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Defining physiological contributions to yield loss in response to irrigation in cotton

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Abstract

Excessive irrigation can reduce cotton yield, but studies assessing the relative contribution of component physiological processes to yield loss are limited. The objective of the current experiment was to quantify irrigation-induced yield loss attributable to Intercepted Photosynthetically Active Radiation (IPAR), Radiation Use Efficiency (RUE) and Harvest Index (HI). For three irrigation treatments (well-watered, over-irrigated, and dryland) during the 2018 and 2019 growing seasons, biweekly measurements of predawn leaf water potential (Ψ_{PD}) and light interception were taken along with measurements of biomass, lint yield, fibre 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 was observed for irrigated treatments, despite the dryland producing lower biomass. Any positive effects of IPAR and RUE on lint yield due to excess irrigation were offset by large declines in HI. We conclude that HI was the dominant contributor to yield loss due to excessive irrigation because reduced boll numbers and average boll mass were observed in plots with the greatest total above-ground biomass.

KEYWORDS
cotton, harvest index, radiation use efficiency, Water excess, yield loss

1 | 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., 2015), yield losses as large as 1,178 kg/ha and losses in net revenue of $697 per ha have been observed due to drought stress. Yield reductions under drought are associated with declines in boll density per unit land area, and to a lesser extent, boll mass (Hu et al., 2018; Sharma et al., 2015; Zhao et al., 2019). Overall fibre quality was also reduced by drought due to increases in fibre micronaire and reductions in length (Gao et al., 2020; Hu et al., 2018). However, excessive irrigation should also be avoided because (a) the costs associated with pumping ground water when it is not needed can decrease economic productivity, (b) unnecessary irrigation events deplete groundwater resources and can exacerbate nutrient leaching concerns, and (c) cotton yield can respond negatively to over-irrigation (Cholpankulov et al., 2005; Grimes et al., 1969; Jackson & Tilt, 1968; Pereira et al., 2009; Willis et al., 1997). 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 (Y) 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; RUE), and the fraction of total dry matter allocated to the economically important part of the crop (Harvest Index; HI) (Monteith, 1972).

$$Y = IPAR \times RUE \times HI$$

Water stress can influence total intercepted photosynthetically active radiation (IPAR). According to a 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. Pettigrew (2004) showed 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, (which governs solar radiation interception), along with photosynthetic efficiency, forms the foundation of crop yield as described in the biophysical model developed by Monteith (1972). Bange et al. (2004) reported a slight reduction in light interception due to water logging related to 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 (Plénet et al., 2000). In cotton, drought negatively affects RUE. 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) and non-irrigated (0.9 g/MJ) plots was significant. At the same time, the fraction of PAR intercepted by the canopy ($IPAR_f$) was similar between the various irrigation treatments. In addition to the effect of RUE and $IPAR_f$, total biomass can also be reduced because water deficit hastens maturity (Chastain et al., 2016; Meeks et al., 2017), reducing the number of days over which PAR is intercepted. Regarding excessive irrigation, a study by Bange et al. (2004) showed a reduction in RUE associated with excessive irrigation (waterlogging) of about 35%. Najeeb et al. (2016) documented significant reductions in photosynthetic rates and yield under waterlogging stress. 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 0.04 (where the well-watered HI was higher). In their experiment, the most important factor determining HI variation was genotype, and the drought effect was relatively small. A study by Kimball and Mauney (1993) showed no significant difference in HI with different levels of irrigation. Hussein et al. (2011) reported no significant difference in HI for cotton grown with four different levels of irrigation. In contrast, Pettigrew (2004) documented 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. (2011) who documented a higher HI in dryland (0.32 ± 0.05) when compared to the non-stressed plants (0.26 ± 0.05).

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., 1961).

As noted in the previous sections, researchers have extensively characterized crop physiological responses to water deficit, but studies quantifying the relative yield losses attributable to each parameter under water excess are non-existent in cotton. The current study 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.

2 | MATERIALS AND METHODS

2.1 | Study site details and general 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 experimental site is classified as Lucy loamy sand, 0 to 5 per cent slopes. 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 statewide Georgia Weather Network (http://www.georgiaweather.net). Weather data are provided in Table 1. Seeds of the cotton (*Gossypium hirsutum* L.) cultivar ST 6,182 GLT (Stoneville®, BASF, United States) were planted on 2 May 2018 and 5 May 2019 at a rate of 9.8 seed/m row length, and the inter-row spacing was 0.91 m. Planting depth was 2.5 cm, 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

TABLE 1 Irrigation, rainfall, total water received from rainfall plus irrigation, average daily minimum and maximum temperature, 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)	T_{min} (°C)	T_{max} (°C)	Total Solar Radiation (MJ/m^2)
2018	Dryland	3.3	81.3	84.6	21.3	32.1	2,621
	100%	21.3	81.3	102.6	21.3	32.1	2,621
	125%	22.3	81.3	103.6	21.3	32.1	2,621
2019	Dryland	6.1	54.7	60.7	21.2	33.7	2,804
	100%	27.0	54.7	80.9	21.2	33.7	2,977
	125%	32.7	54.7	86.6	21.2	33.7	2,977

conducted for all the experimental plots according to University of Georgia Cooperative Extension Service recommendations (Whitaker et al., 2018). Since our irrigation treatments were expected to have a pronounced effect on growth, we will discuss plant growth management in more detail here. Specifically, the plant growth regulator mepiquat chloride (4.2% solution; Pix®) was applied at a rate of 0.7 L per hectare one week prior to the onset of flowering and 1.2 L per hectare two weeks later for all treatments and years. To ensure stand establishment was not a confounding factor in our experiment, all the plots received blanket applications of sprinkler irrigation of 3.3 cm in 2018 and 6.1 cm in 2019. Differential irrigation treatments were initiated when the first floral buds were visible (the 'squaring' stage).

2.2 | 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 (ETc) 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(ET_0) from available weather data and then quantifies ETc by multiplying reference ET_0 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 et al. (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 (12.2 m) wide, with a minimum of 12.2 m buffer between adjacent plots (8 rows of buffer).

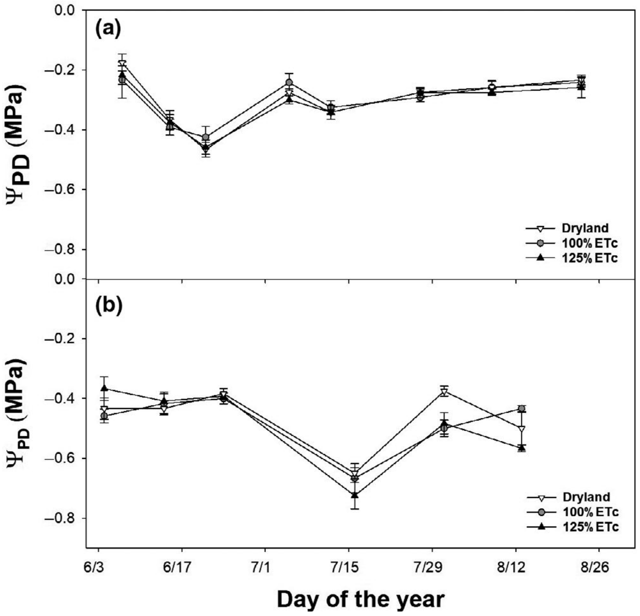

FIGURE 1 Predawn leaf water potential (Ψ_{PD}) for field grown cotton. For three different irrigation treatments during the 2018 (a) and 2019 (b) growing seasons for a field site near Camilla, GA. Values are means ± standard error (*n* = 6 for 2018, *n* = 3 for 2019)

2.3 | Leaf water potential measurements

Predawn leaf water potential (Ψ_{PD}) data were collected between 04:00 and 06:00 hr in approximately two-week intervals during the irrigation treatment period. 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 afterwards, 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, 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.

2.4 | In-season light interception measurements

Light interception measurements were performed between 1,000 and 1,400 hr 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 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 fits 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) and $IPAR_f$ and then summing all daily values from planting until crop maturity. $IPAR_{total}$ is reported in MJ/m^2.

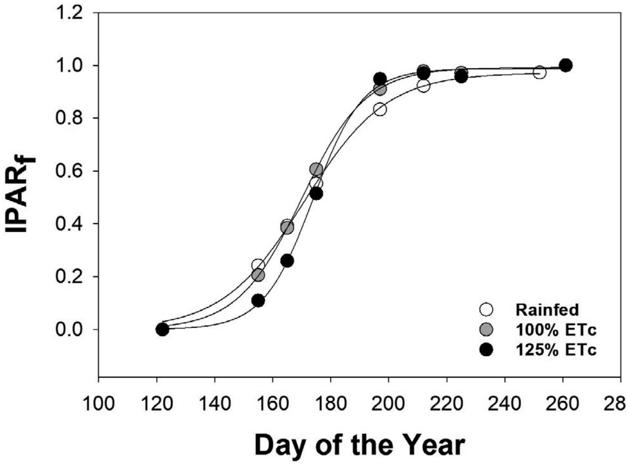

FIGURE 2 Example sigmoidal response of interception of photosynthetically active radiation ($IPAR_f$) to day of the year for three different irrigation treatments measured throughout the 2019 growing season at a field site near Camilla, GA

2.5 | 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 25 September 2018 and 18 September 2019. Harvest dates were 8 October 2018 and 4 October 2019. In both years, a two metre section of each plot was harvested by hand and the number of bolls in each section was counted. Thereafter, the seedcotton from the hand-harvested samples was weighed and ginned. Lint weight was also determined, and lint yield was estimated from the hand-harvested samples. Since lint yield can also be expressed as a function of boll density (bolls m^{-2}), seedcotton mass per boll (g/boll), and lint fraction, these parameters were also calculated for each plot.

In 2018, the only yield data obtained were the hand-harvested samples because Hurricane Michael stripped nearly all the seedcotton off the plant before machine harvest was possible, but in 2019, 2 rows from the centre of each plot were mechanically harvested using a two-row, John Deere 9,930 (John Deere, Moline, IL) spindle cotton picker. Thus, with the exception of yield component correlations (discussed in the statistical analysis section), lint yield data presented for 2018 were from hand-harvested samples, whereas lint yield data for 2019 were from mechanically harvested plots. 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 fibre samples were sent to the USDA classing office in Macon, Georgia to obtain HVI measures of fibre quality, including fibre 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 hr to estimate total above-ground biomass in kg/ha. Harvest index (HI) values were calculated for each plot by dividing lint yield in kg/ha 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.

2.6 | Statistical analysis

Yield losses attributable to IPAR, RUE and HI were calculated according to a simplified path model as described in Earl and Davis (2003), wherein yield loss due to IPAR is calculated first as follows.

$$L(IPAR) = Yc \times \left(1 - \frac{IPARs}{IPARc}\right)$$

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:

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

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:

$$L(H) = (Yc - L(IPAR) - L(TUE)) \times \left(1 - \frac{HIs}{HIc}\right)$$

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 (LSD) test. For all comparative analysis, $p < .05$ was indicative of a significant irrigation effect or significant difference between means. Associations between yield components and lint yield, across both years and all irrigation treatments in the current study, were assessed by calculating Pearson's correlation coefficient for all possible combinations of lint yield, boll density, bolls per plant, boll mass and lint per cent only for hand-harvested samples. All curve fitting and comparative statistical analyses were conducted using JMP® Pro 14.3.0 (SAS, Cary, NC), and graphs were built using SigmaPlot 14.0 (Systat Software Inc., San Jose, CA).

3 | RESULTS

3.1 | 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 2019 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, rainfall totalled 81.3 cm in 2018 and 54.7 cm during 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 6.1 cm 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 (2,621 MJ/m^2), whereas in 2019, there was a difference between the dryland and the irrigated treatments (2,804 MJ/m^2 and 2,977 MJ/m^2 respectively) because the dryland treatment exhibited early maturation and the growing season ended approximately two weeks prior to irrigated treatments. Moreover, all the treatments in 2019 received more cumulative total solar radiation compared to all the 2018 treatments. The 2018 season had a lower (32.1°C) average daily maximum temperature than the 2019 season (33.7°C), but the average minimum temperature was similar for the two years (21.3 and 21.2°C for the 2018 and 2019 seasons, respectively).

TABLE 2 Analysis of variance results for the effect of irrigation on lint yield and HVI fibre quality parameters for the 2018 and 2019 season

	Irrigation effect (*p* value)	
Parameter	**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

To describe seasonal trends in crop water status, biweekly measurements of predawn leaf water potential (Ψ_{PD}) were performed. 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 to the last measurement taken on the 31 July 2019, where the dryland Ψ_{PD} was −0.375 MPa while the 100% ETc and the 125% ETc where −0.5 MPa and −0.483 MPa, 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 −0.175 MPa. For 2019, the lowest value of Ψ_{PD} was recorded in the 125% ETc on 16 July 2019 and it was equal to −0.725 MPa and the maximum value was recorded in the 125% ETc on 14 June 2019, when the measurements started, and it was equal to −0.367 MPa.

3.2 | Lint yield and biomass

Table 2 provides analysis of variance results for the effect of irrigation on lint yield and fibre 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 fibre quality parameters ($p < .05$), 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 with a specific focus on 2019. In 2019, lint yield decreased as the amount of water provided through irrigation increased (Figure 3). The dryland treatment yielded the highest (1,559 kg/ha), and the 125% ETc treatment yielded the lowest (1,241 kg/ha). 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

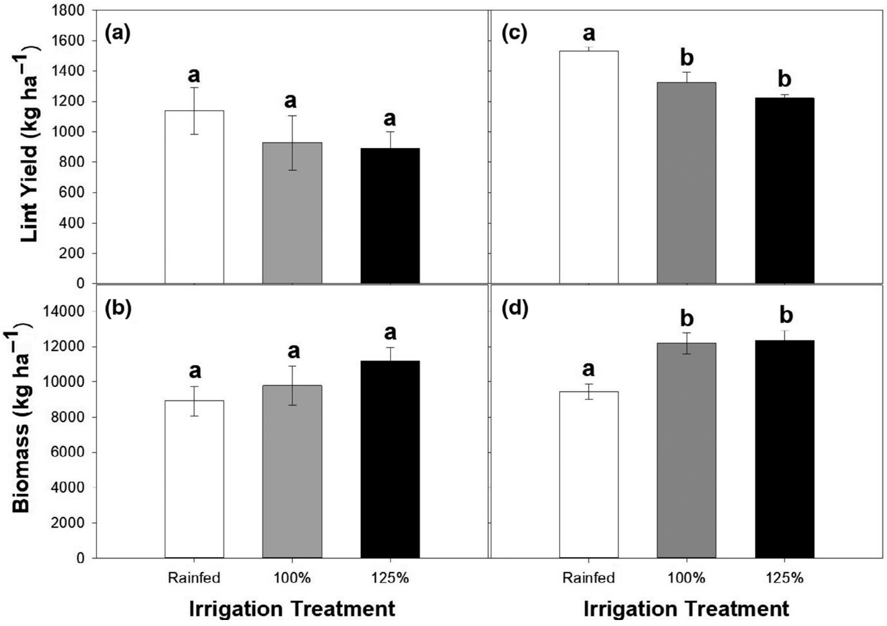

FIGURE 3 Total Lint Yield and Biomass expressed in kg/ha for field grown cotton for three different irrigation treatments during the 2018 (a and b) and 2019 (c and d) growing seasons for a field site near Camilla, GA. Values are means ± standard error (*n* = 6 for 2018 and 3 for 2019)

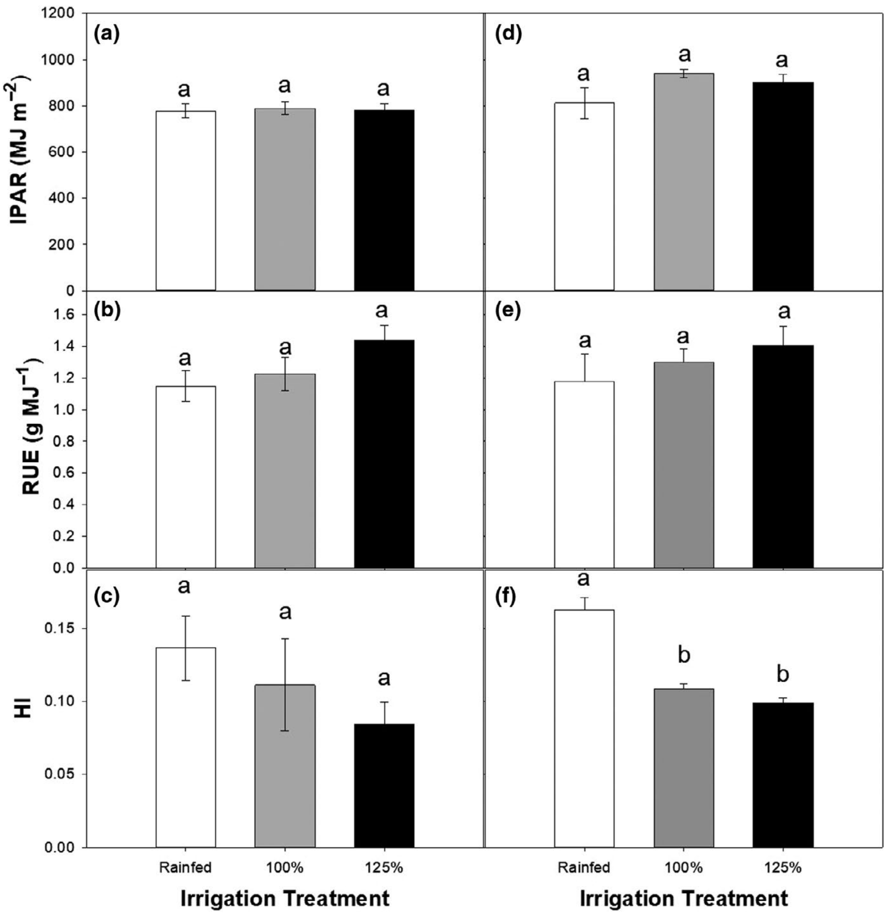

FIGURE 4 Total Intercepted Photosynthetically Active Radiation expressed as MJ/m^2, Radiation Use Efficiency expressed in g/MJ and Harvest Index for field grown cotton for three different irrigation treatments during the 2018 (a-c) and 2019 (d-f) growing seasons for a field site near Camilla, GA. Values are means ± standard error (*n* = 6 for 2018 and 3 for 2019)

2019 season suppressed yield by 267 kg/ha. Conversely, biomass was approximately 30% higher in the irrigated plots (averaging 12,270 kg/ha) than the dryland plots (9,459 kg/ha). Both the 100% ETc and the 125% ETc treatments produced statistically equivalent biomass. Similar trends were observed in 2018, but the irrigation treatment effect was not significant.

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

As shown in Figure 2, the data collected for IPAR$_f$ in 2019 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, 812.13 MJ for the dryland, 939.54 MJ for the 100% ETc and 900.90 MJ 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 for the Dryland to 1.40 g/MJ 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%. Similar trends were also observed for 2018, but no significant irrigation treatment effect was observed for any of the aforementioned parameters.

3.4 | Yield loss contributions and yield component relationships

Figure 5 describes the irrigation-induced yield loss contributions for the three physiological parameters of interest (IPAR, RUE and HI) expressed in kg/ha for the three irrigation treatments. These data are only shown for 2019 since no statistically significant yield loss was observed for 2018. 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 and 167.58 Kg/ha, 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 and 259.45 kg/ha 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 and 769.80 kg/ha for the 100% ETc and 125% ETc, respectively. Thus, the negative impacts of excessive 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 208.9 kg/ha for the 100% ETc and 312.6 kg/ha for the 125% ETc.

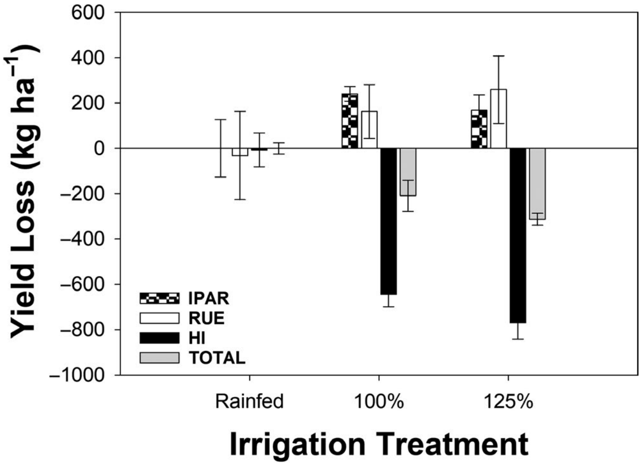

FIGURE 5 Yield losses contribution of Intercepted Photosynthetically Active Radiation (IPAR), Radiation Use Efficiency (RUE) and Harvest Index (HI) expressed as kg/ha for field grown cotton for three irrigation treatments during the 2019 growing season for a field site near Camilla, GA. Values are means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

Correlations between lint yield and yield components such as boll density, boll number per plant, boll mass and lint per cent are provided in Table 3. Lint yield was most strongly and positively associated with boll density per unit land area (*r* = 0.983) and boll number per plant (*r* = 0.960). It was expected that boll density and boll number responses would be similar since stand establishment was uniform across treatments. Lint yield was also significantly and positively associated with boll mass, albeit less so than boll density. In contrast, lint yield across both years of the study was somewhat negatively associated with lint percentage.

4 | DISCUSSION

4.1 | Yield and biomass responses

It is well-established that drought can drastically limit lint yield and economic productivity in cotton by negatively impacting multiple physiological processes (Chastain et al., 2014, 2016; Hu et al., 2018; Meeks et al., 2017). 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, excessive irrigation can also limit lint yield, but the importance of key physiological processes in driving yield loss due to excess irrigation has 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

TABLE 3 Pairwise correlation coefficients for various yield components (Boll Density, Bolls/Plant, Boll mass, Lint percentage), and lint yield for two growing seasons (2018 and 2019) and three irrigation treatments at a field site near Camilla, Georgia

	Bolls/plant	Boll mass	Lint percentage	Lint yield
Boll density	0.9599**	0.6111**	−0.4846*	0.9833**
Bolls/Plant	–	0.6187**	−0.5164**	0.9618**
Boll Mass	–	–	−0.1943	0.7276**
Lint Percentage	–	–	–	−0.4585*

*$p < .05$.
**$p < .01$.

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 fibre 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 1,559 kg/ha while the 125% ETc treatment yielded the lowest at 1,241 kg/ha 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, 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 0.8 cm to 47.7 cm while the yearly yields for the wettest treatments were from 5% to 37% less than the highest yielding treatments. Karam et al. (2006) reported a reduction of yield with increased irrigation, where total irrigation ranged from 47.4 to 57.8 cm in the first year and between 48.3 and 60.2cm in the second year. In addition, yield was 653.4 kg/ha in the dry treatment compared to the wet control yield of 423.3 kg/ha during the first year, while for the second year, the dry treatment yielded 623.9 kg/ha and the control yield was 490.6 kg/ha. This finding of yield reduction due to excessive irrigation is confirmed by other studies (Grimes et al., 1969; Jackson & Tilt, 1968; Letey & Dinar, 1986).

An important result from this study is the increase of biomass associated with over-irrigation (Figure 3): dryland biomass was 9,459 kg/ha while 125% ETc, statistically equivalent to 100% ETc, was 12,270 kg/ha. Similar results are reported in literature (Grimes et al., 1969; Karam et al., 2006; Letey & Dinar, 1986; Wang et al., 2016), confirming that this is a common response of the cotton plant to over-irrigation. By comparison, drought reduces total biomass production in cotton (Zhang et al., 2017).

4.2 | Component factors contributing to yield variability

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 of the aforementioned parameters were the 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 and 168 kg/ha respectively. The study by Zhi et al. (2014) reports a linear relationship between IPAR and Leaf Area Index, and this behaviour, even in other species, is confirmed by other scientific works (Hipps, 1983; Tharakan et al., 2008). 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 for the 100% ETc and 259 kg/ha for the 125% ETc treatments, respectively. Rosenthal and Gerik (1991) reported values of RUE between 1.3 g/MJ and 1.5 g/MJ in non-stressed cotton plants. These values are close to the values reported in Figure 4. Mild drought stress can cause stomatal closure and reduced 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 and 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 HI was 0.11 and 0.10 for the 100% ETc and 125% ETc treatments (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 and 770 kg/ha for the 100% ETc and 125% ETc treatments, when compared 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 treatment was of 209 kg/ha for the 100% ETc and 313 kg/ha for the 125% ETc. Earl and Davis (2003) reported that reduced HI was the largest component responsible for corn yield reduction in mild water deficit stress conditions. In contrast, Heuer and Nadler (2000) reported 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 (Jenkins et al., 1990; Liu et al., 2015). 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; Sharma et al., 2015; 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. Associations between lint yield and yield components across both years of the study indicate that yield reductions due to irrigation excess are primarily associated with the production of fewer bolls per plant and reduced seedcotton mass per boll. This response produces substantial reductions in HI and lint yield, despite an overall increase in biomass production for irrigated plots.

To conclude, this study shows how excess irrigation can suppress yield without suppressing biomass production. For example, the highest yields were observed in plots with the lowest total biomass. Furthermore, 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 excessive irrigation. This decline in HI was largely driven by reductions in boll density and boll mass for plots with the highest levels of total above-ground biomass.

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