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Physiological Response of Cotton to High Night Temperatures

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ABSTRACT

Variable yields of cotton (*Gossypium hirsutum* L.) have been mostly attributed to high day temperatures. However, high night temperatures seem to play a major role due to their effect on respiration by affecting the carbohydrate supply for plant growth and yield. Little is known about the effect of night temperatures on the metabolism of field-grown cotton. This study evaluated the effect of different periods (weeks) of high night temperatures on leaf respiration and photosynthesis, leaf carbohydrate concentration, and fiber yield as determined by the fiber weight per seed. Night temperatures were elevated daily for 4 hours during flowering and boll development and their effect compared with ambient conditions. Results showed that short periods of one week of high night temperatures in the field in 2002 and 2003 had little effect on respiration, whereas the longer period of 4 weeks in 2004 caused a significant increase in respiration. There was also no effect of high night temperatures on respiration of plants cultivated under growth room conditions. Photosynthesis and the leaf carbohydrate content were not affected by the night temperature regimes in either environment. There was a significant increase in boll abscission by the second week of high night temperature treatment under growth room conditions followed by compensation. The only component of yield affected by high night temperature was fiber per seed which would suggest less available carbohydrate. Overall, the high night temperatures had some small effect on respiration, no effect on photosynthesis, and resulted in a decrease in fiber weight.

Keywords: boll abscission, fiber, *Gossypium hirsutum*, respiration, temperature stress

INTRODUCTION

Cotton (*Gossypium hirsutum* L.) is a major row crop in the United States and suffers from extreme yield variability from year to year. These yield variations have been attributed to genetics, management practices, and unfavorable weather conditions (Lewis *et al.* 2000; Robertson 2001) with high temperature considered to be the main environmental factor contributing to reduced yields (Oosterhuis 1994). Although the optimum temperature for cotton growth is between 20 and 30°C (Reddy *et al*. 1991), higher than optimum temperatures often take place in the U.S. Cotton Belt during flowering and boll development, thereby compromising the reproductive efficiency of the crop (Ashraf *et al*. 1994; Reddy *et al*. 2004). Furthermore, Oosterhuis (1994) reported that high night temperatures may be the major contributing factor for yield reduction because of their effect on cotton respiration.

Respiration of growth-room cotton increased twofold with night temperatures of 37°C (Law and Crafts-Brandner 1999). Similarly, Salvucci and Crafts-Brandner (2004) reported that respiration of cotton increased with a Q_{10} (the rate of change of a biological reaction as a consequence of increasing the temperature by 10°C) of 1.86 at night temperatures between 28 and 42.5°C. Elevated respiratory rates not only deplete photoassimilates (Reynolds *et al*. 1990), but also decrease the supply/demand ratios for photosynthates (Reddy *et al*. 1997); therefore, more carbohydrates are utilized by the high respiratory rates at the expense of plant and boll growth (Reddy *et al*. 1996). Under high respiratory rates, fewer carbohydrates are translocated to the developing bolls, the rates of cellulose synthesis during the initial stages of fiber formation decrease and yield declines (Ehlig 1986; Gipson 1986).

How high night temperatures affect plant metabolism and rates of plant growth, boll development, and ultimately yield of field-grown cotton is not clear. Previous studies altered both day and night temperatures without holding day temperatures constant to assess the effect of night temperatures alone. We hypothesize that the shortage of carbohydrate and metabolic energy caused by increased rates of respiration under high night temperatures, with constant day temperatures, result in decreased plant growth and carbohydrate flow to the developing bolls, thus increasing boll abscission and decreasing yield. The objective of this study was to evaluate the effects of periods of high night temperatures on important plant physiological processes such as photosynthesis and respiration, as well as on the plant carbohydrate supply and yield of growth room and field-grown cotton.

MATERIALS AND METHODS

Arrangement of the experiments under field and growth room conditions

Three field experiments were carried out in 2002, 2003 and 2004 on a Captina silt loam (fine-silty, thermic Typic Fragiudults), at the University of Arkansas Agricultural Research and Extension Center in Fayetteville, Arkansas. The early maturing cotton cultivar Suregrow 215BR was sown in mid May (2002 and 2004) and early June (2003) at a row spacing of 0.9 m with a population of 10 plants m^{-1}. Plots were 5 × 2.7 m. Shelters (width × length × height, 4 × 5 × 1 m) were constructed from 2.5-cm i.d. schedule-80 PVC pipes to support a 6-mil transparent plastic covering over the top and elongated sides of the plot, with the ends opened for air flow, for use in elevating temperatures.

Treatments consisted of elevated night temperatures (i.e., temperatures raised ~ 6 to 9°C depending on given ambient conditions) and a control of ambient night temperatures (**Table 1**), with

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three replications. To impose the treatments, ambient temperatures were elevated with one heavy duty factory heater (3VU34 Dayton Electric Co., Niles, IL) per plot. The heaters forced warmed air up the middle two covered rows of the plots. Climatic conditions in each plot were monitored every 15 min with Watchdog sensors (Spectrum Technologies Inc., Plainfield, IL) models 100 and 150 for temperature and relative humidity (RH), respectively. The Watchdog sensors were protected by radiation shields (Radiation Shield 3663, Spectrum Tech. Inc., Plainfield, IL) and positioned 1 m from both ends of the plot at mid canopy. Once the plastic covers were drawn over the top and lateral sides of the PVC shelters at night, the treatments were imposed for 4 hours from sundown at approximately 8:00 p.m. until midnight, after which, the plastic covers were removed. The duration of the temperature treatment, was determined by previous monitoring of the night ambient conditions, which remained high until midnight and started to drop significantly thereafter. In 2002 and 2003, treatments commenced during the third week of flowering and were imposed for 1 and 2 weeks, respectively. In 2004, treatments were initiated in the second week of flowering and were imposed for 4 weeks.

In 2004, a growth room study using the same cotton cultivar Suregrow 215BR was sown in 2.5-L pots filled with soilless horticulture medium (professional growing mix, Sun Gro Horticulture, Bellevue, WA). Initially, all the plants were grown at 30/24°C with a RH of 75%, and 12-h photoperiod. The growth chambers (Conviron, model PGW36, Pembina, ND) were supplied with incandescent and fluorescent lights giving about 800 μmol m^{-2} s^{-1} of photosynthetically active radiation. Water and half-strength Hoagland's nutrient solution (Hoagland and Arnon 1950) were applied twice a week before and after treatment initiation. One week after first flower, plants were assigned to each night temperature treatment and transferred to different growth chambers. The night temperatures imposed were 24°C (control) and 33°C (elevated temperature treatment). These temperatures were chosen to mimic the average ambient, and maximum high night temperature achieved in the field studies. Day temperatures remained at 30°C. Each treatment consisted of six replications. Treatments were imposed for 4 hours each night as in the field studies and the duration of the night temperature treatments was 3 weeks.

Photosynthesis and night respiration measurements

Gas exchange was measured at the end of each week of temperature treatment, except for week 1 in 2003, with a portable LICOR-6000 photosynthesis system (LI-COR Inc, Lincoln, NE). To determine photosynthesis, one reading from each of three plants per plot (field studies) and two readings per plant (growth room) were taken at midday (maximum solar radiation) from the uppermost fully expanded fourth main-stem node leaf from the terminal, which is the standard representative leaf used in cotton studies to sample for nutrient analysis. Dark respiration was measured during the night at about 9:30 p.m., with the same procedures.

Extraction of carbohydrates

Two different procedures were followed for extraction of carbohydrates from cotton leaves in 2003 and 2004. In 2003, the extraction and analysis of nonstructural carbohydrates followed the protocol of Hendrix (1993). Samples were also collected at mid day from the fourth main-stem node leaf at the end of each week-period of temperature treatment. Eighteen leaf disks, six per leaf, excised interveinally with a 0.45-cm diameter punch, were collected from three leaves in each treatment and transferred to 15-ml test tubes containing 80% (v/v) ice-cold ethanol and stored at -80°C until extraction. The reagents used in these assays were obtained from Sigma (Sigma Aldrich, St. Louis, MO). Unknowns were pipetted into microwell plates and measured with a spectrophotometer (Spectra Shell Reader, SLT Lab Instruments, Salzburg, Austria).

In 2004, carbohydrates were extracted from leaf dry matter instead of fresh leaf disks due to the discontinuity of a kit used in the previous extraction method. The procedure of Guo and Oosterhuis (1995) was followed using high performance liquid chromatography (HPLC) for carbohydrate analysis and quantification. Similarly, three leaf samples per plot were collected, kept on ice while in the field, immediately dried in an oven at 50°C for three days and ground and passed through a 2-mm screen. For the extraction, approximately 0.1 g of dried sample was weighed in 1.5-ml microcentrifuge tubes and mixed with deionized water at a 10:1 volume/weight basis. Tubes were transferred to a 70°C deionized water bath for 2 h. Tube contents were vortexed at about 20-min intervals to facilitate extraction. Samples were centrifuged at 13,000 rpm for 10 min at room temperature in order to facilitate collection of the extract. Extracts were collected with 1.5-ml transfer pipettes and passed through 1-ml C_{18} (non-polar), SCX (cation exchange column in H^+ form), and SAX (anion exchange column in acetate form) Alltech extract-clean columns (20500, 209800 and 209600, Alltech Associates, Deerfield, IL) by pushing with a 3-ml syringe at a flow rate of one drop (32 μl) per s. Columns were rinsed previously according to manufacturer instructions. Approximately 0.5 ml of eluate was collected in 1.5-ml microcentrifuge tubes and analyzed with HPLC.

Boll abscission

Boll abscission rates were evaluated only under growth room conditions. This evaluation included daily counts of the number of abscised bolls from all treatments and replications for the duration of the temperature treatments.

Yield

Seedcotton was hand-harvested from a 2-m length in the center of two middle rows in each plot for the determination of the fiber weight per seed (determined by dividing the weight of fiber by the number of seeds). The number of plants, green bolls, open bolls, seeds per unit area, and fiber weight per boll were also recorded (data not shown).

Experimental design and statistical analysis

The experimental design for all studies was a randomized complete block. Temperature response and weeks of treatment were analyzed as split-plots in time with temperature treatment as the whole plot and weekly sampling interval as the subplot. The field studies consisted of three (2002 and 2003) and four (2004) replications per treatment, whereas the growth room study consisted of six replications per treatment. Response variables were compared among treatments at each weekly sampling interval, and the effect of treatments over time (across weeks and across years with no significant treatment by sampling interval interaction) was analyzed with the Least Square Mean Difference (LSD) and the Proc Mix procedure from SAS software version 8.2 (SAS Institute Inc., Cary, NC), respectively. Comparisons of treatment means for weekly sampling intervals and treatment means compared over time were made at $\alpha \leq 0.05$.

RESULTS AND DISCUSSION

Respiration and photosynthesis response to high night temperatures

One or two weeks of elevated night temperatures, 2002 and 2003 respectively, had no significant effect on the respiration of cotton leaves compared with ambient night temperatures (**Table 2**). There was unfortunately a limit on how high the heaters could increase the temperatures in the shelters, and therefore the duration of the imposed temperatures was increased in subsequent years. Furthermore, the ambient temperatures of the field study in 2002 and 2003 were already high (**Table 1**) which could explain the lack of significant effect of the treatments. However, elevated night temperatures from the field study in 2004 increased respiration rates significantly after 2, 3 and 4 weeks. The overall mean increase in respiration for the 4-week period of high night temperatures in 2004 was also significant (P=0.001). Contrary to what we expected, high night temperatures had no significant effect on respiration of cotton leaves after three weeks of exposure under growth room conditions

Table 1 Recorded night and day temperatures under field conditions during the three-season night temperature study, Fayetteville, AR.

	Average temperatures								Average night temperature by period
	Week one		Week two		Week three		Week four		
	Night[z]	Day	Night	Day	Night	Day	Night	Day	
	°C								
2002									
Ambient	23	28							23
Elevated	28	28							28
2003									
Ambient	25	30	24	27					24
Elevated	33	30	32	27					33
2004									
Ambient	21	---[y]	18	---	21	---	22	---	21
Elevated	26	---	23	---	29	---	29	---	27

[z] Average recorded night temperatures for imposition period from 8:00 p.m. until midnight
[y] Lost temperature data

Table 2 Night respiration measured after each week-period of ambient and elevated night temperatures under field and growth room conditions, Fayetteville, AR.

Treatment	Week				Mean[z]	P value[y]
	One	Two	Three	Four		
	μmol CO_2 m^{-2} s^{-1}					
2002						
Ambient	2.75 a[x]					
Elevated	2.32 a					
2003						
Ambient	--[w]	3.01 a				
Elevated	--	3.65 a				
2004						
Ambient	1.18 a	1.05 b	1.19 b	1.12 b	1.14 b	
Elevated	1.76 a	2.45 a	2.56 a	1.76 a	2.13 a	0.001
Growth room (2004)						
Control	0.94 a	1.13 a	1.09 a		1.05 a	0.75
Elevated	0.80 a	1.31 a	1.16 a		1.09 a	

[z] Effect of night temperature treatments over time
[y] P value for the effect of night temperature treatments over time
[x] Means followed by the same letter within a column and underlined study are not significantly different (P≤0.05)
[w] Not measured

(**Table 2**). These results are not in agreement with Salvucci and Crafts-Brandner (2004) and Bunce and Ziska (1996) who reported on the sensitivity of respiration in cotton and soybean leaves to both elevated night temperatures and CO_2 levels under controlled growth conditions. Furthermore, no report of the response of cotton to elevated night temperatures under field conditions is available, and our research is the first to attempt to show the effect of elevated night temperatures alone in the field on cotton despite the difficult problems of conducting such field work in a variable environment.

Although we observed an increase in the respiration of cotton with high night temperatures in one out of three years, the fact that this increase was only significant in the field study may indicate that growth conditions along with night temperature fluctuations (**Table 1**) played a major role. We hypothesize that perhaps exposure to a constant high night temperature, as happened in the growth room study, resulted in acclimation and therefore no significant effect on respiration could be observed. Previous studies in potato and citrus roots reported acclimation of respiration as an effect of exposure to increased temperatures after 7 and 4 days respectively, all under controlled conditions (Bryla *et al*. 1997; Illeperuma *et al*. 1998). Similarly, Bunce (2007) reported the acclimation of soybean leaf respiration, and hence no differences in respiration rates when measured in long-term growth temperatures of 20, 25, and 30°C, also under controlled growth conditions. Our results showed that the respiration of field-grown cotton can be affected by the high night temperature conditions and also by the duration of the night temperature stress. This was observed in the field study in 2004 where there was a greater effect on respiration with average elevated night temperatures of 27°C (6°C above ambient) over 4 weeks compared to that under 33°C (average 8°C above ambient) in 2003 for 2 weeks only (**Table 2**). Furthermore, it is thought that the practical difficulty in imposing temperature treatments in the field resulted in inadequate replications to detect significant differences in respiration due to the elevated night temperatures.

The photosynthetic activity of field-grown cotton leaves, following high night temperatures, did not show the same response of respiration to high night temperatures (**Table 3**). There are several reports of high day temperatures on photosynthesis in cotton, but only limited work on the effect of high night temperatures. Photosynthesis, post exposure to the second week of treatments, decreased significantly (P≤0.05) in the 2003 study coincident with the highest temperature season (**Table 1**). This response could have resulted from a combined high night and high day temperature effect on photosynthesis. No treatment differences were observed in the 2002 and 2004 seasons where both day and night temperatures were milder compared to the 2003 season (**Table 1**). Overall, a small numerical trend was evident for the elevated night temperature treatments to decrease photosynthesis compared with the control both under field and growth room conditions (**Table 3**). Previous reports have also shown no effect of night temperatures on the photosynthetic activity of lettuce (*Lactuca sativa* L.), tomato (*Lycopersicum esculentum* L.) and soybean (*Glycine max* (L.) Merr.) (Frantz *et al*. 2004). The lack of photosynthesis response under high night temperatures in the 2002 and 2004 studies could probably be attributed to favorable day temperature conditions that allowed compensation for the night temperature stress; conversely, we expected an effect on photosynthesis due to the energy loss from the elevated respiration.

Table 3 Photosynthesis after each week-period of ambient and elevated night temperatures under field and growth room conditions, Fayetteville, AR.

Treatment	Week				Mean[z]	P value[y]
	One	Two	Three	Four		
	---------- µmol CO_2 m^{-2} s^{-1} ----------					
2002						
Ambient	31.70 a[x]					
Elevated	30.67 a					
2003						
Ambient	--[w]	24.77 a				
Elevated	--	21.07 b				
2004						
Ambient	28.01 a	24.22 a	31.71 a	29.92 a	28.46	0.45
Elevated	29.66 a	24.44 a	28.85 a	27.14 a	27.52	
Growth room (2004)						
Control	12.47 a	16.24 a	17.12 a		15.28	
Elevated	13.42 a	15.00 a	16.42 a		14.94	0.53

[z] Effect of night temperature treatments over time
[y] P value for the effect of night temperature treatments over time
[x] Means followed by the same letter within a column and underlined study are not significantly different (P≤0.05)
[w] Not measured

Table 4 Sugar concentration in cotton leaves after each week-period of ambient and elevated night temperatures under field conditions, Fayetteville, AR.

Sugar	Treatment	Week				Mean[z]	P value[y]
		One	Two	Three	Four		
		---------- mg g^{-1} ----------					
2003							
Glucose	Ambient	4.24 a[x]	2.13 a			3.18	0.38
	Elevated	2.29 a	1.21 a			1.75	
Fructose	Ambient	4.91 a	3.50 a			4.21	0.26
	Elevated	2.21 a	2.16 a			2.18	
Sucrose	Ambient	13.81 a	11.48 a			12.65	0.46
	Elevated	12.04 a	8.48 a			10.26	
2004							
Glucose	Ambient	1.45 a	1.48 a	0.69 a	1.12 a	1.18	0.30
	Elevated	1.29 a	1.49 a	0.64 a	1.03 a	1.11	
Fructose	Ambient	0.79 a	0.80 a	0.38 a	0.53 a	0.62	0.71
	Elevated	0.71 a	0.85 a	0.40 a	0.49 a	0.61	
Sucrose	Ambient	2.29 a	1.66 a	0.32 a	2.41 a	1.67	0.02
	Elevated	1.42 a	0.97 a	0.40 a	2.59 a	1.34	

[z] Effect of night temperature treatments over time
[y] P value for the effect of night temperature treatments over time
[x] Means followed by the same letter within a column and underlined study are not significantly different (P≤0.05)

Effect of high night temperatures on carbohydrates

There was not significant effect of treatments, however, a consistent numerical trend of carbohydrate reduction in fourth-node leaves under elevated night temperatures was observed in the 2003 and 2004 field studies (**Table 4**). In 2003, numerically lower concentration of glucose, sucrose and fructose in fourth-node cotton leaves was observed under elevated night temperatures after 1 and 2 weeks of treatment exposure (**Table 4**). Likewise, the field study in 2004 showed no significant effects of high night temperatures on the sugar concentration in fourth-node cotton leaves at 1, 2, 3 or 4 weeks after treatment initiation, and neither in the 2004 growth room trial (data not shown). On the other hand, the overall effect of the 4-week period of elevated night temperatures in the 2004 field study significantly decreased sucrose concentration (P=0.02) in cotton leaves which coincided with the observed increase in night respiration (**Table 2**). Diurnal carbon metabolism in cotton plants responds to night temperatures, as well as to the temperatures experienced during the day (Warner *et al*. 1995); therefore, it is possible that the mild ambient night temperature conditions during the implementation of the 2004 trial plus the relatively small effect on photosynthesis may have helped to prevent a major loss in the carbohydrate concentration of fourth main-stem node leaves. As mentioned earlier, the practical difficulty of operating the necessary equipment for imposing the temperature treatments in this experiment under field conditions at night limited the number of replications and thus may have also contributed to the lack of a significant effect by elevated night temperatures on the sugar concentration of cotton.

Boll abscission

Rates of boll abscission in the growth room study increased significantly under high night temperatures during the second week of temperature treatment; in contrast, by the end of the third week, boll abscission under elevated night temperatures was not different from that under control night temperatures (**Table 5**). Again, it is possible that the subsequent acclimation to elevated temperatures helped to overcome the earlier effect of the high night temperature stress. The current results agree with the findings of Reddy *et al*. (1991) that showed high rates of fruit abscission in cotton plants grown at 35/25°C and 40/30°C compared to those at the optimum 30/20°C. However, in the two studies these authors conducted both day and night temperatures were changed and, therefore, could not determine the specific effect of elevated night temperature alone as was accomplished in the present study.

Fiber weight per seed

There was a consistent numerical trend each year under the elevated night temperature stress for a reduction of fiber weight per seed (**Fig. 1**), and this measurement was significantly lower across years (P=0.05) compared to that under ambient night temperatures. High night temperatures had also no significant effect on the number of bolls or seeds per unit area, or fiber weight per boll (data not shown).

Table 5 Cumulative boll abscission (based on daily counts) at the end of each week period of night temperature treatments under growth room conditions, Fayetteville, AR, 2004.

Treatment	Week			Mean[z]	P value[y]
	One	Two	Three		
	---------- # plant^{-1} ----------				
Control	0.00 a[x]	0.00 b	2.00 a	0.67	0.14
Elevated	0.67 a	2.00 a	2.00 a	1.56	

[z] Effect of the night temperature treatments over time
[y] P value for the effect of night temperature treatments over time
[x] Means followed by the same letter within a column are not significantly different (P≤0.05)

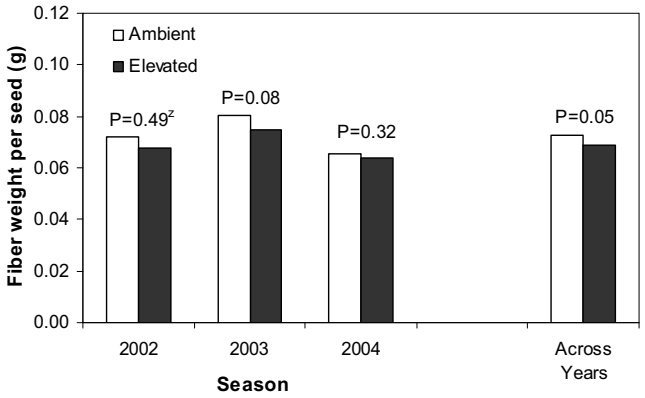

Fig. 1 Fiber weight per seed at harvest from three seasons of field studies. [z] P value for the effect of night temperature treatments overtime.

The results on fiber weight per seed demonstrate the effect of elevated night temperatures on cotton fiber production. Even though these trials were carried out in seasons where temperatures were not as high as usually occurs in the U.S. Cotton Belt, a significant detrimental effect of higher-than-optimum night temperatures was still observed over time on the fiber yield of field-grown cotton. The productivity of cotton is highly influenced by the temperatures that the crop experiences during the growing season (Warner and Burke 1993). Moreover, since the commercial production of cotton is located in areas that normally experience well above optimum temperatures at night, reductions in fruiting, boll development and yield would be expected (Gipson and Joham 1968). Furthermore, high temperatures accelerate the boll maturation period and, thereby, do not allow the bolls to reach their genetic potential (Reddy *et al*. 1996). This last observation was also confirmed in our field study in 2004. A visual evaluation (8 weeks after flowering) of the percentage of open bolls in the control and elevated night temperature treatments showed that about 40% of the bolls were open in the high night temperature plots compared to 20% in the control plots (data not shown).

CONCLUSIONS

Night temperatures have been reported to play a significant role in the physiology of field-grown cotton through their effect on respiration. However, in our studies high night temperatures only increased respiration in one out of three years and also not in the growth chamber. The significant effect of high night temperatures in 2004 may have been related to the lower ambient temperatures in that year allowing a larger difference compared to the high temperature treatment to be recorded. The longer 4 week period of stress in 2004 may have also been a contributory factor to the significant effect observed on respiration. The practical difficulty in imposing temperature treatments in the field probably resulted in inadequate replications to detect significant differences in respiration due to the elevated night temperatures.

Leaf photosynthesis was not sensitive to high night temperatures, perhaps due to a compensatory effect that also masked the effect on the carbohydrate balance of the plant. The consistent numerical trend across seasons and weeks within each season observed for decreased carbohydrate under high night temperatures was an indication of a compromised carbohydrate supply for plant growth and boll development. Furthermore, the observed effect on boll abscission confirmed that during the reproductive stage of cotton, the main sinks for carbohydrates are the developing bolls. Even though this effect was only observed during the second week of the high night temperature stress in our growth room experiment, these results still confirm that a restriction in the supply of carbohydrates results in fewer bolls, reducing the fiber yield and the productivity of the cotton crop. This effect needs to be addressed under field conditions in future studies.

Although the effect of elevated night temperatures on fiber weight per seed was not significant in individual seasons, the significant decrease in the fiber weight per seed across years indicated the deleterious effect of extreme night temperatures on fiber production. This decrease was important because fiber weight per seed, together with seed number per hectare, constitute the basic components of yield in cotton. The lack of significant effect of high night temperatures on fiber weight per seed in individual years was likely due in part to inadequate replications (due to equipment restrictions), shorter periods of high night temperature stress and to plant compensation during the remainder of the boll developing period associated with mild day temperatures. Nevertheless, the consistent numerical reductions in fiber weight per seed recorded each year support our hypothesis that high night temperatures are detrimental for yield of cotton and also cause yield variability due to its effects on respiration and the carbon balance of the plant.

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