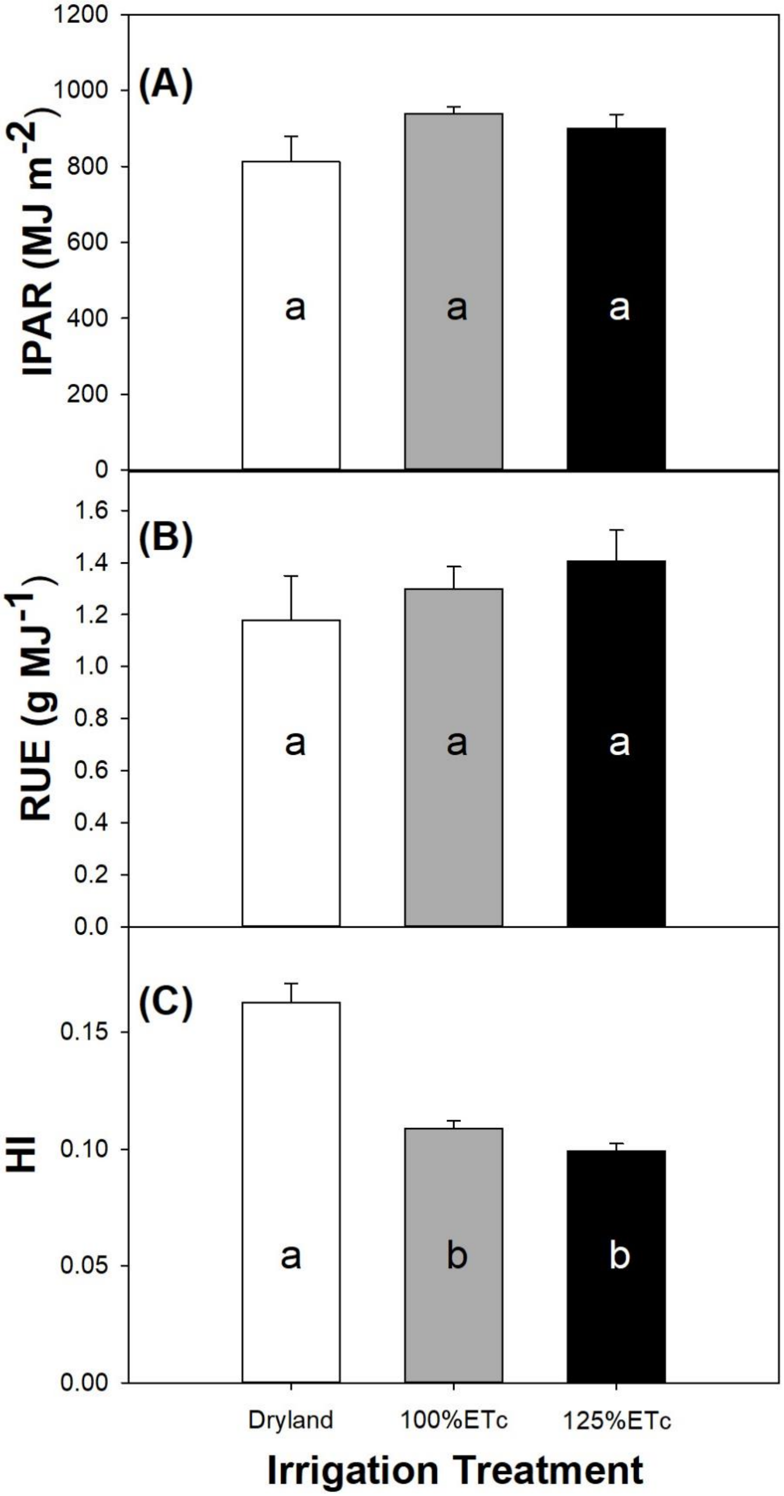

(A)
IPAR (MJ m^{-2})
0
200
400
600
800
1000
1200
a
a
a
(B)
RUE (g MJ^{-1})
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
a
a
a
(C)
HI
0.00
0.05
0.10
0.15
a
b
b
Dryland
100%ETc
125%ETc
Irrigation Treatment

Figure 4

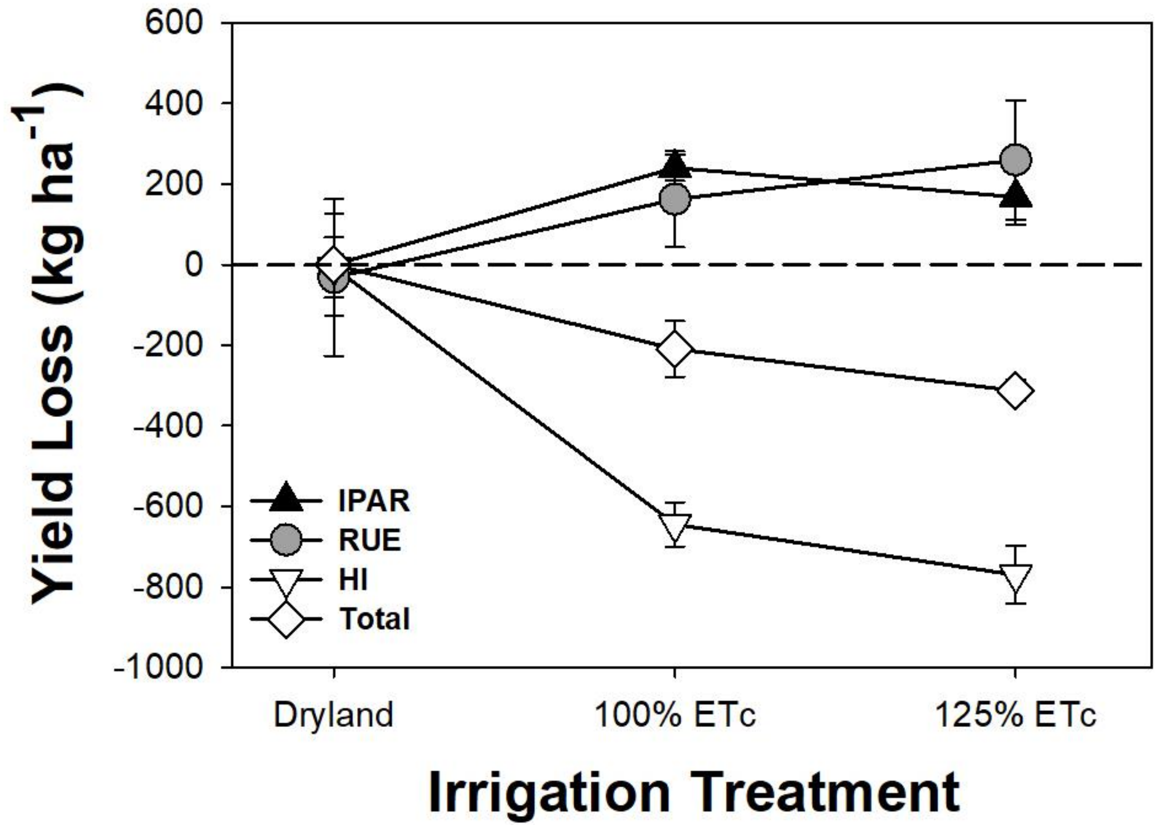

Yield Loss (kg ha^{-1})
600
400
200
0
-200
-400
-600
-800
-1000
IPAR
RUE
HI
Total
Dryland
100% ETc
125% ETc
Irrigation Treatment

Figure 5

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CHAPTER 3

CONCLUSIONS

The current experiment was designed to quantify the relative contributions of cumulative Intercepted Photosynthetically Active Radiation (IPAR), Radiation Use Efficiency (RUE) and Harvest Index (HI) to yield loss in response to irrigation. While the current experiment included a dryland treatment, a well-watered control designed to provide ETc requirements as described in Vellidis et al. (2014), and an over-irrigated treatment, there was no significant irrigation treatment effect on lint yield or fiber quality during the 2018 season. By comparison, irrigation treatment had a pronounce effect on lint yield during the 2019 season, where the amount of water applied was negatively associated with yield.

Firstly, the Dryland treatment had the highest yield with 1559 kg ha^{-1} while the 125% ETc treatment yielded the lowest at 1241 kg ha^{-1} and the 100% ETc treatment’s yield was statistically similar to the 125%ETc treatment.

Biomass increased with over-irrigation: Dryland biomass was 9,459 kg ha^{-1} while 125%ETc (that was statistically equivalent to 100%ETc) was 12,270 kg ha^{-1}: biomass was 30% higher in irrigated treatments than in dryland treatments.

In 2019, component parameters contributing to yield were differentially affected: there was not a significant effect of irrigation treatment on RUE or IPAR although numerically, the mean values for each the aforementioned parameters were highest in the over-irrigated treatment.

In assessing yield loss contributions attributable to each parameter, it is apparent that IPAR was calculated to have a positive impact on yield, where IPAR in the 100%ETc and 125% ETc treatments would have contributed 240 kg ha^{-1} and 168 kg ha^{-1} respectively.

Mean RUE values increased with an increase in irrigation amount, though not statistically. Similarly to IPAR, RUE had a positive contribution to yield for the 100%ETc and 125% ETc. Here, yield contribution due to RUE was respectively 162 kg ha^{-1} for the 100% ETc and 259 kg ha^{-1} for the 125% ETc treatments. It is reasonable to assume that non-waterlogging, water-replete conditions would have a positive impact on RUE.

Finally, HI was significantly higher in the non-irrigated treatment. Dryland HI was 0.16 while the 100%ETc HI was 0.11 and the 125%ETc was 0.10. In contrast with the previous two physiological parameters, HI had a much larger and negative effect on final yield of the 100% ETc and 125% ETc treatments. In fact, the yield loss attributable to this factor was 644 kg ha^{-1} and 770 kg ha^{-1} for the 100% ETc and 125% ETc treatments, relative to the dryland treatment. Thus, the negative impacts of excess irrigation on HI substantially offset any positive effects of IPAR or RUE on yield, resulting in substantial total yield losses relative to the Dryland. Overall, the total yield loss compared to the Dryland was of 209 kg ha^{-1} for the 100%ETc and 313 kg ha^{-1} for the 125%Etc.

Additionally, based on visual observations, Rainfed plants, despite being substantially shorter than irrigated plants, had conspicuously higher boll retention. It is reasonable to say that our dryland plants received growth limiting levels of water deficit but not sufficient stress to cause increased boll abscission as reported in the previously mentioned papers.

The irrigation scheduling approach utilized in the current study made use of an ETc modelling approach described by Vellidis et al., 2014, however, this approach did not provide a measure of crop water status, which is be important for determining if the crop actually requires irrigation to prevent yield limiting stress. A reliable measure of plant water status is Predawn Leaf Water Potential (Ψ_{PD}), and the lowest value of Ψ_{PD} recorded for the Dryland treatment in the entire experiment was -0.65MPa and only occurred on one of the sample days during the season. This indicated that the Dryland crop was rarely, if ever, under yield limiting drought stress during this experiment and would not have required irrigation. Thus, the results described herein, reiterate the need to either refine existing irrigation scheduling approaches or to incorporate plant-based measures of water stress into irrigation management decisions.