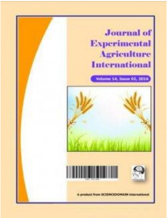

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# Effects of Irrigation Timing on Water Economy, Growth, and Yield of Water Stressed Cotton

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### *Authors' contributions*

*This work was carried out in collaboration between all authors. Author CJF designed the study and wrote the final version of the manuscript. Author HDRC conducted the 2014 study as part of his graduate research towards a MS degree, analyzed the 2014 data, and wrote a first draft of the manuscript. Author JCC managed the operation of the Drought Tolerance Laboratory, assisted in the data collection in 2014, and collected and analyzed the 2015 experimental data. Author WJG formatted the manuscript for publication. All authors read and approved the final manuscript.*

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## ABSTRACT

**Aims:** Objectives were to evaluate the effects of timed irrigations on plant biomass and seed-cotton production, plant leaf area, whole-plant transpiration, and transpiration per unit leaf area.
**Study Design:** A complete randomized design with four replications.
**Place and Duration of Study:** Study was conducted in the Drought Tolerance Laboratory at the Texas A&M AgriLife Research and Extension Center near Corpus Christi, TX during the 2014 and 2015 growing seasons.
**Methodology:** One plant per pot of the cultivar Phytogen 375 was grown in the greenhouse; pots were irrigated during nighttime with 0.5 L of a modified Hoagland's nutrient solution to prevent pot weight changes affecting the calculations of hourly daytime transpiration. A computerized system developed to convert whole-plant transpiration from changes in pot weight included an algorithm to remove nighttime weight data "noise" related to pot weight data collection when excess water drainage occurs, that otherwise would affect hourly and daily whole-plant transpiration calculations.

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**Results:** The full irrigation treatments applied during different phenological stages had significant impact on production of biomass, leaf area, and seed-cotton, as well as whole-plant transpiration and transpiration per unit leaf area. Seed-cotton production per plant increased 49% in 2015 when irrigation was applied during MH-FB and FB-MB, but not when applied late during MB-OB. These effects could not be confirmed in 2014, although not significant numerical differences due to experimental data variation were pointing to comparable effects.

**Conclusion:** The slope of the linear regression of seed-cotton on cumulative whole-plant transpiration (CWPT), which represents the overall impact of irrigation on plant seed-cotton production regardless of their timing, showed that seed-cotton per plant increased 1.063 and 0.554 g per L of CWPT increase in 2014 and 2015, respectively. This difference illustrates the effect of environmental conditions affecting the overall response of plant seed-cotton production to irrigation.

*Keywords: Drought-prone; soil water deficit; yield-limiting; water stress.*

## 1. INTRODUCTION

Soil water deficit is the most dominant yield-limiting environmental factor in drought-prone croplands. In general, the exposure of plants to soil water deficits results in the sequential inhibition of expansive growth, transpiration, and photosynthesis [1]. While plants exposed to water deficits conserve water by limiting leaf area growth and/or closing stomata [2], their growth performance and yield are ultimately adversely affected [3,4].

Where a source of irrigation water is available, farmers seeking to improve and stabilize crop yields and to use water more efficiently usually resort to deficit irrigation practices, particularly when driven by dwindling water resources and/or higher pumping costs. Since deficit irrigation usually exposes a crop to some degree of soil water deficit and water stress, the strategy should be to apply the limited irrigation during the crop's drought-sensitive growing stages. Studies have shown that cotton is sensitive to water stress during flowering and fruit development [5,6]. Water deficits reduce the total number of fruiting positions in cotton as a result of a general reduction in shoot growth [7,8] and decreased fruit retention [9,10]. As cited by Loka et al. [11], studies have shown that early flowering is the most sensitive stage to water deficits [12], whereas other studies concluded that peak flowering is the most sensitive [13] or even at the end of flowering [14].

The challenge is to decide when is best to apply the limited amount of irrigation to alleviate the detrimental effects of water stress, and this requires a better understanding of the crop responses to the timing of irrigation during the growing season. In general, successful production of cotton in semiarid, short-growing-season environments requires adequate water supply during the early reproductive phase to minimize square shedding and increase boll retention and during mid-bloom to secure boll growth and fiber production. This concept was confirmed in a three-year study, which evaluated yield responses of a medium maturity cotton to early termination of irrigation (at first bloom), medium termination (at 3 weeks after first bloom), and late or normal termination (at 6 weeks after first bloom or first open boll) [15]. This study, however, did not provide an answer to when is the best time during the growing season to apply one irrigation to a cotton crop that is growing under moderate water stress.

Most of the work on the effects of irrigation on cotton has focused on yield under variable field growing conditions. Quantifying these effects under controlled environments, particularly in what relates to sheltering from rainfall, securing soil uniformity, and controlling irrigation water supply would allow for a greater accuracy in the assessment of the water economy, growth, and yield responses of cotton to timing of irrigation. This would lead to a better understanding of the responses of cotton to deficit irrigation and help improve the management of cotton grown under deficit irrigation.

In this paper we present data describing whole-plant responses of cotton grown in a rain-shelter under moderate water-deficiency and deficit-irrigated conditions; the latter applied at three phenological periods from match-head square stage to first open boll stage. The objectives of this study were to evaluate the effects of timed irrigations on plant biomass and seed-cotton production, plant leaf area, whole-plant transpiration, and transpiration per unit leaf area of cotton grown under moderate water-deficient conditions.

## 2. MATERIALS AND METHODS

The study was conducted in the Drought Tolerance Laboratory at the Texas A&M AgriLife Research and Extension Center near Corpus Christi during the 2014 and 2015 cotton growing seasons. This facility consists of two joined greenhouse structures modified to operate as rain shelters and equipped with an automated irrigation system controlling the irrigation of individual pots and a computerized network of electronic load cell-based lysimeters for high frequency measurement of individual pot weights from which to calculate daily whole-plant water transpiration.

Seeds of the cultivar Phytogen 375 (PHY375), which is an early-medium maturity variety, were germinated at room temperature for planting. When the radicles reached a length of about 0.015 m, four germinated seeds were hand-planted in 13.5-L pots on April 2nd in 2014 and on April 8th in 2015. The planted pots were later thinned to one plant per pot when plants reached the 3rd true leaf stage. To minimize maximum soil water availability as a source of environmental variation affecting plant growth and plant water economy, all pots were equally filled with 11.4 L of dry fritted clay soil medium. This soil medium has a high volumetric water holding capacity of about 0.46 L $L^{-1}$ [16]. Drained water holding capacity of pots was 4.1 L of which about 60% (2.46 L) was available to plants. Prior to planting, the soil in the pots was covered with finely perforated aluminum foil (60 uniformly distributed needle-size perforations) and thoroughly wetted. The aluminum foil was used with the double purpose of minimizing soil water loss due to evaporation and allowing uniform distribution of irrigation water across the soil surface. Two diagonal cuts were made in the aluminum foil to expose a central soil area for planting the seeds. Upon planting, all pots were irrigated daily with 0.5 L of a modified Hoagland's nutrient solution [17]. Since the rates of plant transpiration during night are minimal, irrigation was applied during nighttime to prevent pot weight changes affecting the calculations of hourly daytime transpiration. The computerized system developed to convert whole-plant transpiration from changes in pot weight included an algorithm to remove nighttime weight data "noise" related to pot weight data collection when excess water drainage occurs that otherwise would affect hourly and daily whole-plant transpiration calculations. Irrigation was set at 2 minutes per day at 0.25 L $min^{-1}$ when plants were small, but increased to 3 minutes per day as plants increased in size.

The experimental design included a water-deficient control treatment and three timed full irrigation treatments applied at different phenological stages of development, namely from match head square (MH) to first bloom (FB), from FB to mid bloom (MB), and from MB to first open boll (OB). Daily irrigation varied throughout the testing period according to treatments and plant development (Table 1). Length of daily irrigation times was maintained at 2 minutes from MH to FB, but increased to 3 minutes thereafter until the end of tests as plants increased in size. Irrigation flow rates were increased to 0.8 L min-1 when the full irrigation treatments were applied. Upon termination of each water full-irrigation treatment, irrigation was returned to the control's level. The tests were initiated on May 7th in 2014 and on May 14th in 2015 when plants reached the MH phenological stage and terminated on August 14th in 2014 and on July 20th in 2015. The study was laid out as complete randomized design with four replications. Every replication of each treatment had three individually potted plants. Of these three plants, one was permanently assigned to a mini lysimeter while the other two plants were spares to be used as replacement if needed.

Daily whole-plant transpiration (DWPT) was calculated as the 24-hr sum of hourly whole-plant transpiration. The hourly whole-plant transpiration was calculated as the pot weight differences between consecutives hours. It was assumed that changes in pot weight between consecutive hours was practically all due to transpiration and only minimally affected by changes in plant biomass. Soil evaporation was also assumed to be negligible, since the top surface of the pot was covered with reflective aluminum foil with needle-made tiny holes.

Plant height (PH) and plant leaf area (PLA) data were obtained at the start and end of each water regime treatments. At the end of the test, plants were harvested individually to measure their seed-cotton yield. In 2014, plant leaf area was calculated by applying a non-destructive method developed by Carvalho et al. [18] consisting in measuring the length of the central vein of main stem leaves and counting the number of leaves in the related branch. In 2015, plant leaf area was estimated using a linear regression of PLA on PH developed with 2014 data (PLA=0.5083*PH-0.0708; R2=0.92877).

**Table 1. Treatment specifications for the water economy study evaluating the effects of one-time exposure to irrigation at different phenological stages; match-head square (MH) to first bloom (FB), FB to mid bloom (MB), MB to first open boll (OB)**

| | Phenological stages | | | |
|---|---|---|---|---|
| **Treatments** | **MH-FB** | **FB-MB** | **MB-OB** | **OB-Harvest** |
| Water-Stressed Control | 0.5 L $d^{-1}$ | 0.75 L $d^{-1}$ | 0.75 L $d^{-1}$ | 0.75 L $d^{-1}$ |
| Full irrigation MH-FB | 1.6 L $d^{-1}$ | 0.75 L $d^{-1}$ | 0.75 L $d^{-1}$ | 0.75 L $d^{-1}$ |
| Full irrigation FB-MB | 0.5 L $d^{-1}$ | 2.40 L $d^{-1}$ | 0.75 L $d^{-1}$ | 0.75 L $d^{-1}$ |
| Full irrigation MB-OB | 0.5 L $d^{-1}$ | 0.75 L $d^{-1}$ | 2.40 L $d^{-1}$ | 0.75 L $d^{-1}$ |
| Date range of stages 2014 | May 8- May 29 | May 30-Jun 19 | Jun 20-Jul 10 | Jul 11-Aug 14 |
| Date range of stages 2015 | May 14-Jun 5 | Jun 6-Jun 23 | Jun 24-Jul 17 | Jul 18-Jul 20 |

Weather conditions during the studies, which are best summarized by the daily variation of reference potential evapotranspiration (RPET), were measured by an automated field weather station located approximately 100 m east of the Drought Tolerance Laboratory (Fig. 1). RPET was calculated at hourly steps using the Penman-Monteith equation and applying the reference standard method described by Pereira et al. [19]. Experimental data (sums, averages, standard deviations, and coefficients of variation) were summarized using Excel 2010 (Microsoft Corporation, Redmond, WA) and statistical analyses including ANOVA, mean separations, and contrasts were performed using SAS 9.2 (SAS Institute, Cary, NC).

## 3. RESULTS AND DISCUSSION

Weather conditions during the test period in 2014 and 2015 were different (Fig. 1). While the progression of RPET during the MH-FB stage was smoothly increasing with small daily variations in 2015, there were spikes of high evaporative demand early and about half-way during this development stage in 2014. A spike of high evaporative demand also occurred in 2014 at the start of the first bloom to mid bloom stage but then followed by smooth increase towards the end of this stage. Distinctly, the atmospheric evaporative demands during the first bloom to mid bloom and the mid bloom to first open boll stages were much lower in 2015 than in 2014, due primarily to cloudiness and high air humidity (data not shown).

Plant leaf area (PLA) at the start of tests (MH) was uniform among treatments in both years with the exception of the irrigation FB-MB and MB-OB treatments in 2015, which were both 15% greater than the control (Table 2). The water-deficient control plants increased PLA 3.78 and 2.62 fold during the MH-FB phase of vegetative development in 2014 and 2015, respectively, but did not exhibit any change thereafter during the fruit growing reproductive phase. Test plants not subjected to full irrigation during the MH-FB stage exhibited comparable PLA increases comparable to the control in both years ranging from 3.22 to 3.56 fold in 2014 and from 2.47 to 2.67 fold in 2015.

PLA growth increased 5.11 and 4.08 fold when full irrigation was applied during MH-FB in 2014 and 2015, respectively; 35 and 56% greater PLA than the control in 2014 and 2015, respectively (Table 2). This increased PLA of the irrigated MH-FB treatment over the control was maintained during the FB-MB stage (32 and 56% larger PLA than the control in 2014 and 2015, respectively), also maintained (54%) during MB-OB in the less evapotranspiration demanding 2015, but lost due to leaf senescence during this late stage in the high evapotranspiration demanding 2014 (Fig. 1).

PLA growth increased 2.09 and 1.54 fold when full irrigation was applied during FB-MB in 2014 and 2015, respectively; 81 and 58% greater PLA than the control in 2014 and 2015, respectively (Table 2). This increased PLA of the irrigated MH-FB treatment over the control was maintained (57%) during MB-OB in the less evapotranspiration demanding 2015, but lost due to leaf senescence (21% decrease from MB to OB stage) during this late stage in the high evapotranspiration demanding 2014 (Fig.1).

Full irrigation applied during MB-OB did not increase PLA in 2014 due to a high atmospheric evaporative demand, but it increased PLA 1.31 fold in the less evaporative demanding 2105 (Table 2). PLA of plants under this late irrigation treatment in 2015 was 49% higher than the water deficient control.

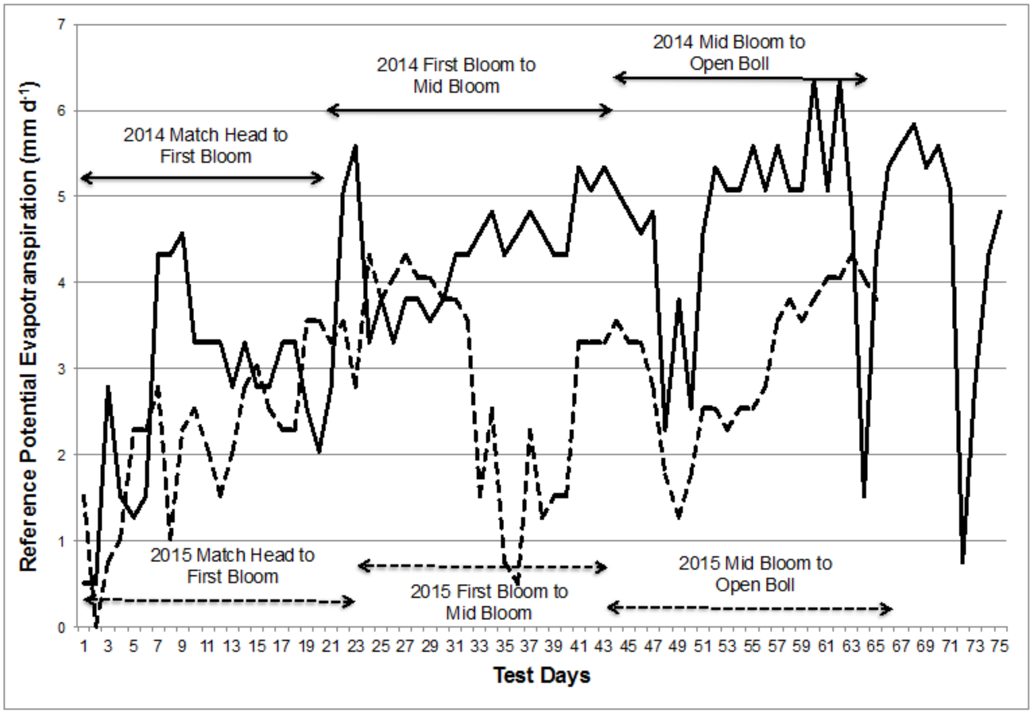


**Fig. 1. Progression of reference potential evapotranspiration (mm d-1) during the phenological treatment periods in 2014 and 2015.**

Overall, all irrigation treatments exhibited significant increases in PLA over the water-deficient control. The decrease of leaf area growth in cotton with limiting water supply is well documented [8,20,21,22,23,24,25,26]. Full irrigation increased PLA, but its impact depended on the development stage and the environmental conditions. The largest impact of full irrigation on PLA occurred when applied during the pre-bloom vegetative phase; about 4 to 5 fold increase. When applied at a later post-first bloom reproductive stage, the impact of full irrigation was somewhat decreased; about 1.5 to 2 fold increase during the FB-MB stage and further decreased to none to 1.3 fold during the MB-OB stage, with the higher impacts associated with a lower atmospheric evaporative demand. The decreasing post-first bloom trend impact of irrigation on PLA can be explained by a decreasing potential production of new leaves as plants began to allocate more photosynthetic substrate to fruit growth than to vegetative growth; a long recognized cotton growth characteristic [27,28,29,30].

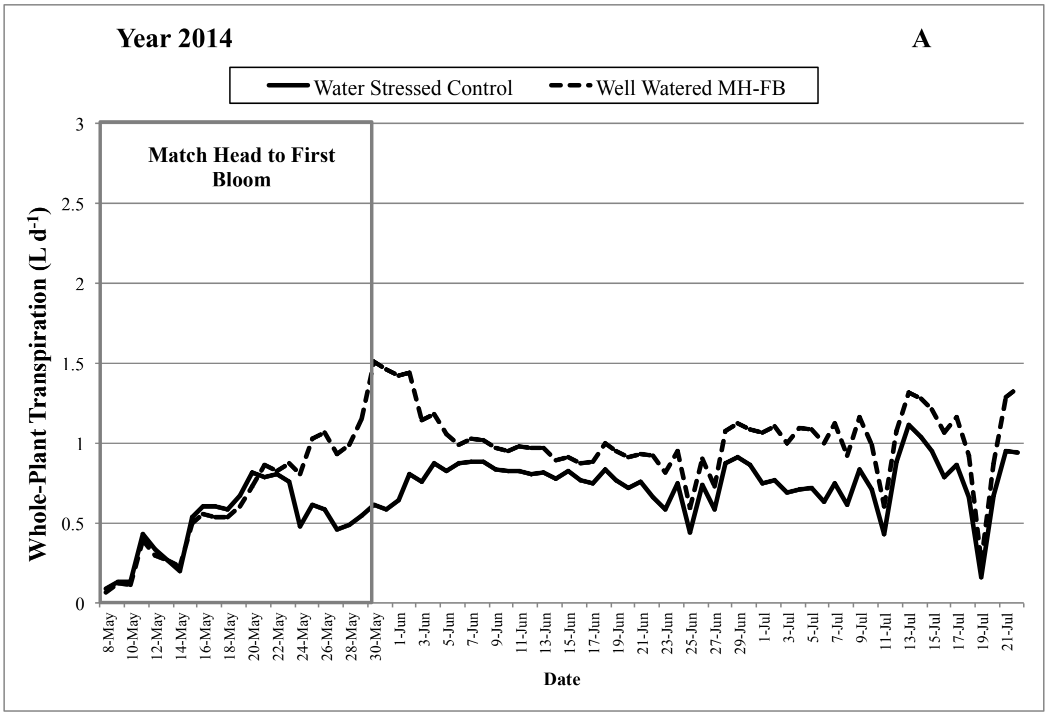
Progressions of DWPT (daily whole-plant transpiration) during the span of the tests showed distinct patterns for each of the water regime treatments in both years (Figs. 2,3). Day-to-day variation of DWPT values throughout the tests resulted mostly from daily variations in weather conditions (Fig. 1), but variation trends over several days resulted from longer-term shifts in weather conditions and changes in PLA caused by leaf expansive growth, production of new leaves, and leaf senescence.

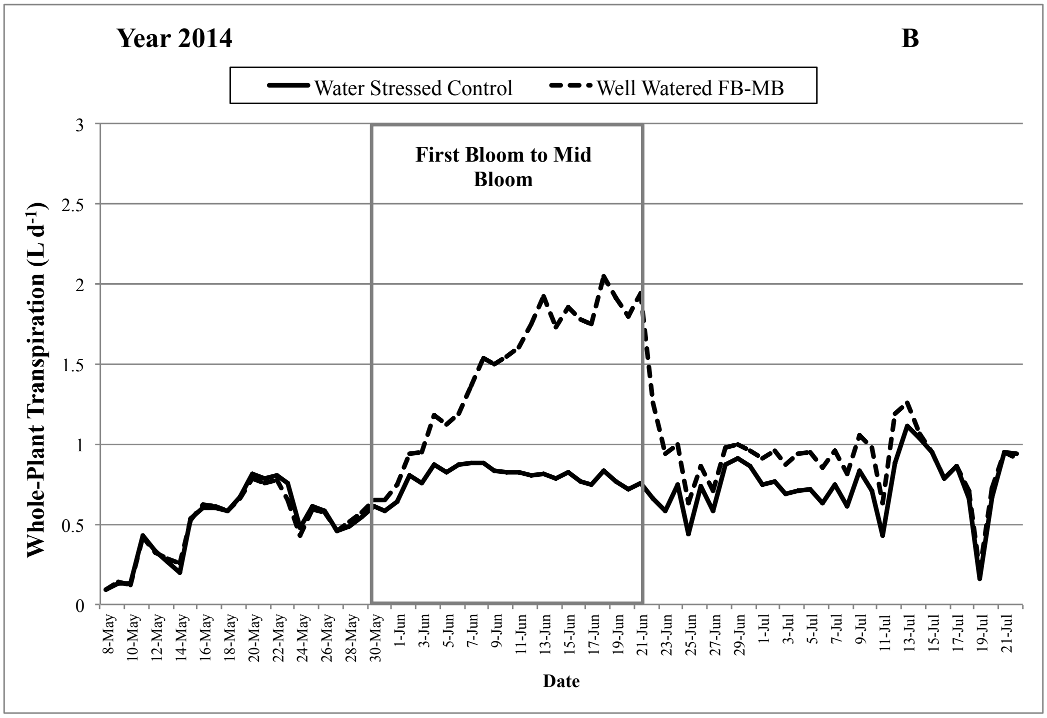
DWPT in water-deficient control plants exhibited a moderate increase during the first half to three quarters of the MH-FB phase of development in both years to about 0.6 and 0.75 L $d^{-1}$ in 2015 and 2014, respectively, and stabilized in both years to about 0.6 L $d^{-1}$ towards the end of the phase (Figs. 2,3). This increase in DWPT resulted from the combined effects of increasing leaf area per plant and increasing atmospheric evaporative demand (Table 2, Fig. 1). Thereafter until OB stage, DWPT in the water-deficient control fluctuated slightly around 0.75 and 0.5 L $d^{-1}$ in 2014 and 2015, respectively. Atmospheric potential evapotranspiration demands during FB-MB and MB-OB were higher in 2014 than in 2015 (Fig. 1). This leveling of DWPT values resulted primarily from a slowed down production of new leaves as water-deficient conditions inhibited leaf production [8,20,21,22,23,24,25,26] and as plants began to allocate more photosynthetic substrate to fruit growth than vegetative growth [27,28,29,30]. This slowed down of PLA growth in 2014 and 2015 is shown in Table 2.

All three full irrigation treatments showed marked increases in DWPT upon initiation of the irrigations (Figs. 2,3). The increases exhibited during MH-FB were somewhat comparable in 2014 and 2015 (Figs. 2A,3A) since the environmental conditions were not too dissimilar (Fig. 1). The increases in DWPT exhibited during the FB-MB and MB-OB phases, however, were much greater in 2014 than in 2015, as the atmospheric potential transpiration demands were much higher in 2014 than in 2015 (Figs. 1,2,3). Once full irrigation stopped at the end of the treatments applied, DWPT declined near the level of the water-deficient control plants within 4 to 6 days as the soil water storage was progressively decreased to the water-deficient control level (this response is only shown in Figs. 2A, 2B, 3A, and 3B for treatments applied during MH-FB and FB-MB).

**Table 2. Plant leaf area (PLA) at four phenological stages across the water-deficient control and three timed full irrigation treatments in 2014 and 2015. PLA for 2015 was estimated using the linear regression of PLA on plant height PH data obtained in 2014 (PLA=0.5083*PH-0.0708; R2=0.92877)**

| **Year** | **Plant leaf area ($m^2$)** | | | |
|---|---|---|---|---|
| | **Match head** | **First bloom** | **Mid bloom** | **First open boll** |
| **Treatment** | **Square (MH)** | **(FB)** | **(MB)** | **Boll (OB)** |
| **2014** | | | | |
| Water-Deficient Control | 0.09 a (b) | 0.34 b (a) | 0.37 c (a) | 0.38 a (a) |
| Irrigated MH-FB | 0.09 a (b) | 0.46 a (a) | 0.49 b (a) | 0.48 a (a) |
| Irrigated FB-MB | 0.09 a (d) | 0.32 b (c) | 0.67 a (a) | 0.53 a (b) |
| Irrigated MB-OB | 0.09 a (c) | 0.29 b (b) | 0.33 c (b) | 0.49 a (a) |
| **2015** | | | | |
| Water-Deficient Control | 0.13 b (c) | 0.34 c (b) | 0.36 b (ab) | 0.37 b (a) |
| Irrigated MH-FB | 0.13 b (c) | 0.53 a (b) | 0.56 a (a) | 0.57 a (a) |
| Irrigated FB-MB | 0.15 a (c) | 0.37 bc (b) | 0.57 a (a) | 0.58 a (a) |
| Irrigated MB-OB | 0.15 a (c) | 0.40 b (b) | 0.42 b (b) | 0.55 a (a) |





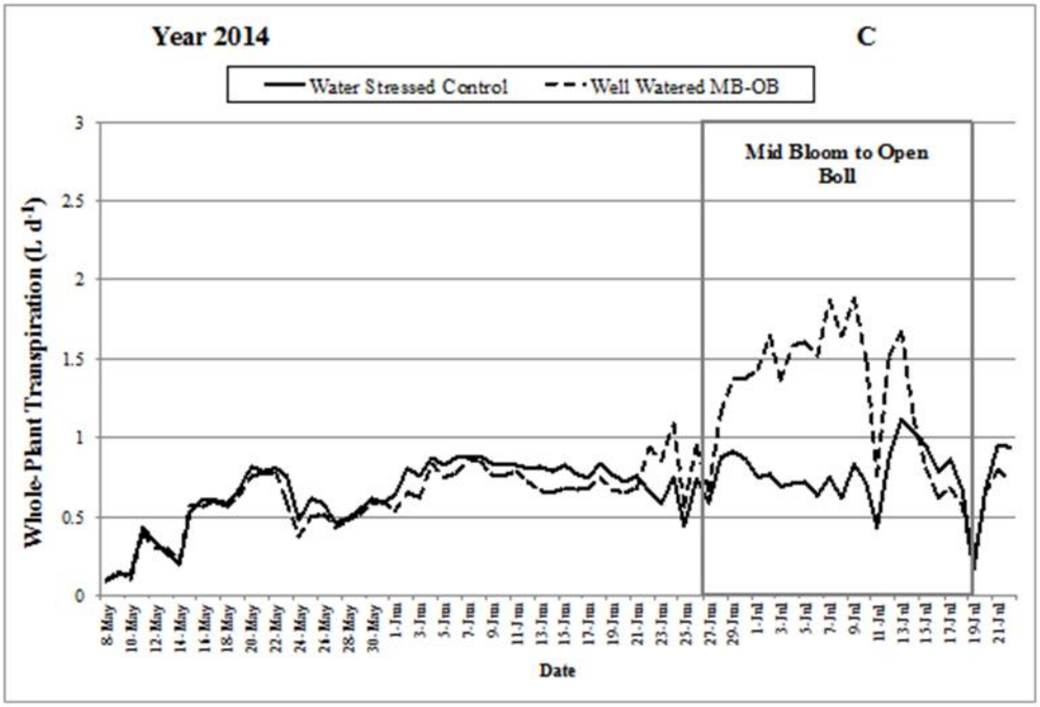
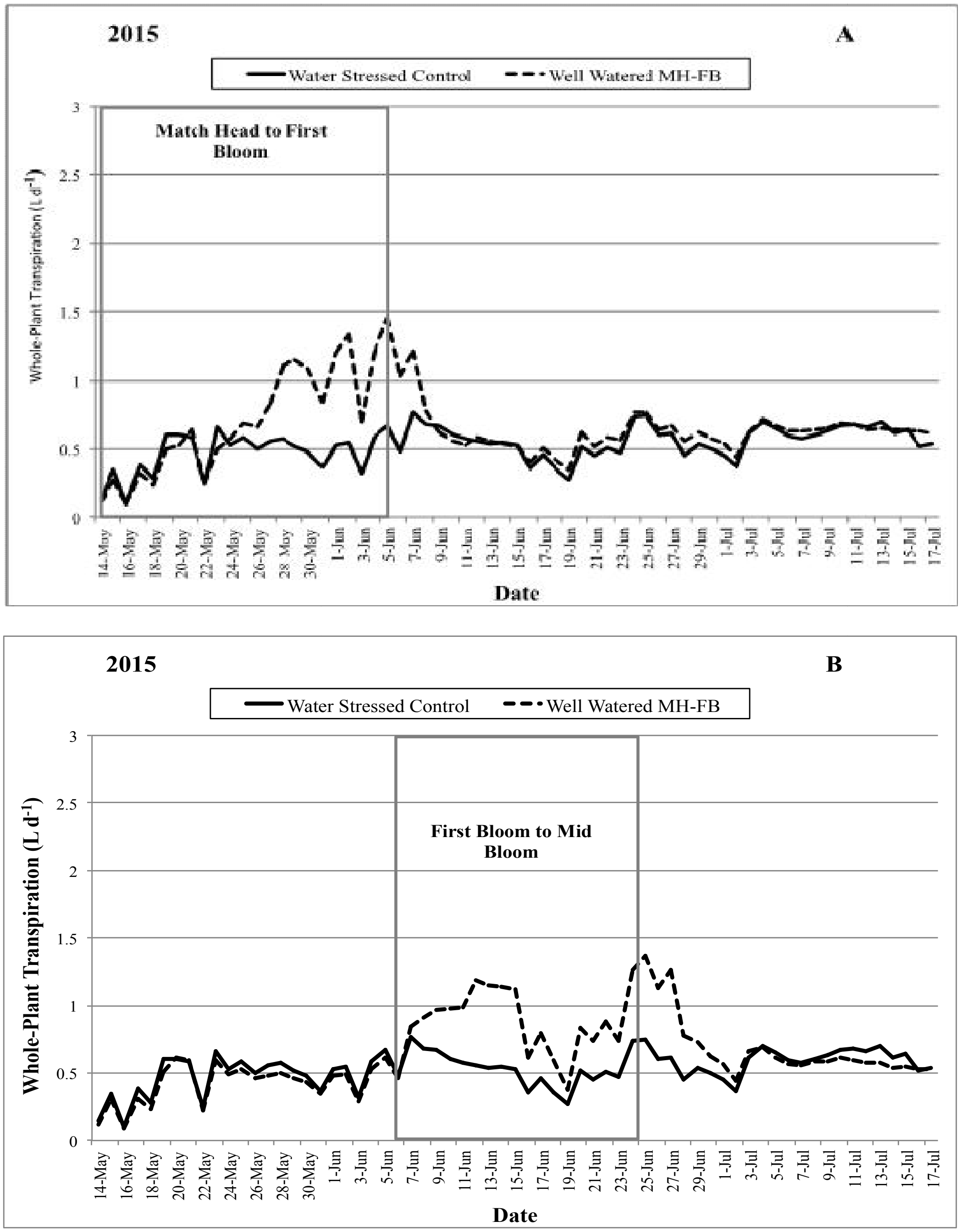


**Fig. 2. Average whole-plant daily transpiration (L day$^{-1}$) data (average of four replications) for the water-deficient control and the three full irrigation treatments during the 2014 season. (A) water-deficient control vs full irrigation from match-head square to first bloom; (B) water-deficient control vs full irrigation from first bloom to mid bloom; (C) water-deficient control vs full irrigation from mid bloom to first open boll**

The increases in DWPT exhibited by the full irrigation treatments resulted from marked increases in PLA (Table 2) and transpiration per unit leaf area (Table 3). Transpiration per unit leaf area increased 56, 38, and 77% in 2014 and 35, 52, and 15% in 2015 with the irrigation treatments applied during MH-FB, FB-MB, and MB-OB, respectively. Irrigation supply leads to plant rehydration, which in turn leads to enhancement of the production of new leaves, leaf expansion, and leaf conductance for transpiration associated with stomatal opening. It has been long established and documented that stomatal closure is the main cause of the reduction in leaf transpiration to water deficiency [1,31,32]. Conversely, these findings support the



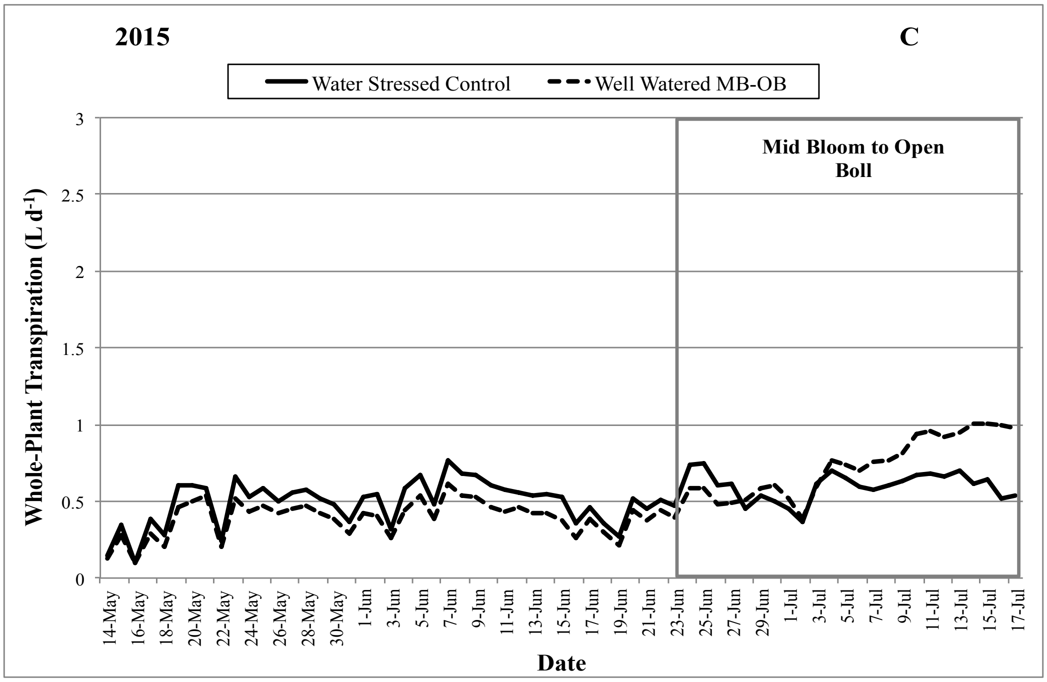


**Fig. 3. Average whole-plant daily transpiration (L day$^{-1}$) data (average of four replications) for the water-deficient control and the three full irrigation treatments during the 2015 season. (A) water-deficient control vs full irrigation from match-head square to first bloom; (B) water-deficient control vs full irrigation from first bloom to mid bloom; (C) water-deficient control vs full irrigation from mid bloom to first open boll**

theory that stomatal opening is the main cause of increase transpiration upon water stress alleviation by irrigation. An increase of leaf conductance upon plants rehydrating and regaining leaf turgor has been reported by Bielorai and Hopmans [1]. Consequently, increases in leaf conductance would lead to higher rates of transpiration per unit leaf area, as exhibited by all full irrigation treatments (Table 3). For the sake of simplification, the complex interconnected processes involved in the response of plants to irrigation can be described as follows. The increase in soil water content due to irrigation leads to an increased plant soil water uptake, increased water transport to leaves, regain of leaves' turgor as water transport to leaves is meets (and exceeds) the transpiration demand, and stomata opening in response to increased leaf turgor. More detailed descriptions of plant water dynamics in the form of simulation models have been published elsewhere [2,33,34,35,36,37].

The distinct patterns of DWPT shown by the water regime treatments were reflected on the cumulative whole-plant transpiration (CWPT) per phenological stage (Table 4). CWPT was increased 24 and 91% over the untreated water-deficient control with full irrigation applied during MH-FB in 2014 and 2015, respectively. After returning to the water-deficient water regime, CWPT of the treated plants remained higher than that of the control plants during the FB-MB and MB-OB stages in both years; 36 and 45% during FB-MB in 2014 and 2015, respectively, while 38 and 32% during MB-OB in 2014 and 2015, respectively. When full irrigation was applied during FB-MB, CWPT was increased 82 and 203% over the water-deficient control in 2014 and 2015, respectively. As was observed with the early full irrigation after it was stopped, a higher CWPT was observed during MB-OB; 37 and 46% in 2014 and 2015, respectively. CWPT was increased 80 and 52% over the water-deficient control when it was applied during MB-OB in 2014 and 2015, respectively. As was discussed above in relation to the DWPT responses, the increases in CWPT exhibited by the full irrigation treatments resulted from marked increases in PLA (Table 2) and leaf conductance for transpiration (Table 3) upon rehydration.

Upon termination of the irrigation treatment, CWPT remained higher (although to a lesser extent) than the water-deficient control during the following stages even after returning to the water deficient regime. It is apparent that this response is related to the lasting effect of increased PLA (Table 2) and, in the case of the stage immediately following the irrigation treatment, a delayed decline in leaf conductance while soil moisture is being depleted to the water-deficient control level (Figs. 2A, 2B, 3A, and 3B).

There were differences among experimental treatments in total plant dry biomass production in 2014 and 2105 (Table 5). In 2014, full irrigation applied during MH-FB and FB-MB increased total plant biomass growth 39 and 37%, respectively, over the water-deficient control, but it had no effect when applied late during MB-OB. In 2015, all full irrigation treatments increased total plant biomass growth over that of the water-deficient control; 42% when applied during MH-FB, 67% when applied during FB-MB, and 29% when applied during MB-OB. The larger responses exhibited during FB-MB and MB-OB in 2015 can be related to the lower atmospheric potential transpiration demands than those occurring during in 2014 (Fig. 1). Studying plant responses to evaporative flux, Ritchie and Burnett [38] found that cotton crops greatly decreased growth and above ground dry biomass production when grown under droughty rain-fed conditions.

The response of seed-cotton production per plant to full irrigation treatments was different between the years (Table 5). In 2014, although irrigation treatments applied during MH-FB and FB-MB indicated numerical advantages in seed-cotton production per plant over the water-deficient control, these differences were not statistical significant due to high coefficients of variation of experimental data. In 2015, however, full irrigation applied during MH-FB and FB-MB both increased seed-cotton yield per plant 49% over the water-deficient control, but it had no effect on seed-cotton yield when applied late during MB-OB. In the more stressful atmospheric environment of 2014, the number of bolls per plant with irrigation during MH-FB and FB-MB indicate a numerical advantage over the water-deficient control (47 and 50%, respectively) but these differences were not statistical significant. Under the less stressful atmospheric environment in 2015, the number of harvested bolls per plant increased 31 and 34% over that of the water-deficient control (20 and 21 vs. 15 average bolls per plant) when irrigation was applied during MH-FB and FB-MB, respectively. Snowden et al. [39] studied the effects of the timing of episodic drought and found that events during early flowering and peak bloom caused significant reductions in yields, and fruit retention.

The results presented above regarding the effect of irrigation timing on plant seed-cotton yield are in contrast with previous findings reported on an almost identical preliminary study [40] where only irrigation applied during MB-OB increased 41% seed-cotton production per plant over the water-deficient control. It is noted that atmospheric evaporative demands during that 2013 study were much higher than those occurring in 2014 and 2015. According to the data presented by Fernandez et al. [40], irrigation increased plant growth when applied during MH-FB, as indicated by increases in plant height, which would lead to a rapid onset of water stress upon stopping the irrigation. Furthermore, irrigation applied during FB-MB did not increase seed-cotton per plant over the water-deficient control since this treatment led to a lower average boll weight. Alternatively, irrigation applied late during MB-OB increased seed-cotton per plant by preventing a decrease in average boll weight.

Since CWPT integrates the effects of PLA and transpiration per unit leaf area over the phenological periods during which the full irrigation treatments were applied, this variable was found useful for expressing the alleviation of the moderate water deficit applied to the test plants. Linear regressions of dry seed-cotton yield per plant on CWPT obtained by pairing 16 values (four water regime treatments x four replications) for both years 2014 and 2015 showed clear significant increasing trends with increasing values of CWPT from match-head square (MH) stage to first open boll (OB) stage (Fig. 4). The slopes of the linear regressions represent the average response of plant seed-cotton yield to changes in CWPT regardless of the timing of the full irrigation treatments applied to the test plants. Seed-cotton per plant increased 1.063 and 0.554 g per L of CWPT increase in 2014 and 2015, respectively. The increase in seed-cotton yield per plant resulting from irrigation was almost half lower in 2015 than in 2014, as a result of the lesser stressful environment (lower atmospheric transpiration demands) in 2015 than in 2014.

**Table 3. Average daily transpiration per unit leaf area across phenological stages for the water-deficient control and the three timed full irrigation treatments in 2014 and 2015. Phenological stages are: match-head square (MH) to first bloom (FB), FB to mid bloom (MB), and MB to first open boll (OB)***

| Year | Daily transpiration per unit leaf area (L $m^{-2}$) | | |
|---|---|---|---|
| | Phenological stages | | |
| **Treatment** | **MH-FB** | **FB-MB** | **MB-OB** |
| **2014** | | | |
| Water-Deficient Control | 1.634 b | 2.250 b | 2.235 b |
| Irrigated MH-FB | 2.549 a | 2.028 b | 2.451 b |
| Irrigated FB-MB | 1.797 b | 3.098 a | 2.011 b |
| Irrigated MB-OB | 1.786 b | 2.316 b | 3.947 a |
| **2015** | | | |
| Water-Deficient Control | 2.007 b | 1.498 b | 1.650 b |
| Irrigated MH-FB | 2.710 a | 1.387 b | 1.404 b |
| Irrigated FB-MB | 2.032 b | 2.277 a | 1.552 b |
| Irrigated MB-OB | 1.706 b | 1.262 b | 1.896 a |

**Means with different letters are significantly different at the 5% level.*

**Table 4. Cumulative whole-plant transpiration (CWPT) per phenological stage across the four timed irrigation treatments in 2014 and 2015***

| Year | Cumulative whole-plant transpiration per stage (L) | | |
|---|---|---|---|
| | Phenological stages | | |
| **Treatment** | **MH-FB** | **FB-MB** | **MB-OB** |
| **2014** | | | |
| Water-Deficient Control | 10.9 b | 17.3 c | 14.7 c |
| Irrigated MH-FB | 13.5 a | 23.5 b | 20.3 b |
| Irrigated FB-MB | 10.8 b | 31.5 a | 20.2 b |
| Irrigated MB-OB | 10.2 b | 15.5 c | 26.4 a |
| **2015** | | | |
| Water-Deficient Control | 10.7 b | 9.4 c | 14.5 b |
| Irrigated MH-FB | 20.4 a | 13.6 b | 19.2 a |
| Irrigated FB-MB | 12.1 b | 19.1 a | 21.2 a |
| Irrigated MB-OB | 10.8 b | 9.3 c | 22.1 a |

** Means with different letters are significantly different at the 5% level.*

**Table 5. Total dry biomass and seed-cotton per plant for the well watered control and the three timed water deficit treatments in 2014 and 2015***

| Treatment | 2014 | | 2015 | |
|---|---|---|---|---|
| | **Biomass** | **Seed-Cotton** | **Biomass** | **Seed-Cotton** |
| | **(g $plant^{-1}$)** | **(g $plant^{-1}$)** | **(g $plant^{-1}$)** | **(g $plant^{-1}$)** |
| Water-Deficient Control | 183 b | 59.0 a | 146 c | 45.1 b |
| Irrigated MH-FB | 254 a | 66.9 a | 207 b | 67.0 a |
| Irrigated FB-MB | 250 a | 76.2 a | 244 a | 67.1 a |
| Irrigated MB-CB | 202 b | 59.1 a | 189 b | 56.7 ab |

**Means with different letters are significantly different at the 5% level*

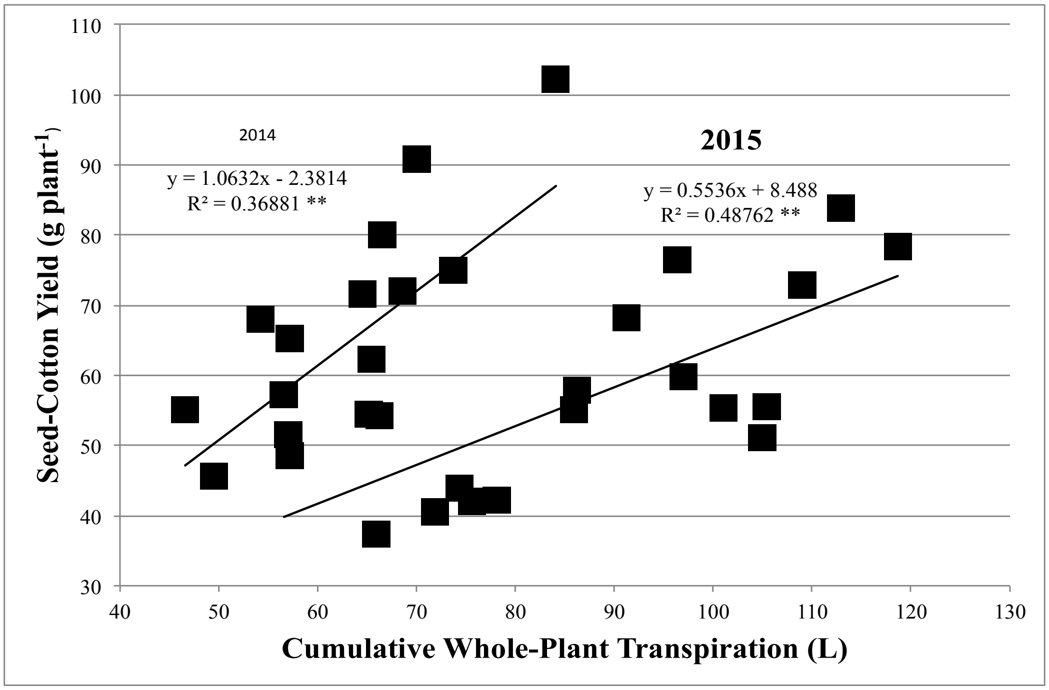


**Fig. 4. Seed-cotton per plant as a function of cumulative whole-plant transpiration from match-head square (MH) to first open boll (OB) during the 2014 and 2015 irrigation timing studies**

## 4. CONCLUSIONS

The two-year study conducted under rain-sheltered and controlled-irrigation conditions made it possible to quantify significant cotton whole-plant responses to irrigation applied at three different phenological stages. The weather conditions during the two-year study (2014 and 2015), as assessed by the atmospheric evapotranspiration demand, were not too different during the MH-FB stage, but they were distinctly different during the phase of boll growth and development from first bloom to first open boll. The atmospheric evaporative demands were much lower in 2015 than in 2014. This incidental difference in environments amplified the range of conditions under which the responses to irrigation were quantified.

With only few exceptions, the full irrigation treatments applied during different phenological stages had significant impact on plant's production of biomass, leaf area, and seed-cotton, as well as whole-plant transpiration and transpiration per unit leaf area. The responses to these plant variables showed to be different between years and this was attributed to environmental differences as assessed by the atmospheric evaporative demand, particularly from first bloom to first open boll.

The irrigation treatment applied during MH-FB in 2014 increased dry biomass per plant 39%, PLA 35%, CWPT 24%, transpiration per unit leaf area 56%, but had no significant effect on seed-cotton yield per plant, while in 2015 it increased dry biomass per plant 42%, PLA 56%, CWPT 91%, transpiration per unit leaf area 35%, and seed-cotton yield per plant 49%. The irrigation treatment applied during FB-MB in 2014 increased dry biomass per plant 37%, PLA 81%, CWPT 82%, transpiration per unit leaf area 38%, but had no significant effect on seed-cotton yield per plant, while in 2015 it increased dry biomass per plant 67%, PLA 58%, CWPT 203%, transpiration per unit leaf area 52%, and seed-cotton yield per plant 49%. The irrigation treatment applied during MB-OB in 2014 did not increased dry biomass per plant nor PLA, increased CWPT 80% and transpiration per unit leaf area 77%, but had no significant effect on seed-cotton yield per plant, while in 2015 it increased dry biomass per plant 29%, PLA 49%, CWPT 52%, transpiration per unit leaf area 15%, but had no significant effect on seed-cotton yield per plant.

Seed-cotton production per plant was increased 49% in 2015 when irrigation was applied during MH-FB and FB-MB, but not when it was applied late during MB-OB. These effects could not be confirmed in 2014, although not significant numerical differences due to experimental data variation were pointing to comparable effects. The slope of the linear regression of seed-cotton on CWPT, which represents the overall impact of irrigation on plant seed-cotton production regardless of their timing, showed that seed-cotton per plant increased 1.063 and 0.554 g per L of CWPT increase in 2014 and 2015, respectively. This difference, which resulted from the less stressful environment in 2015, illustrates the effect of environmental conditions affecting the overall response of plant seed-cotton production to irrigation.

## COMPETING INTERESTS

Authors have declared that no competing interests exist.

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