Received: 8 September 2021 | Accepted: 21 February 2022 | Published online: 9 July 2022

DOI: 10.1002/csc2.20749

Crop Science

ORIGINAL RESEARCH ARTICLE

Crop Physiology & Metabolism

Irrigation management impacts on cotton reproductive development and boll distribution

Matthew T. Herritt | **Alison Thompson** | **Kelly Thorp**

USDA-ARS, U.S. Arid Land Agricultural Research Center, Maricopa, AZ 85138, USA

Correspondence
Matthew T. Herritt, USDA-ARS, U.S. Arid Land Agricultural Research Center, Maricopa, AZ 85138, USA.
Email: matthew.herritt@usda.gov

Assigned to Associate Editor Glen Ritchie.

Abstract

Cotton (*Gossypium hirsutum* L.) reproductive development is affected by irrigation management and reduced soil moisture, leading to yield impacts. This study was conducted to determine how irrigation timing and reduced soil moisture affects the distribution of cotton reproductive structures throughout the canopy. Reduced soil moisture was achieved through varied irrigation amounts based on recommendations from an agroecosystem model. Plants from each irrigation treatment were destructively sampled bi-weekly and squares, green bolls, and abscissions were counted on mainstem fruiting branches. Plant height, leaf area, and dry weights of squares, flowers, and green bolls were measured. Reduced irrigation from first square to peak bloom reduced the number of green bolls in the lower middle quarter of mainstem nodes, where most bolls are located. Reproductive development and growth were most sensitive to reduced soil moisture treatments and irrigation rates from squaring to peak bloom, whereas the period from peak bloom to 90% open boll was unaffected by irrigation rates.

1 | INTRODUCTION

Cotton (*Gossypium hirsutum* L.) provides a renewable natural fiber resource for textile production. The rise in the global population has increased the demand for fiber to meet textile manufacturing needs. To meet increased fiber production demands, U.S. cotton breeders have focused on increasing cotton fiber yields. However, meeting the increasing fiber needs is complicated due to global climate uncertainty. Increasing cotton fiber yields is a complicated endeavor when considering the future global climate that plants will be grown in and requires breeders to increase yield in conditions that are projected to limit yield.

Future climate predictions include reduced rainfall; water supplies for irrigation in many cotton production regions are now threatened by ongoing drought and competition from the urban sector. Previous studies have shown that reduced soil moisture negatively influences crop growth, development, and yield (Basal et al., 2009; Gerik et al., 1996; Grimes et al., 1969; Lokhande & Reddy, 2014; McMichael & Hesketh, 1982; Pettigrew, 2004). Cotton fiber yield is positively related to the number of bolls per plant (Grimes et al., 1969). Reduced soil moisture has been shown to impact the number of bolls and can vary from being as low as 3.9 bolls per plant to as high as 7.7 bolls per plant, resulting in fiber yield loss (Basal et al., 2009; Lokhande & Reddy, 2014; Wang et al., 2016). The number of bolls per plant is a complicated metric affected by management decisions and environmental conditions at every reproductive stage. To better understand how cotton is affected by reduced soil moisture, additional information is required to discern how the number of bolls per plant is affected. Understanding how cotton fiber yield is affected

Abbreviations: DAP, days after planting.

by reduced soil moisture is further affected by the severity and timing of the reduced soil moisture.

The impact of reduced soil moisture on cotton yield depends on the developmental stage during which the reduced soil moisture occurred, in addition to the severity and duration (Bray, 2004; Loka et al., 2012). Early stages in cotton's reproductive cycle have been shown to be sensitive to reduced soil moisture (Ungar et al., 1989). Square development, beginning approximately 25 days after planting (DAP), has been shown to be reduced and bud shedding to be increased in response to reduced soil moisture (Ungar et al., 1989). Flowering, beginning between 56 and 63 DAP, has been shown to be reduced in response to reduced soil moisture (Orgaz et al., 1992).

The severity of reduced soil moisture has varied effects on the number of bolls per plant. Basal et al (2009) observed, on average, 3.85 fewer bolls on cotton plants that received half of the required irrigation amounts to return the soil moisture level to field capacity. Lokhand and Reddy (2014) observed a reduction of 7.7 bolls per plant with 60% of the required irrigation amount to replace soil water lost by evapotranspiration. Grimes et al (1970) reported that water deficits during flowering impacted the number of bolls per plant and was associated with reduced fiber yield. Therefore, more attention must be given to the timing and severity of reduced soil moisture and how these impact cotton fiber yield. Additionally, many studies do not report how reduced soil moisture treatments affect reproductive developmental stages; this requires further scrutiny.

Cotton has been shown to preferentially retain and lose bolls at different canopy levels in response to abiotic stress, including water deficit. Higher fruiting branches and fruiting positions further from the main stem have been shown to have fewer bolls with reduced soil moisture (Pettigrew, 2004; Snowden et al., 2014), whereas the lower canopy levels, where most bolls are located, are more likely to be retained in response to reduced soil moisture (Wang et al., 2016). Studies that reported boll distribution in response to reduced soil moisture did not incorporate irrigation timing treatments to test responses to soil moisture deficit during sensitive reproductive stages. Understanding how varied irrigation timings affect boll distribution could provide valuable information to better inform cotton management decisions. Opportunities to reduce irrigation management can be identified at times when boll retention is less impacted, which could improve cotton water productivity.

To provide information about how cotton responds to reduced soil moisture timing and severity, a field experiment was undertaken at the University of Arizona's Maricopa Agricultural Center in 2016, 2017, and 2018. The effects of the irrigation amounts and timings on yield, water productivity and fiber quality were previously reported (Thorp et al., 2020). However, the report did not present or analyze the cotton plant mapping data, which shows the impact of irrigation management treatments on flower and boll distribution. The goals of the present work were to (a) determine the effects of irrigation management that include first square, peak bloom and 90% open boll on cotton biomass development; (b) identify reproductive stages and square and boll development patterns that were impacted by the irrigation management variability that include first square, peak bloom and 90% open boll; and (c) determine how irrigation management that include first square, peak bloom and 90% open boll impacted boll distribution in primary boll distribution areas.

Core Ideas

- A 60% irrigation rate from squaring to 90% open boll was most impactful on growth and development.
- Reduced irrigation impacted the middle of plant canopy, which reduced fiber yield.
- Management can avoid these losses with 20% irrigation savings from square to peak bloom.

2 | MATERIALS AND METHODS

2.1 | Field experiment

As described by Thorp et al. (2020), a cotton field study was conducted during the summers of 2016, 2017, and 2018 at the Maricopa Agricultural Center near Maricopa, Arizona (33.079˚ N, −111.977˚ W, 360 m asl). Briefly, a randomized block design was used with four replications of each block and 16 total irrigation treatments per block. Irrigation rates included a combination of four irrigation rates applied during two distinct periods of the growing season, first square to peak bloom and peak bloom to 90% open boll. The cotton genotype used for the study was Deltapine 1549 B2XF (Monsanto). Irrigation rates were 60, 80, 100 and 120% of the recommended irrigation amount from the CSM-CROPGRO-Cotton agroecosystem model (Thorp et al., 2017). The environment was hot and dry with daily minimum and maximum temperatures regularly exceeding 25 ˚C and 40 ˚C, respectively, and rainfall never exceeded 10% of the total water received. To address the objectives of the present study, treatment combinations from Thorp et al. (2020) that aligned with the present objectives were used (Table 1). Plant sampling data were aggregated among three irrigation treatment strategies, which varied irrigation rates at different times: (a) irrigation strategy 1 varied irrigation rates (60, 80, 100 and 120%) from first square to peak bloom and received the 100% irrigation rate from peak bloom to 90% open boll; (b) irrigation strategy 2 received the

TABLE 1 Timing of irrigation treatments for three irrigation strategies

	Irrigation models				
	Emergence till first square	First square	Peak bloom	Day after peak bloom	90% open bolls
	%				
Strategy 1	100	60	60	100	100
	100	80	80	100	100
	100	100	100	100	100
	100	120	120	100	100
Strategy 2	100	100	100	60	60
	100	100	100	80	80
	100	100	100	100	100
	100	100	100	120	120
Strategy 3	100	60	60	60	60
	100	80	80	80	80
	100	100	100	100	100
	100	120	120	120	120

100% irrigation rate during first square to peak bloom and varied irrigation rates from peak bloom to 90% open boll; and (c) irrigation strategy 3 received one of the four irrigation rates consistently from first square to 90% open boll (Table 1).

2.2 | Plant sampling and mapping

Cotton plants were destructively sampled on a 2-wk schedule. Three plant sampling locations in each plot were randomly selected and flagged at the beginning of the season. On each sampling date, the tenth plant along the row from each sampling flag was cut at the soil surface, yielding three plants total per plot. The sampling flag was then moved to mark the current sampling location, from which the tenth plant was collected on the next sampling date and so on. Sampled plants were bagged and placed on ice in coolers prior to transport to cold rooms at the laboratory facilities to await further processing.

Leaves were removed from each of the three plants per plot leaving the petioles intact on the stems. The total leaf area of each sample was measured on a leaf area meter (model 3100, Li-Cor). The numbers of total mainstem nodes and prefruiting nodes were counted on each plant. Plants were then mapped by specifying the order of squares, white flowers, green bolls, mature bolls, and abscised sites on each fruiting branch for each node. Following plant mapping, the plants were further dissected to separate stems, squares, green bolls, and mature bolls per plot. Plant parts were bagged and oven-dried at 65 ˚C with ventilation until constant weight was achieved. Dry weights of each sample were measured and recorded.

To conduct the present analysis, the mapping data was used to count each type of reproductive structure on each fruiting branch, giving information on the vertical distribution of reproductive structures as impacted by the water management treatments. Nodes above white flower was recorded to track maturity (Supplemental Table S1) (Bourland et al., 2001). The counts of reproductive structures from two nodes for a total of 16, 17, and 16 levels from 2016, 2017, and 2018 respectively. Until all nodes in a level were present, no data were specified.

2.3 | Statistical analysis

Data for the three plants sampled were averaged to represent each irrigation rate × irrigation strategy for each DAP in all growing seasons. For each trait (height, total nodes, weights of squares, flowers, green bolls, or mature bolls, and node levels for number of squares, abscissions, and green bolls), a linear model was fitted to the data using SAS v9.4 (SAS Institute). The model for each year was as follows:

$$\begin{aligned} Y_{ijkl} = \mu &+ \mathrm{DAP}_i + \mathrm{Strategy}_j + \mathrm{Rate}_k + \mathrm{Rep}_l \\ &+ \left(\mathrm{DAP}_i \times \mathrm{Strategy}_j\right)_{ij} + \left(\mathrm{DAP}_i \times \mathrm{Rate}_k\right)_{ik} \\ &+ \left(\mathrm{Strategy}_j \times \mathrm{Rate}_k\right)_{jk} + \left(\mathrm{DAP}_i \times \mathrm{Rep}_l\right)_{il} \\ &+ \left(\mathrm{Strategy}_j \times \mathrm{Rep}_l\right)_{jl} + \left(\mathrm{Rate}_k \times \mathrm{Rep}_l\right)_{kl} \\ &+ \left(\mathrm{DAP}_i \times \mathrm{Strategy}_j \times \mathrm{Rate}_k\right)_{ijk} \\ &+ \left(\mathrm{Strategy}_j \times \mathrm{Rate}_k \times \mathrm{Rep}_l\right)_{jkl} + \varepsilon_{ijklm} \end{aligned}$$

Rep and all interactions were treated as random

$$\text{with } \varepsilon_{ijklm} = \text{Var}\left(\varepsilon_{ijklm}\right) = \sigma^2\text{Cov}\left(\varepsilon_{ijklm}, \varepsilon_{ijklm}\right) = \rho\sigma^2,\ i \neq i'$$

where Y_{ijk} is the trait, μ is the grand mean, DAP_i is the effect of the *i*th DAP, $Strategy_j$ is the effect of the *j*th irrigation strategy, $Rate_k$ is the effect of the *k*th irrigation rate, Rep_l is the effect of the *l*th replication, $(DAP_i \times Strategy_j)_{ij}$ is the interaction effect between the *i*th DAP and *j*th irrigation strategy, $(DAP_i \times Rate_k)_{ik}$ is the interaction effect between the *i*th DAP and *k*th irrigation rate, $(Strategy_j \times Rate_k)_{jk}$ is the interaction effect between the *j*th irrigation strategy and *k*th irrigation rate, $(DAP_i \times Rep_l)_{il}$ is the interaction effect between the *i*th DAP and *l*th replication, $(Strategy_j \times Rep l)_{jl}$ is the interaction effect between the *j*th irrigation strategy and *l*th replication, $(Rate_k \times Rep_l)_{kl}$ is the interaction effect between the *k*th irrigation rate and *l*th replication, $(DAP_i \times Strategy_j \times Rate_k)_{ijk}$ is the interaction effect between the *i*th DAP, *j*th irrigation strategy and *k*th irrigation rate, $(Strategy_j \times Rate_k \times Rep_l)_{jkl}$ is the interaction effect between the *j*th irrigation strategy, *k*th irrigation rate, and *l*th replication, and ε_{ijkl} is the random error term following a normal distribution with mean 0 and variance σ^2. The residual variance, ε_{ijkl}, was modeled using a correlated error variance structure that incorporated a constant, non-zero, correlation term (ρ) among error terms to account for correlation among the days on which measurements were taken on the same experimental unit, the plots. All terms were fitted as fixed effects. Tests of fixed effects were conducted using the Kenward Roger approximation for the calculation of degrees of freedom. Difference matrixes for each Year × DAP × Timing are presented in supplemental material (Supplemental Tables S1, S2, and S3). Only data with significant differences ($p \leq .05$) between irrigation rates from at least 2 yr are presented.

3 | RESULTS

3.1 | Effects of irrigation strategy and rate on square number in cotton canopy quarters

No irrigation strategy had a significant ($p \leq .05$) effect on the number of squares in Levels 7 and below (Nodes 1–14) or above Level 14 (Nodes 27 and 28). In 2017 and 2018 on 84 and 97 DAP, respectively, irrigation Strategy 1 had fewer squares present in Level 8 (Nodes 15 and 16) with the 60% irrigation rate than the 100% irrigation rate (Figure 1; Supplemental Table S2). In 2017 and 2018 on 112 and 111 DAP, respectively, irrigation Strategy 1 had fewer squares present in Level 11 (Nodes 21 and 22) with the 60% irrigation rate than the 120% irrigation rate (Figure 1; Supplemental Table S2). In 2017 and 2018 on 112 and 125 DAP, respectively, irrigation Strategy 1 had fewer squares present in Level 12 (Nodes 23 and 24) with the 60% irrigation rate than the 120% irrigation rate. In 2016 and 2018 on 98 and 111 DAP, respectively, irrigation Strategy 3 had fewer squares present in Level 10 (Nodes 19 and 20) with the 60% irrigation rate than the 120% irrigation rate (Figure 2; Supplemental Table S2). In 2016 and 2017 on 112 and 112 DAP, respectively, irrigation Strategy 3 had fewer squares present in Level 12 (Nodes 23 and 24) with the 60% irrigation rate than the 100% irrigation rate (Figure 2; Supplemental Table S2). In 2016 and 2017 on 112 and 112 DAP, respectively, irrigation Strategy 3 had fewer squares present in Level 13 (Nodes 25 and 26) with the 60% irrigation rate than the 100% irrigation rate. In 2016 and 2017 on 126 and 126 DAP, respectively, irrigation Strategy 3 had fewer squares present in Level 14 (Nodes 27 and 28 with the 60% irrigation rate than the 120% irrigation rate.

3.2 | Effects of irrigation strategy and rate on number of abscissions in cotton canopy quarters

No irrigation strategy had a significant ($p \leq .05$) effect on the number of abscissions above Level 17 (Nodes 27 and 28). In 2017 and 2018 on 84 and 83 DAP, respectively, irrigation Strategy 1 had fewer abscissions present in Level 1 (Nodes 1 and 2 with the 60% irrigation rate than the 100% irrigation rate (Figure 3; Supplemental Table S3). In 2017 and 2018 on 112 and 111 DAP, respectively, irrigation Strategy 1 had fewer abscissions present in Level 8 (Nodes 15 and 16) with the 60% irrigation rate than the 120% irrigation rate (Figure 3; Supplemental Table S3). In 2016 and 2018 on 140 and 146 DAP, respectively, irrigation Strategy 1 had fewer abscissions present in Level 14 (Nodes 27 and 28) with the 60% irrigation rate than the 120% irrigation rate. In 2016 and 2017 on 112 and 112 DAP, respectively, irrigation Strategy 2 had fewer abscissions present in Level 10 (Nodes 19 and 20) with the 80% irrigation rate than the 120% irrigation rate (Figure 4; Supplemental Table S2). In 2016, 2017, and 2018 on 112, 112, and 111 DAP, respectively, irrigation Strategy 3 had fewer abscissions present in Level 7 (Nodes 13 and 14) with the 60% irrigation rate than the 120% irrigation rate (Figure 5; Supplemental Table S2). In 2016 and 2018 on 112 and 111 DAP, respectively, irrigation Strategy 3 had fewer abscissions present in Level 8 (Nodes 15 and 16) with the 60% irrigation rate than the 120% irrigation rate (Figure 5; Supplemental Table S2). In 2016, 2017, and 2018 on 112, 112, and 111 DAP, respectively, irrigation Strategy 3 had fewer abscissions present in Level 9 (Nodes 17 and 18) with the 60% irrigation rate than the 120% irrigation rate. In 2016, 2017, and 2018 on 112, 112, and 111 DAP, respectively, irrigation Strategy 3 had fewer abscissions present in Level 10 (Nodes 19 and 20) with

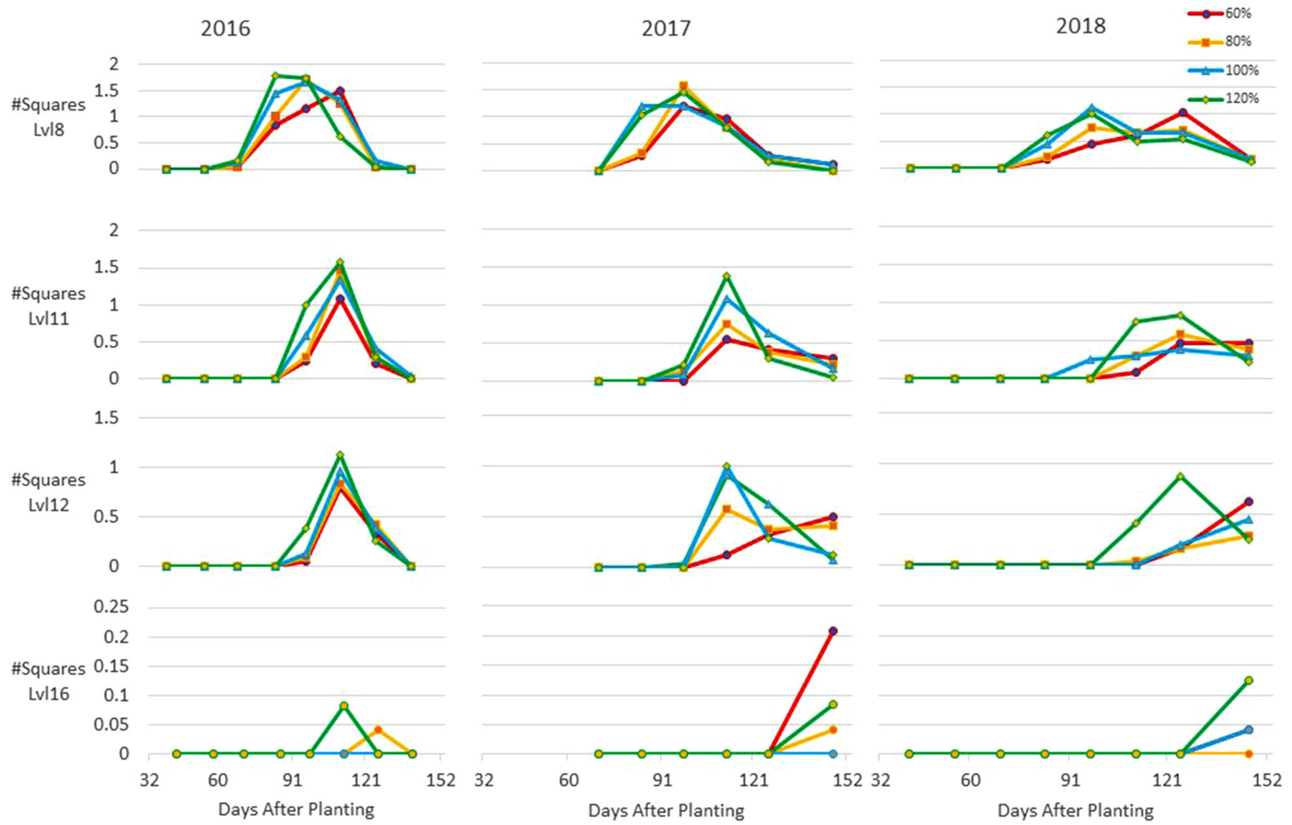

FIGURE 1 Number of squares present in Levels (Lvl) 8, 11, 12, and 16 in 2016, 2017, and 2018 with irrigation Strategy 1. Data points represent the mean value from each day of year × irrigation rate ($n = 4$) for each day of year and year

FIGURE 2 Number of squares present in Levels (Lvl) 10, 12, 13, and 14 in 2016, 2017, and 2018 with irrigation Strategy 3. Data points represent the mean value from each day of year × irrigation rate ($n = 4$) for each day of year and year

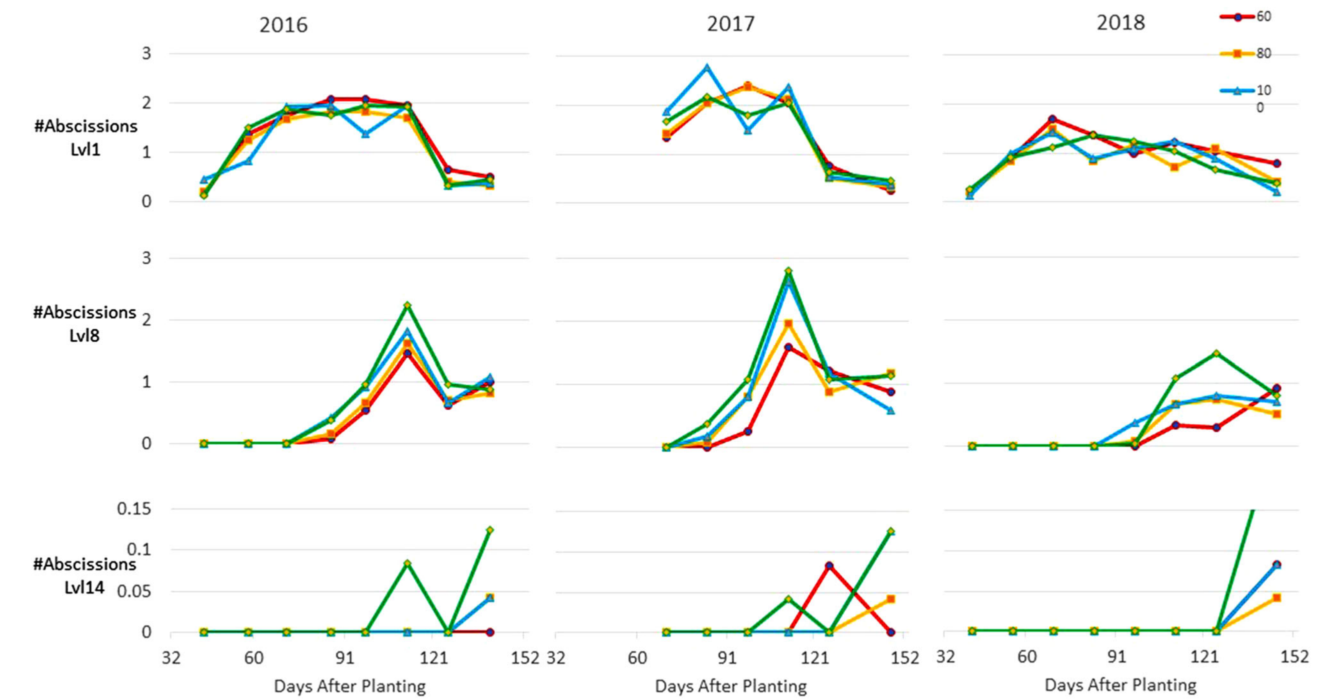

FIGURE 3 Number of abscissions present in Levels (Lvl) 1, 8, and 14 in 2016, 2017, and 2018 with irrigation Strategy 1. Data points represent the mean value from each day of year × irrigation rate ($n = 4$) for each day of year and year

FIGURE 4 Number of abscissions present in Level (Lvl) 10 in 2016, 2017, and 2018 with irrigation Strategy 2. Data points represent the mean value from each day of year × irrigation rate ($n = 4$) for each day of year and year

the 60% irrigation rate than the 120% irrigation rate (Figure 6; Supplemental Table S2). In 2016 and 2018 on 140 and 146 DAP, respectively, irrigation strategy had fewer abscissions present in Level 11 (Nodes 21 and 22) with the 80% irrigation rate than the 120% irrigation rate (Figure 6; Supplemental Table S2).

3.3 | Effects of irrigation strategy and rate on green boll number in cotton canopy quarters

No irrigation strategy had a significant ($p \leq .05$) effect on the number of green bolls below Level 9 (Nodes 17 and 18). In 2016 and 2017 on 140 and 147 DAP, respectively, irrigation Strategy 1 had fewer green bolls present in Level 15 (Nodes 29 and 30) with the 60% irrigation rate than the 120% irrigation rate (Figure 7; Supplemental Table 4). In 2016 and 2018 on 126 and 125 DAP, respectively, irrigation Strategy 3 had fewer green bolls present in Level 9 (Nodes 17 and 18) with the 60% irrigation rate than the 120% irrigation rate (Figure 7; Supplemental Table S4). In 2016 and 2018 on 126 and 125 DAP, respectively, irrigation Strategy 3 had fewer green bolls present in Level 11 (Nodes 21 and 22) with the 60% irrigation rate than the 120% irrigation rate.

3.4 | Effects of irrigation strategy and rate on cotton plant height and node number

In 2016 on DAP 86 and 98, the plant height from plants that received the 60% rate with irrigation strategy 1 was shorter

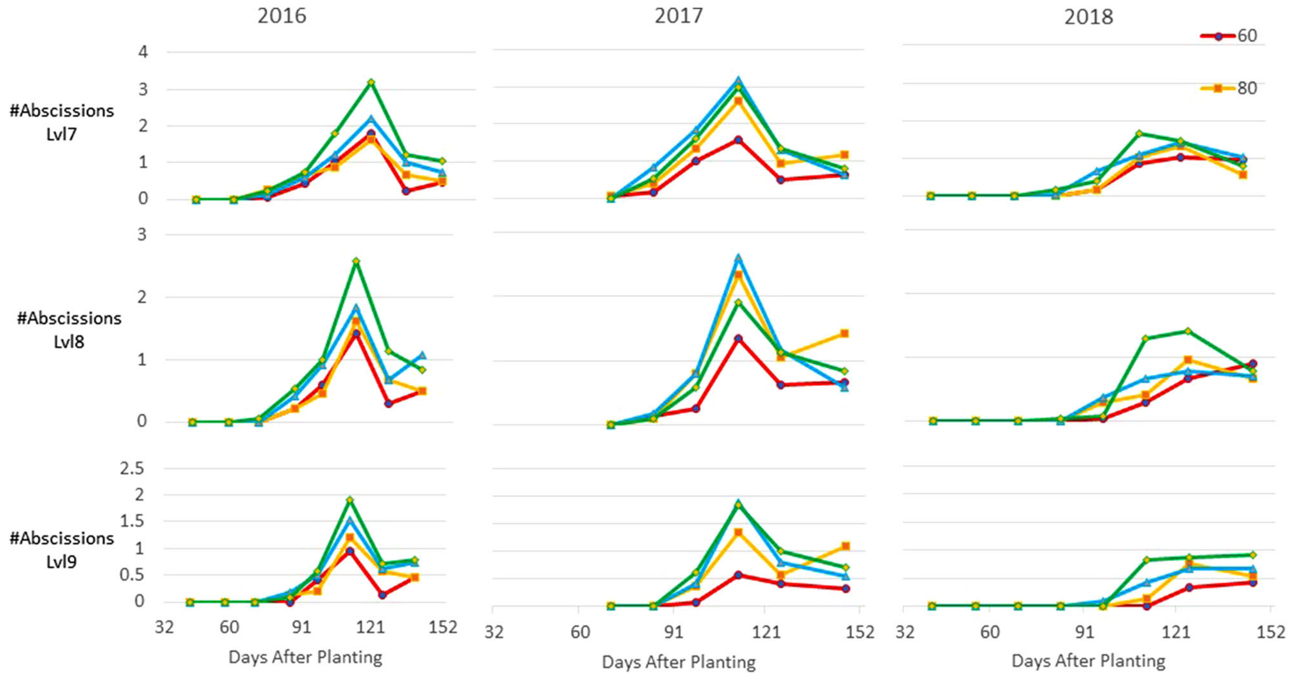

FIGURE 5 Number of abscissions present in Levels (Lvl) 7, 8, and 9 in 2016, 2017, and 2018 with irrigation Strategy 3. Data points represent the mean value from each day of year × irrigation rate ($n = 4$) for each day of year and year

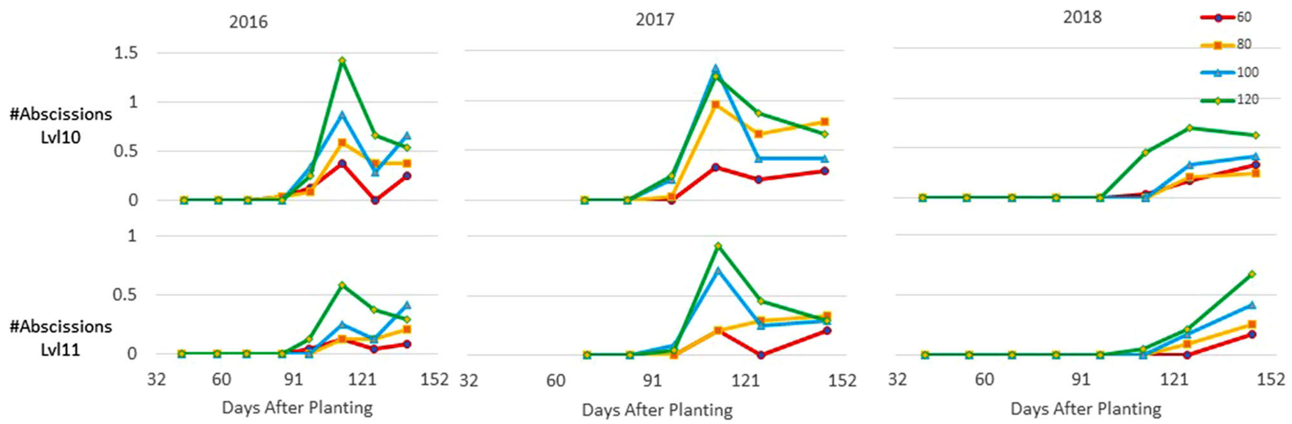

FIGURE 6 Number of abscissions present in Levels (Lvl) 7, 8, and 9 in 2016, 2017, and 2018 with irrigation Strategy 3. Data points represent the mean value from each day of year × irrigation rate ($n = 4$) for each day of year and year

than that for the 100 and 120% irrigation rates. In 2016 on DAP 112, the plant height from plants that received 60% rate with irrigation strategy 1 was shorter than that for the 120% irrigation rate (Table 2). In 2017 on DAP 98 and 112, the plant height from plants that received with the 60% rate with irrigation strategy 3 was shorter than that for the 100 and 120% irrigation rates (Table 3). In 2018 on DAP 97, 111, and 125, the plant height from plants that received the 60% rate with irrigation strategy 1 was shorter than that for the 100% and 120% irrigation rate (Table 4). Irrigation strategy 2 resulted in no differences in height among irrigation rates. In 2016 on DAP 86, the plant height from plants that received the 60% rate with irrigation strategy 3 was shorter than that for the 100 and 120% irrigation rate. In 2016 on DAP 98, 112, 126, and 140, the plant height from plants that received the 80% rate with irrigation strategy 3 was shorter than that for the 120% irrigation. In 2018 on DAP 97 and 111, the plant height from plants that received the 60% rate with irrigation strategy 3 was shorter than that for the 100 and 120%. In 2018 on DAP 97, the plant height from plants that received that 80% rate with irrigation strategy 3 was shorter than that for the 100 and 120% irrigation rates. In 2018 on DAP 111, 125, and 146, the

TABLE 2 Mean nodes plant height and leaf area from irrigation strategies 1, 2, and 3 (Strategy) from days after planting (DAP) for 60, 80, 100, and 120% irrigation rates (Irr) in 2016

	DAP	Plant height				Nodes				Stem weight				Leaf area			
Strategy	Irr	60	80	100	120	60	80	100	120	60	80	100	120	60	80	100	120
		cm				No.				g				cm^2			
1	43	14.0	15.5	15.3	15.5	7.7	7.8	8.4	8.3	1.26	1.55	1.56	1.57	438	473	491	492
	58	38.6	39.5	40.9	44.8	13.8	14.4	13.8	15.0	14.36	15.20	15.26	21.23	3381	3085	2874	3850
	71	69.8	69.7	76.8	81.1	18.8	19.2	20.1	20.3	43.71	44.76	55.12	63.33	8129	8059	9947	11293
	86	88.5	92.5	115.8	119.9	22.8	23.2	24.3	24.8	74.96	81.79	117.53	110.06	10751	11512	62300	16368
	98	100.8	110.9	136.8	136.7	25.4	26.5	27.0	29.3	90.76	118.64	136.36	166.14	13379	16101	17520	20708
	112	120.8	129.3	141.0	153.1	29.8	29.8	30.8	31.6	149.79	163.63	188.00	199.29	19726	19207	19644	20440
	126	122.8	135.0	146.8	156.8	31.3	33.3	33.0	33.8	48.27	70.24	75.47	75.31	5511	6483	6871	6742
	140	123.3	135.0	163.5	162.3	31.8	31.8	33.5	32.5	57.69	73.22	96.16	94.07	5786	6741	8029	7031
2	43	16.7	15.4	15.3	15.3	9.1	8.6	8.4	8.4	1.83	1.56	1.56	1.78	542	483	491	548
	58	44.9	42.8	40.9	41.3	14.0	14.5	13.8	13.5	17.00	18.13	15.26	11.69	3388	3514	2874	2416
	71	83.8	79.9	76.8	77.7	19.9	20.3	20.1	19.4	56.58	60.12	55.12	63.13	10314	10979	9947	10942
	86	123.8	116.7	115.8	113.9	24.7	24.5	24.3	24.7	128.17	140.10	117.53	101.82	18674	19134	62300	15375
	98	143.8	137.6	136.8	135.3	28.1	27.8	27.0	28.6	173.48	150.76	136.36	179.33	20942	18298	17520	23353
	112	155.8	160.3	141.0	151.0	31.7	32.9	30.8	29.8	215.52	260.04	188.00	203.02	20381	25867	19644	22696
	126	172.8	170.5	146.8	174.8	33.8	33.8	33.0	35.8	90.10	103.56	75.47	98.97	6791	8380	6871	8849
	140	154.5	171.5	163.5	169.0	30.8	34.5	33.5	33.8	97.25	136.67	96.16	81.84	6785	9311	8029	6645
3	43	15.1	16.6	15.3	15.0	7.8	9.1	8.4	8.0	1.66	1.48	1.56	1.39	515	561	491	432
	58	35.6	38.8	40.9	44.4	13.9	13.9	13.8	14.3	12.65	13.67	15.26	16.85	2526	2811	2874	3233
	71	65.6	72.4	76.8	84.6	18.6	19.5	20.1	19.8	39.08	47.57	55.12	55.26	7173	8979	9947	10102
	86	82.8	101.6	115.8	121.7	22.3	23.4	24.3	24.5	75.92	85.30	117.53	129.61	11024	11023	62300	19802
	98	95.0	117.4	136.8	146.3	25.3	26.1	27.0	28.6	111.62	111.17	136.36	163.22	14850	15080	17520	20273
	112	104.5	129.3	141.0	166.8	28.3	30.1	30.8	32.3	124.13	163.68	188.00	237.49	14530	16784	19644	23431
	126	99.3	122.0	146.8	180.0	26.8	29.3	33.0	36.8	30.18	43.11	75.47	106.70	3297	5128	6871	9236
	140	108.3	128.0	163.5	177.3	27.0	29.3	33.5	35.0	48.03	53.84	96.16	83.14	4391	4709	8029	5651

TABLE 3 Mean nodes plant height and leaf area from irrigation Strategies 1, 2, and 3 (Strategy) from days after planting (DAP) for 60, 80, 100, and 120% irrigation rates (Irr) in 2017

	DAP	Plant height				Nodes				Stem weight				Leaf area			
Strategy	Irr	60	80	100	120	60	80	100	120	60	80	100	120	60	80	100	120
		cm				No.				g				cm^2			
1	70	33.8	43.9	51.3	56.0	16.0	17.8	18.5	18.3	14.80	27.94	33.73	34.31	2218	3191	5340	5627
	84	47.3	59.1	74.5	83.4	19.8	25.3	23.1	23.7	34.16	39.56	67.25	89.14	4830	5849	9977	13302
	98	61.8	76.4	93.1	104.3	24.4	25.8	25.9	27.1	46.26	62.94	77.75	110.66	7897	10358	12067	16100
	112	85.9	98.2	116.9	127.7	27.6	29.8	31.1	32.2	84.61	104.85	134.29	170.44	14614	15945	17974	21814
	126	107.5	118.5	121.8	143.3	31.8	31.5	35.3	32.8	45.88	44.52	64.92	52.28	5955	5418	6562	5842
	147	129.8	121.5	128.3	148.3	35.3	37.3	32.3	35.8	48.11	47.24	50.30	74.70	4305	4362	4672	5669
2	70	50.2	48.3	51.3	49.3	18.5	18.3	18.5	17.4	31.61	28.85	33.73	27.09	5628	4609	5340	4220
	84	72.6	72.3	74.5	66.8	22.7	23.2	23.1	22.3	84.49	65.09	67.25	52.09	11925	9619	9977	7926
	98	87.5	90.6	93.1	88.3	26.7	27.3	25.9	25.8	86.83	97.80	77.75	86.26	13145	14556	12067	13644
	112	99.8	108.6	116.9	116.8	29.8	29.6	31.1	29.4	101.97	110.37	134.29	128.35	13939	15665	17974	19123
	126	113.8	118.5	121.8	145.5	30.3	31.3	35.3	33.8	48.69	41.28	64.92	52.20	5100	4428	6562	5553
	147	112.5	114.8	128.3	141.3	33.0	32.5	32.3	36.0	64.08	39.74	50.30	51.38	4949	3485	4672	5678
3	70	37.3	48.4	51.3	52.9	16.5	18.3	18.5	18.8	24.17	28.11	33.73	31.10	2605	4176	5340	4950
	84	55.3	66.3	74.5	72.7	20.7	21.7	23.1	22.2	37.39	59.49	67.25	55.96	5186	8485	9977	8360
	98	61.4	78.4	93.1	93.9	23.3	25.3	25.9	26.8	46.44	74.87	77.75	97.50	7587	11770	12067	14644
	112	75.7	97.8	116.9	122.2	25.6	29.8	31.1	30.0	66.74	93.26	134.29	128.52	10574	14442	17974	17827
	126	78.3	111.0	121.8	142.8	29.0	32.8	35.3	35.8	32.64	49.20	64.92	60.52	3765	6007	6562	7155
	147	94.3	123.8	128.3	142.3	30.8	35.0	32.3	36.5	45.58	60.00	50.30	61.72	3942	5779	4672	5348

TABLE 4 Mean nodes plant height (cm), leaf area (cm2) from irrigation Strategy 1, 2 and 3 (Strategy) from days after planting (DAP) for 60, 80, 100, and 120% irrigation rates (Irr) in 2018

	DAP	Plant height				Nodes				Stem weight				Leaf area			
Strategy	Irr	60	80	100	120	60	80	100	120	60	80	100	120	60	80	100	120
		cm				No.				g				cm^2			
1	43	18.6	21.6	21.9	22.8	8.6	8.4	8.5	8.6	1.71	2.40	1.61	1.94	436	607	413	490
	58	34.4	41.5	43.3	42.6	12.1	13.3	13.4	12.8	9.17	12.04	9.02	10.54	1535	1877	1466	1601
	71	54.3	69.3	67.4	73.8	16.9	18.1	17.5	17.0	21.34	18.78	30.39	28.72	3358	3005	4559	4349
	86	71.4	86.1	92.6	97.4	20.3	20.3	21.1	22.1	44.06	41.24	44.15	32.76	5932	5454	6333	4712
	98	78.1	98.8	114.3	118.5	21.8	23.5	26.0	24.9	60.64	71.66	65.32	61.96	7878	9512	8974	7876
	112	81.4	105.6	116.1	127.4	25.0	26.6	26.6	28.6	63.65	71.36	74.75	68.28	7622	10093	8728	8752
	126	88.6	106.5	111.9	135.4	26.1	28.3	28.0	31.6	91.51	88.95	84.07	68.83	9389	8919	7953	7261
	140	128.0	120.3	133.3	140.0	34.8	32.0	33.5	36.0	48.57	70.87	55.40	52.50	3864	5171	5256	4266
2	43	19.9	20.3	21.9	20.5	8.4	8.5	8.5	8.5	1.60	2.12	1.61	1.75	406	527	413	439
	58	41.5	39.5	43.3	40.4	13.3	12.4	13.4	12.9	10.58	6.08	9.02	9.77	1629	1045	1466	1461
	71	68.4	60.4	67.4	67.3	17.5	16.9	17.5	17.8	32.18	23.61	30.39	23.94	4683	3485	4559	3499
	86	95.1	87.5	92.6	86.4	21.8	20.0	21.1	21.1	53.96	39.86	44.15	42.93	7882	5424	6333	6034
	98	110.5	101.5	114.3	100.5	25.5	23.6	26.0	24.0	62.58	58.99	65.32	69.52	8316	8118	8974	9235
	112	113.6	107.9	116.1	110.4	27.0	26.9	26.6	27.0	58.16	69.93	74.75	69.10	7372	8131	8728	8536
	126	113.9	113.1	111.9	113.6	29.5	29.4	28.0	29.6	91.25	96.49	84.07	78.34	8692	10018	7953	8890
	140	113.5	127.8	133.3	122.0	30.3	33.5	33.5	31.8	52.34	54.62	55.40	66.66	3990	3903	5256	5250
3	43	21.1	21.1	21.9	21.0	8.3	8.9	8.5	8.1	1.52	1.75	1.61	1.91	391	425	413	454
	58	39.6	35.1	43.3	46.8	13.0	11.8	13.4	13.1	10.51	11.23	9.02	6.85	1708	1855	1466	1195
	71	60.1	61.1	67.4	74.0	16.9	17.8	17.5	17.5	27.38	25.16	30.39	24.48	4187	3985	4559	3794
	86	66.3	78.0	92.6	98.3	18.8	20.4	21.1	21.4	45.05	38.56	44.15	42.55	6512	5176	6333	6055
	98	82.8	89.9	114.3	122.8	21.8	23.3	26.0	24.9	68.65	65.45	65.32	46.84	9285	8859	8974	6596
	112	83.4	98.5	116.1	131.1	22.9	25.6	26.6	29.0	71.19	83.83	74.75	76.90	7843	9758	8728	9001
	126	91.9	102.4	111.9	135.0	27.3	29.0	28.0	29.9	99.13	78.40	84.07	82.86	9846	8256	7953	8987
	140	104.8	109.5	133.3	152.8	32.0	32.0	33.5	34.8	47.82	67.07	55.40	50.36	4340	5343	5256	4342

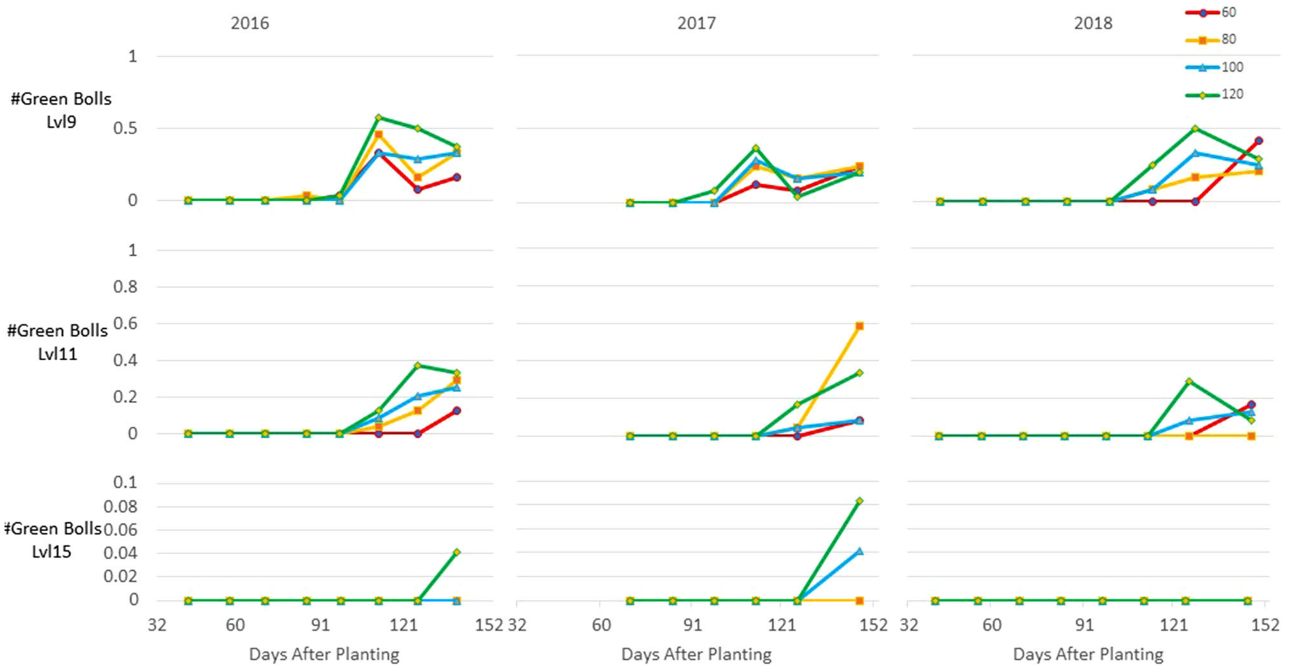

FIGURE 7 Number of green bolls present in Levels (Lvl) 9, 11, and 15 in 2016, 2017, and 2018 with irrigation Strategy 3. Data points represent the mean value from each day of year × irrigation rate ($n = 4$) for each day of year and year

plant height from plants that received the 80% rate with irrigation strategy 3 was shorter than that for the 120% irrigation rate.

In 2016 and 2018 on DAP 98 and 125, respectively, with irrigation strategy 1, the 60% irrigation rate resulted in fewer nodes than the 120% irrigation rate (Tables 2 and 4). In 2016 and 2018 on DAP 112 and 111, respectively, with irrigation strategy 3, the 60% irrigation rate resulted in fewer nodes than the 120% irrigation rate. No significant differences were identified between irrigation rates for irrigation strategy 2.

3.5 | Effects of irrigation strategy and rate on biomass accumulation

Irrigation strategy 1, 2, and 3 had no consistent effects between irrigation rates for weights of squares, flowers, green bolls, or mature bolls. In 2016 and 2017 on DAP 98 and 98, respectively, with irrigation strategy 1, stem weight was lower with the 60% irrigation rate compared with the 120% irrigation rate (Tables 2 and 3). In 2016 and 2017 on DAP 112 and 112, respectively, with irrigation strategy 3, the 60% irrigation rate resulted in less stem weight than the 120% rate. Irrigation strategy 2 had no differences between irrigation rates for stem weight. In 2016 and 2017 on DAP 98 and 112, respectively, with irrigation strategy 1, the 60% irrigation rate resulted in less leaf area than the 120% irrigation rate (Tables 2 and 3). In 2016 and 2017 on DAP 112 and 112, respectively, with irrigation strategy 3, the 60% irrigation rate resulted in less leaf area than the 120% rate. Irrigation strategy 2 had no differences among irrigation rates for leaf area.

4 | DISCUSSION

4.1 | Deficit irrigation impacts on cotton reproductive development

Over the course of the season, cotton plants received one of four irrigation rates that followed one of three irrigation strategies. Irrigation rates were 60, 80, 100, and 120% amounts based on irrigation recommendations from an irrigation scheduling model. Irrigation strategies were one of the four irrigation rates from first square to peak bloom and then 100% for rest of the season (Strategy 1), 100% up to peak bloom then one of four irrigation amounts from peak bloom to 90% open boll (Strategy 2), and one of the irrigation rates from first square to 90% open boll (Strategy 3).

Reduced irrigation from squaring to peak bloom (Strategy 1) reduced the number of squares present in the lower middle quarter of cotton plants (Levels 5–8, Nodes 9–16). Schaefer et al., 2018 showed a reduction in bolls from lower nodes (below Node 8) in response to reduced irrigation prior to flowering. Reduced irrigation from squaring to 90% open boll (Strategy 3) reduced the number of squares present in the lower middle, whereas the number of squares in the lowest (Levels 1–4, Nodes 1–8) and upper middle (Levels 9–12, Nodes 17–24) and uppermost (Levels 13–16, Nodes 25–32) quarters of cotton plants were unaffected by the irrigation rates or strategies. Cotton yield was reduced with reduced irrigation in early vegetative growth (Mitchell-McCallister et al., 2020). However, the impacts of reduced irrigation on reproductive development was not reported. Shedding of squares by cotton in response to drought has been previously reported (Bruce & Römkens, 1965; Eaton, 1955; Grimes et al., 1970; McNamara et al., 1940). It is possible that reproductive growth follows the nutritional theory of boll shedding, where bolls that can be supplied with N, carbohydrates, and other nutrients are kept on the plant (Eaton, 1955). Squares in the lower middle quarter of the canopy can be prioritized and provided nutrients despite reduced irrigation early in the season, and upper middle canopy squares are sacrificed to ensure that lower squares continue to progress through reproductive development. Gerik et al. (1996) concluded that photosynthetic capacity may be the underlying reason that a short-season cotton variety outyielded other varieties regardless of the water stress level. Reduced irrigation is likely leading to reduced source strength, which limits the number of squares that can be provided an adequate supply of nutrients and carbohydrates. As such, the full year of reduced irrigation limited the amount of nutrients the cotton plants could supply to reproductive growth, leading to the sacrifice of even the lower middle canopy squares. When irrigation was limited earlier in the reproductive development (Strategy 1), enough nutrients could still be provided to reproductive growth lower in the canopy that were further along in reproductive development. Reducing the source strength early in reproductive development would limit the number of squares that are generated and retained. Additional studies will be needed to determine the effects of irrigation rates and timing on cotton flowering and how that affects flower abortion and boll shedding. Reduced irrigation from first square to peak bloom (Strategy 2) impacted cotton development at a critical stage between squares and green bolls. These effects were observed through developmental stages that never recovered even when irrigation rates were returned to 100% of the recommendation.

Overall, reduced irrigation reduced the number of green bolls present in the lower middle quarter (Levels 5–8, Nodes 9–16) of cotton plants. Similar results have been reported with full-year irrigation treatments (like irrigation strategy 3 herein), but without the within-canopy resolution of the present study (Zhao et al., 2019). McMicheal et al. (1973) reported that bolls were sensitive to reduced irrigation and tended to be abscised during the first 14 d post anthesis. It is likely that reduced irrigation during strategies 1 and 3 reduced source strength; therefore, reduced nutrients going to the lower middle quarter of reproductive structures on plants. The reduced nutrients led to less development of green bolls in these canopy quarters, or increased abscissions of reproductive structures. Additional studies are required to determine the critical periods of sensitivity to drought and the most influential reproductive stage on cotton yield loss under drought stress.

Yield reduction was associated with the 60% irrigation rate in Strategy 1 (Thorp et al., 2020). However, the 80% irrigation rate maintained reasonable yields with Strategy 1. The results in the present study indicate that the reduction in yield associated with the 60% irrigation rate in timing Strategy 1 were a result of reduced boll numbers in the lower middle quarter of plants. The lack of yield impact of the 80% irrigation rate with Strategy 1 and lack of impact on the number of green bolls indicate that more finely timed irrigation rates during the lower middle and upper middle plant canopy development could provide additional water savings for cotton production. The present study has reaffirmed the importance of boll per plant for determining cotton yield and has expanded the findings for four unique canopy levels.

4.2 | Effects of reduced irrigation on cotton growth

In general, plants that received less irrigation were smaller and had fewer nodes (Figures 1 and 2). Reduced irrigation was previously shown to reduce cotton height and node number (Snowden et al., 2014). In the present study, plant height and node number were not affected by irrigation strategy 2. When drought occurred earlier in the season with younger plants (Strategy 1), plant height and node number were reduced. When drought occurred earlier and persisted for the rest of the season (strategy 3), the effects on plant height were more pronounced. Previous studies have shown that plant height is sensitive to drought when drought occurs with younger cotton plants (Desclaux et al., 2000; Snowden et al., 2014). A previous study involving greenhouse-grown cotton found similar results when irrigation was withheld from plants aged 38 d (Pace et al., 1999). Providing cotton with enough irrigation early in the season to reach their full height potential is critical to ensure maximum boll development later in the season. However, potential for boll development, because node number was not affected by strategy 1, could lead to yield maintenance. The effects of boll development and retention in differing canopy architectures also needs to be investigated.

5 | CONCLUSION

Irrigation rates at 60% of the recommendation from a cotton irrigation model from squaring to peak bloom and from squaring to 90% open boll were most impactful on cotton growth and development. The 60% rate was most impactful on boll development in the middle of cotton plants when this occurred during first square to peak bloom. Reproductive growth was inhibited by the 60% irrigation rate and was primarily in the middle of the plant canopy, leading to reduced boll numbers, which was associated with reduced fiber yield. Additional studies with irrigation treatments coinciding with reproductive development stages are required to determine the developmental stage that has the most impact on cotton fiber yield. This can better inform irrigation decisions that lead to additional water saving without impacting fiber yield.

ACKNOWLEDGMENTS

For help with the plant sampling and mapping activities, the authors would like to acknowledge Suzette Maneely, Matt Hagler, Cassie Farwell, Josh Cederstrom, Sara Harders, Ryan Sullivan, Alanna Zubler, Dylan Polo, and Frank Sherwood.

AUTHOR CONTRIBUTIONS

Matthew Herritt: Conceptualization; Data curation; Formal analysis; Investigation; Writing – original draft. Alison Thompson: Conceptualization; Supervision; Writing – review & editing. Kelly Thorp: Conceptualization; Methodology; Project administration; Resources; Supervision; Writing – review & editing.

CONFLICT OF INTEREST

Authors declare no conflicts of interest.

ORCID

Matthew T. Herritt https://orcid.org/0000-0002-8307-8123

REFERENCES

Basal, H., Dagdelen, N., Unay, A., & Yilmaz, E. (2009). Effects of deficit drip irrigation ratios on cotton (*Gossypium hirsutum* L.) yield and fibre quality. *Journal of Agronomy and Crop Science*, *195*(1), 19–29. https://doi.org/10.1111/j.1439-037X.2008.00340.x

Bourland, F. M., Benson, N. R., Vories, E. D., Tugwell, N. P., & Danforth, D. M. (2001). Measuring maturity of cotton using nodes above white flower. *Journal of Cotton Science*, *5*(1), 1–8.

Bray, E. A. (2004). Genes commonly regulated by water-deficit stress in *Arabidopsis thaliana*. *Journal of Experimental Botany*, *55*(407), 2331–2341. https://doi.org/10.1093/jxb/erh270

Bruce, R., & Römkens, M. J. M. (1965). Fruiting and growth characteristics of cotton in relation to soil moisture tension. *Agronomy Journal*, *57*(2), 135–140. https://doi.org/10.2134/agronj1965.00021962005700020003x

Desclaux, D., Huynh, T. T., & Roumet, P. (2000). Identification of soybean plant characteristics that indicate the timing of drought stress. *Crop Science*, *40*(3), 716–722. https://doi.org/10.2135/cropsci2000.403716x

Eaton, F. M. (1955). Physiology of the cotton plant. *Annual Review of Plant Physiology*, *6*(1), 299–328. https://doi.org/10.1146/annurev.pp.06.060155.001503

Gerik, T., Faver, K., Thaxton, P., & El-Zik, K. J. C. (1996). Late season water stress in cotton: I. Plant growth, water use, and yield. *Crop Science*, *36*(4), 914–921. https://doi.org/10.2135/cropsci1996.0011183X003600040017x

Grimes, D., Miller, R., & Dickens, W. L. (1970). Water stress during flowering of cotton. *Acta Agronomica Sinica*, *24*(3), 4–6.

Grimes, D. W., Yamada, H., & Dickens, W. L. (1969). Functions for cotton (*Gossypium hirsutum* L.) production from irrigation and nitrogen fertilization variables: I. Yield and evapotranspiration. *Agronomy Journal*, *61*(5), 769–773. https://doi.org/10.2134/agronj1969.00021962006100050035x

Loka, D. A., & Oosterhuis, D. M. (2012). Water stress and reproductive development in cotton. In Oosterhuis, D. M., & Cothren, J. T. (Eds.), *Flowering and fruiting in cotton* (pp. 51–58). The Cotton Foundation. https://www.cotton.org/foundation/upload/FLOWERING-AND-FRUITING-IN-COTTON.pdf

Lokhande, S., & Reddy, K. R. (2014). Reproductive and fiber quality responses of upland cotton to moisture deficiency. *Agronomy Journal*, *106*(3), 1060–1069. https://doi.org/10.2134/agronj13.0537

McMichael, B. L, & Hesketh, J. D. (1982). Field investigations of the response of cotton to water deficits. *Field Crops Research*, *5*, 319–333. https://doi.org/10.1016/0378-4290(82)90034-X

McMichael, B. L., Jordan, W., & Powell, R. J. A. J. (1973). Abscission processes in cotton: Induction by plant water deficit. *Agronomy Journal*, *65*(2), 202–204. https://doi.org/10.2134/agronj1973.00021962006500020005x

McNamara, H. C., Hooton, D. R., & Porter, D. D. (1940). *Differential growth rates in cotton varieties and their response to seasonal conditions at Greenville, Tex*. USDA.

Mitchell-McCallister, D., Williams, R. B., Bordovsky, J., Mustian, J., Ritchie, G., & Lewis, K. (2020). Maximizing profits via irrigation timing for capacity-constrained cotton production. *Agricultural Water Management*, *229*, 105932. https://doi.org/10.1016/j.agwat.2019.105932

Orgaz, F., Mateos, L., & Fereres, E. (1992). Season length and cultivar determine the optimum evapotranspiration deficit in cotton. *Agronomy Journal*, *84*(4), 700–706. https://doi.org/10.2134/agronj1992.00021962008400040031x

Pace, P., Cralle, H. T., El-Halawany, S. H., Cothren, J. T., & Senseman, S. A. (1999). Drought-induced changes in shoot and root growth of young cotton plants. *The Journal of Cotton Science*, *3*(4), 183–187. https://www.researchgate.net/publication/228455020_Drought-induced_changes_in_shoot_and_root_growth_of_young_cotton_plants

Pettigrew, W. (2004). Moisture deficit effects on cotton lint yield, yield components, and boll distribution. *Agronomy Journal*, *96*(2), 377. https://doi.org/10.2134/agronj2004.0377

Schaefer, C. R., Ritchie, G. L., Bordovsky, J. P., Lewis, K., & Kelly, B. (2018). Irrigation timing and rate affect cotton boll distribution and fiber quality. *Agronomy Journal*, *110*(3), 922–931. https://doi.org/10.2134/agronj2017.06.0360

Snowden, M. C., Ritchie, G. L., Simao, F. R., & Bordovsky, J. P. (2014). Timing of episodic drought can be critical in cotton. *Agronomy Journal*, *106*(2), 452–458. https://doi.org/10.2134/agronj2013.0325

Thorp, K., Thompson, A., & Bronson, K. (2020). Irrigation rate and timing effects on Arizona cotton yield, water productivity, and fiber quality. *Agricultural Water Management*, *234*, 106146. https://doi.org/10.1016/j.agwat.2020.106146

Thorp, K. R., Hunsaker, D. J., Bronson, K. F., Andrade-Sanchez, P., & Barnes, E. M. (2017). Cotton irrigation scheduling using a crop growth model and FAO-56 methods: Field and simulation studies. *Transactions of the ASABE*, *60*(6), 2023–2039. https://doi.org/10.13031/trans.12323

Ungar, E., Kletter, E., & Genizi, A. (1989). Early season development of floral buds in cotton. *Agronomy Journal*, *81*(4), 643–649. https://doi.org/10.2134/agronj1989.00021962008100040018x

Wang, R., Ji, S., Zhang, P., Meng, Y. L., Wang, Y. H., Chen, B. L., & Zhou, Z. G. (2016). Drought effects on cotton yield and fiber quality on different fruiting branches. *Crop Science*, *56*(3), 1265–1276. https://doi.org/10.2135/cropsci2015.08.0477

Zhao, W. Q., Wang, R., Hu, W., & Zhou, Z. G. (2019). Spatial difference of drought effect on photosynthesis of leaf subtending to cotton boll and its relationship with boll biomass. *Journal of Agronomy and Crop Science*, *205*(3), 263–273. https://doi.org/10.1111/jac.12320

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Herritt, M. T., Thompson, A., & Thorp, K. (2022). Irrigation management impacts on cotton reproductive development and boll distribution. *Crop Science*, *62,* 1559–1572. https://doi.org/10.1002/csc2.20749