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Cultivar variation in cotton photosynthetic performance under different temperature regimes

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Abstract

Cotton (*Gossypium hirsutum* L.) yields are impacted by overall photosynthetic production. Factors that influence crop photosynthesis are the plants genetic makeup and the environmental conditions. This study investigated cultivar variation in photosynthesis in the field conditions under both ambient and higher temperature. Six diverse cotton cultivars were grown in the field at Stoneville, MS under both an ambient and a high temperature regime during the 2006–2008 growing seasons. Mid-season leaf net photosynthetic rates (P_N) and dark-adapted chlorophyll fluorescence variable to maximal ratios (F_v/F_m) were determined on two leaves per plot. Temperature regimes did not have a significant effect on either P_N or F_v/F_m. In 2006, however, there was a significant cultivar × temperature interaction for P_N caused by PeeDee 3 having a lower P_N under the high temperature regime. Other cultivars' P_N were not affected by temperature. FM 800BR cultivar consistently had a higher P_N across the years of the study. Despite demonstrating a higher leaf F_v/F_m, ST 5599BR exhibited a lower P_N than the other cultivars. Although genetic variability was detected in photosynthesis and heat tolerance, the differences found were probably too small and inconsistent to be useful for a breeding program.

Additional key words: abiotic stress; gas exchange; maximum quantum yield; thermotolerance; water-use efficiency.

Introduction

Current climate change projections indicate substantial global surface temperature increases by the end of the 21st century. These temperature increases can result in productivity losses across the current US cotton production belt (Reddy *et al*. 2002, Pettigrew 2008). Although an optimum temperature range for cotton growth has been defined as 20 to 30°C by Reddy *et al*. (1991), as 23.5 to 32°C by Burke *et al*. (1988), and as 25.5°C for peak reproductive potential (Lokhande and Reddy 2014), there is no consensus yet on optimal temperature range for cotton as the plant response to temperature varies among developmental stages and different plant parts (Burke and Wanjura 2009). In addition, cotton is grown successfully in climate where temperatures often exceed 40°C, such as India and Pakistan (Oosterhuis and Snider 2011). Many times during a growing season in the mid-southern US cotton production belt, the daily maximum temperature exceeds the optimal range proposed by Reddy *et al*. (1991).

Although compromised reproductive growth may be the most obvious consequence resulting from high temperature stress (Pettigrew 2008, Snider *et al*. 2009), the photosynthetic capacity of the leaves can also be impacted (Perry *et al*. 1983, Feller *et al*. 1998, Crafts-Brandner and Law 2000, Crafts-Brandner and Salvucci 2000, 2004; Snider *et al*. 2013).

Discovering heat-tolerant cotton lines would be desirable in mitigating some of the damage inflicted by high temperature stress. Genotypic heat tolerance has been investigated for cotton with varying degrees of success. Neither Bednarz and van Iersel (2001) nor Pettigrew (2008) found genetic differences among a limited pool of cotton genotypes evaluated. However, Cottee *et al*. (2010) and Snider *et al*. (2010) were both able to document genotypic differences in heat tolerances between two cotton genotypes. The heat tolerant genotypes maintained higher P_N and chlorophyll (Chl) fluorescence variable to maximal ratio (F_v/F_m) under high temperature than did the more heat-susceptible genotypes. In addition, Snider *et al*. (2013) identified genotypic variability in PSII thermotolerance (the temperature causing a 15% decline in maximum quantum yield) among three commercial cotton cultivars. Heat stress has been shown to inhibit

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Abbreviations: C_i – intercellular CO_2 concentration; Chl – chlorophyll; DAP – days after planting; E – transpiration rate; F_0 – minimal chlorophyll fluorescence; F_m – maximal chlorophyll fluorescence; F_v – variable chlorophyll fluorescence; F_v/F_m – chlorophyll fluorescence variable to maximal ratio; g_s – stomatal conductance; P_N – net photosynthetic rate; WUE – water-use efficiency.

reproductive stress in cotton by decreasing the photosynthetic properties of the subtending source leaves (Snider *et al*. 2009). Despite the genotypic differences identified, Oosterhuis and Snider (2011) concluded that, as of yet, not enough genotypic heat tolerance variation has been identified to be exploited for improved thermotolerance by plant breeders.

Identifying genotypic variation in photosynthesis is important because photosynthesis is one of the basic physiological processes underpinning dry matter production and ultimately yield. Some genotypic differences in cotton photosynthesis have been identified (Rosenthal and Gerik 1991, Pettigrew *et al*. 1993, Pettigrew and Meredith 1994, 2012; Quisenberry *et al*. 1994, Pettigrew and Turley 1998, Clement *et al*. 2013), but additional differences could be useful in breeding efforts to improve seasonal crop photosynthesis and ultimately yield.

Overall improvement in photosynthesis and also tolerance to high temperature stress under field conditions would therefore be desirable traits. The objectives of this research were to investigate possible genetic differences in heat tolerance and photosynthesis for a diverse group of cotton genotypes when grown in the field under ambient and high temperature conditions.

Materials and methods

Cotton plot production techniques: Field studies were conducted at Stoneville, MS, during the 2006–2008 growing seasons. Six cotton cultivars were grown each year on a highly productive Bosket fine sandy loam (fine-loamy, mixed, thermic Mollic Hapludalf) soil. The six cultivars grown in 2006 were DPL 50, Dixie King, FM 800BR, PeeDee 3, SG 125, and ST 5599BR. The cultivars were chosen to represent a diversity of breeding programs, year of release, maturity, and leaf shape. For the years 2007–2008, DPL 445BR was substituted for SG 125 with the other five cultivars remaining the same. This cultivar substitution was made because we were not able to obtain SG 125 seed in 2007–2008. The cultivar subplots consisted of one row 7.62 m in length with a 1-m row spacing. There were a total of six cultivar subplots per each temperature treatment main plot. Two border rows were planted to separate the temperature main plots. Plots were planted on 28 April 2006, 1 May 2007, and 23 April 2008. Initially the plots were overseeded and then hand thinned at the second or third true leaf stage to a uniform density of 9 plants m^{-1} of row or approximately 97,000 plants ha^{-1}. Each spring, 112 kg(N) ha^{-1} was applied to the experimental area in a pre-plant application of a urea-ammonium nitrate solution. The experimental area was furrow irrigated (approximately 2.54 cm of water for each event) as needed each growing season to minimize moisture deficit stress. Irrigation was applied three times in 2006, two times in 2007, and three times in 2008. Recommended insect and weed control methods were applied each growing season as needed.

Temperature treatments: Half of the plots were exposed to ambient air temperatures (ambient) and the other half exposed to slightly warmer than ambient temperatures (heat). The warmer temperature regime was generated by placing 30-cm × 6-m *Redi-Heat* propagation mats (*Phytotronics*, *Inc*., Earth City, MO, USA) between the rows on 30-cm-tall × 30-cm-wide × 6-m long wooden racks as previously described (Pettigrew 2008). Eight mats were used per main plot. Mounting the mats on wooden racks allowed the furrow irrigation to flow underneath the mats. The heating mats were powered from early July through early September, a period corresponding to the stages of growth from early bloom through boll filling. Power supplied to the heating mats was controlled using *Redi-Heat R-FT4* thermostats (*Phytotronics*, *Inc*., Earth City, MO, USA) set at the thermostat's upper temperature limit of 38°C. These heating mats raised the canopy temperature of the heat plots approximately 1°C above the ambient temperature (Pettigrew 2008). Canopy temperatures in each temperature main plot were monitored and recorded every 30 min at an approximately 1-m height location in the canopy during the months of July and August in 2006 using *Hobo H8 Pro Temp* (*Onset Computer Corp*., Bourne, MA, USA) data loggers. These temperature sensor-equipped data loggers were mounted inside solar radiation shields at the previously mentioned 1-m canopy height.

Gas-exchange measurements were conducted on leaves from the plots using a *CI-310* portable photosynthesis system (*CID*, *Inc*., Camas, WA, USA). Measurements were taken on the youngest, fully expanded, disease-free, and sunlit leaves in each plot, typically the fourth leaf down from the apical terminal. All measurements were taken with the leaves oriented perpendicular to the sun with the PPFD reaching the leaf surface ≥ 1,600 μmol m^{-2} s^{-1}. Measurements were collected on two leaves per plot with the average of those two measurements used for later statistical analyses. The gas-exchange measurements were made from 94 to 98 d after planting (DAP) in 2006, 86 to 90 DAP in 2007, and 80 to 86 DAP in 2008.

Chl fluorescence: Following the gas-exchange measurements, dark-adaption cuvettes were placed on the same leaves used to measure gas exchange for subsequent Chl fluorescence determinations in 2006 and 2008. Leaves were dark adapted for at least 15 min prior to Chl fluorescence measurements. Dark-adapted Chl variable fluorescence to maximal fluorescence (F_v/F_m) ratios were measured using a *Hansatech Fluorescence Monitoring System* (*Hansatech Instruments Ltd*., Norfolk, UK) in 2006. In 2008, the F_v/F_m measurements were taken using an *Opti-Sciences OS1-FL Modulated Fluorometer* (*Opti-Sciences*, Hudson, NH, USA). Measurements were

collected on two leaves per plot with the average of those two measurements used for later statistical analyses.

Experimental design and data analyses: The experimental design utilized was a randomized complete block design with a split plot treatment arrangement. Temperature regimes were the main plots and cultivars were the subplots. There were six cultivar subplots randomly assigned within each temperature regime main plot for a total of 12 experimental units per replicate. The study consisted of five replicates. Statistical analyses were performed by analyses of variance (*PROC MIXED*; *SAS Institute*, USA) (Littell *et al*. 1996). The year 2006 was analyzed separately because a different collection of cultivars was utilized that year. Data from 2007 and 2008 were averaged together due to the consistency of the temperature and cultivar responses across the years. Temperature and cultivar means were averaged across each other when no significant temperature by cultivar interaction was detected. Means were separated by using protected LSD at the $P \leq 0.05$ level.

Results

Temperature: The heat treatment raised the average, maximum, and minimum canopy temperatures just under 1°C relative to the ambient temperature treatment (Table 1). These slight temperature increases were consistent with the temperature increase generated by the same canopy temperature elevating technique and system as previously reported from an earlier study (Pettigrew 2008).

Cultivar gas-exchange differences: The collections of cotton cultivars utilized in 2006 differed in their photosynthetic performance (Table 2). FM 800BR had the highest photosynthetic rate (P_N) and stomatal conductance (g_s) among the cultivars. FM 800BR is an okra leaf–type cultivar and the higher leaf P_N of this okra leaf–type cultivar is consistent with the results reported previously (Pettigrew *et al*. 1993). In contrast to the reduced g_s exhibited by the okra leaf–type genotype in the Pettigrew *et al*. (1993) study, FM 800BR demonstrated the highest g_s. Differences in stomatal behavior between the two studies may be related to the different genetic backgrounds in which the okra leaf trait was expressed.

Genetic differences in gas-exchange parameters were also detected among the second collection of cultivars utilized in 2007 and 2008 (Table 3). FM 800BR, in addition to the newly added cultivar DPL 445BR, exhibited the highest leaf P_N of the cultivars evaluated. The P_N of Dixie King, PeeDee 3, and ST 5599BR were all lower than that produced by either FM 800BR or DPL 445BR. DPL 50 had a more intermediate P_N. In contrast to 2006, no cultivar differences in g_s were observed during the 2007–2008 period.

Temperature by cultivar interaction: Despite the fact that there was not a significant temperature main effect ($P>F$ = 0.23) (data not shown) in 2006, there was a significant temperature regime by cultivar interaction ($P>F$ = 0.02) lurking behind the previously reported cultivar differences in 2006 (Table 4). The cultivar PeeDee 3 was responsible for this significant interaction as its P_N under the heat temperature regime was 15% lower than its P_N under the ambient temperature regime. None of the other cultivars demonstrated a significant photosynthetic difference between temperature regimes that year.

Table 1. Average canopy air temperatures (± SE, n = 5) measured at approximately 1-m height during the months of July and August as affected by two canopy air temperature (ambient and heat) in the year 2006.

Temperature regime	Temperature [°C]	Maximum temperature [°C]	Minimum temperature [°C]
Ambient	26.9 ± 0.02	33.6 ± 0.08	21.7 ± 0.08
Heat	27.5 ± 0.05	34.2 ± 0.10	22.4 ± 0.05

Table 2. Cultivar differences in gas exchange (± SE, n = 10) averaged across two temperature regimes at Stoneville, MS, in 2006. ns – not significantly different at the $P \leq 0.05$ level. C_i – intercellular CO_2 concentration; E – transpiration rate; g_s – stomatal conductance; P_N – net photosynthetic rate; WUE – water-use efficiency.

Cultivar	P_N [μmol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	C_i [μmol mol^{-1}]	WUE [μmol(CO_2) mmol^{-1}(H_2O)]	g_s [mmol m^{-2} s^{-1}]
DPL 50	22.49 ± 0.85	3.79 ± 0.53	344 ± 3	8.57 ± 2.10	193 ± 30
Dixie King	20.64 ± 0.79	4.13 ± 0.41	341 ± 2	6.64 ± 1.26	200 ± 25
FM 800BR	23.13 ± 0.69	4.67 ± 0.34	341 ± 2	5.35 ± 0.49	224 ± 19
PeeDee 3	20.05 ± 0.71	3.56 ± 0.36	343 ± 2	6.93 ± 1.05	153 ± 22
SG 125	21.54 ± 0.73	4.06 ± 0.66	341 ± 3	12.00 ± 6.22	194 ± 44
ST 5599BR	19.60 ± 0.71	3.86 ± 0.50	342 ± 2	8.51 ± 3.28	166 ± 24
LSD 0.05	1.76	0.61	4^{ns}	6.45^{ns}	41

Table 3. Cultivar differences in gas exchange (± SE, n = 20) averaged across two temperature regimes and the years 2007–2008 at Stoneville, MS. ns – not significantly different at the $P \leq 0.05$ level. C_i – intercellular CO_2 concentration; E – transpiration rate; g_s – stomatal conductance; P_N – net photosynthetic rate; WUE – water-use efficiency.

Cultivar	P_N [µmol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	C_i [µmol mol^{-1}]	WUE [µmol(CO_2) mmol^{-1}(H_2O)]	g_s [mmol m^{-2} s^{-1}]
DPL 445BR	23.67 ± 0.68	2.56 ± 0.11	341 ± 2	10.12 ± 0.66	137 ± 8
DPL 50	22.65 ± 0.78	2.59 ± 0.13	339 ± 2	9.83 ± 0.79	135 ± 12
Dixie King	22.07 ± 0.66	2.55 ± 0.16	340 ± 3	9.57 ± 0.60	130 ± 10
FM 800BR	23.64 ± 0.55	2.42 ± 0.18	345 ± 3	12.09 ± 1.50	131 ± 12
PeeDee 3	21.05 ± 0.89	2.45 ± 0.15	343 ± 3	9.28 ± 0.50	135 ± 13
ST 5599BR	21.76 ± 0.60	2.73 ± 0.10	342 ± 3	8.47 ± 0.36	143 ± 10
LSD 0.05	1.45	0.28^{ns}	5^{ns}	1.78	30^{ns}

Table 4. Cultivar differences in gas exchange (± SE, n = 5) for two temperature regimes at Stoneville, MS, in 2006. † – comparison of temperature regimes within a cultivar; ‡ – comparison of cultivars within a temperature regime; ns – not significantly different at the $P \leq 0.05$ level. C_i – intercellular CO_2 concentration; E – transpiration rate; g_s – stomatal conductance; P_N – net photosynthetic rate; WUE – water-use efficiency.

Temperature	Cultivar	P_N [µmol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	C_i [µmol mol^{-1}]	WUE [µmol(CO_2) mmol^{-1}(H_2O)]	g_s [mmol m^{-2} s^{-1}]
Ambient	DPL 50	22.34 ± 0.73	3.68 ± 0.80	342 ± 3	7.82 ± 1.90	178 ± 45
	Dixie King	19.34 ± 1.28	3.95 ± 0.80	340 ± 3	8.10 ± 2.44	184 ± 44
	FM 800BR	23.01 ± 0.60	4.82 ± 0.48	341 ± 1	5.22 ± 0.77	237 ± 24
	PeeDee 3	21.61 ± 0.74	3.73 ± 0.67	342 ± 2	7.57 ± 2.00	163 ± 42
	SG 125	20.16 ± 0.64	3.77 ± 1.28	341 ± 4	17.90 ± 13.94	159 ± 56
	ST 5599BR	18.74 ± 0.69	3.40 ± 0.88	342 ± 2	11.88 ± 6.50	140 ± 38
Heat	DPL 50	22.63 ± 1.63	3.91 ± 0.78	345 ± 5	9.33 ± 3.99	209 ± 45
	Dixie King	21.94 ± 0.59	4.32 ± 0.29	343 ± 3	5.19 ± 0.39	215 ± 27
	FM 800BR	23.25 ± 1.33	4.53 ± 0.52	342 ± 5	5.48 ± 0.71	212 ± 31
	PeeDee 3	18.47 ± 0.69	3.38 ± 0.36	343 ± 4	6.30 ± 0.88	142 ± 21
	SG 125	22.91 ± 1.02	4.35 ± 0.76	341 ± 4	6.10 ± 1.13	230 ± 66
	ST 5599BR	20.45 ± 1.20	4.32 ± 0.48	343 ± 4	5.15 ± 0.76	193 ± 28
	LSD 0.05 †	2.77	1.25^{ns}	8^{ns}	9.9^{ns}	62
	LSD 0.05 ‡	2.49	0.86	5^{ns}	9.1^{ns}	59

Table 5. Cultivar differences in chlorophyll fluorescence parameter (± SE, n = 10) averaged across two temperature regimes for the years 2006 and 2008 at Stoneville, MS. F_0 – minimal chlorophyll fluorescence; F_m – maximal chlorophyll fluorescence; F_v – variable chlorophyll fluorescence; F_v/F_m – chlorophyll fluorescence variable to maximal ratio. ns – not significantly different at the $P \leq 0.05$ level.

Year	Cultivar	F_v/F_m	F_0	F_m	F_v
2006	DPL 50	0.7754 ± 0.0096	209 ± 7	937 ± 16	728 ± 20
	Dixie King	0.7775 ± 0.0093	203 ± 7	919 ± 14	716 ± 18
	FM 800BR	0.7739 ± 0.0042	216 ± 3	958 ± 12	742 ± 13
	PeeDee 3	0.7786 ± 0.0100	217 ± 7	986 ± 16	769 ± 22
	SG 125	0.7977 ± 0.0078	199 ± 7	986 ± 16	787 ± 17
	ST 5599BR	0.8103 ± 0.0087	191 ± 6	1,017 ± 20	826 ± 24
	LSD 0.05	0.0193	15	40	46
2008	DPL 445BR	0.7607 ± 0.0032	419 ± 5	1,759 ± 19	1,340 ± 18
	DPL 50	0.7615 ± 0.0051	409 ± 6	1,725 ± 21	1,316 ± 23
	Dixie King	0.7581 ± 0.0057	420 ± 7	1,745 ± 21	1,325 ± 25
	FM 800BR	0.7671 ± 0.0048	431 ± 9	1,858 ± 31	1,428 ± 28
	PeeDee 3	0.7619 ± 0.0051	425 ± 5	1,796 ± 22	1,371 ± 25
	ST 5599BR	0.7725 ± 0.0059	408 ± 6	1,806 ± 29	1,398 ± 31
	LSD 0.05	0.0137^{ns}	17	64	68

Similar to the 2006 growing season, there was not a significant temperature response for P_N ($P>F$ = 0.98) during the 2007–2008 growing seasons (data not shown). There also was no significant temperature by cultivar interaction for P_N ($P>F$ = 0.42) during the 2007–2008 growing seasons (data not shown), which was in contrast to the significant interaction observed in 2006. The 2006 interaction was caused principally by the response of the cultivar PeeDee 3 to the different temperature regimes, however, the photosynthetic decline seen in 2006 for PeeDee 3 when grown under the heat temperature regime was not evident in either 2007 or 2008.

Chl fluorescence: No significant temperature regime main effect ($P>F$ = 0.98 in 2006 and 0.48 in 2008) or temperature by cultivar interactions ($P>F$ = 0.96 in 2006 and 0.26 in 2008) were detected for Chl fluorescence F_v/F_m ratios or the components that make it up during either years when Chl fluorescence measurements were taken (data not shown). Significant cultivar differences were detected in F_v/F_m during both 2006 and 2008 (Table 5). ST 5599BR had a greater F_v/F_m ratio than all the other cultivars in 2006 except for SG 125. In 2008, ST 5599BR again had the greatest F_v/F_m but it was only statistically greater than Dixie King. The greater F_v/F_m ratio for ST 5599BR came about principally due to its lower initial Chl fluorescence level (F_0) compared to most of the other cultivars. This greater F_v/F_m ratio for ST 5599BR contrasted with its lower P_N relative to most of the other cultivars (Tables 2, 3).

Discussion

Cultivar variation to temperature: In general, the minor temperature rise generated under field conditions by the heat treatment did little to impact photosynthetic performance of the leaves tested even though it was enough to produce a yield reduction (Pettigrew 2008). The exception to this was the response of the cultivar PeeDee 3. It was more sensitive to the photosynthetic (P_N) depression caused by the higher temperatures than the other cultivars in 2006. Unfortunately, this trend for PeeDee 3 was not observed in either 2007 or 2008. Similarly, Snider *et al.* (2013) also found inconsistency in genotypic variation for heat tolerance as a particular cotton cultivar (PHY 499) exhibited a greater PSII thermotolerance than two other cultivars in one environment but not a second. Snider *et al.* (2015) reported that photosynthetic heat tolerance could be affected by the developmental stage of the plant. Hall *et al.* (2014) also reported that younger cotton leaves had greater heat tolerance than older leaves possibly due to alterations in the fatty acids composition of the membranes. These finding could help to explain some of the inconsistency across environments for a suspected genetic heat tolerance trait, as there may have been subtle developmental or leaf age differences across the environments for the cultivars. Others have been able to detected genotypic differences in heat tolerance when they were able to raise canopy temperature to levels that were more extreme than that achieved in this study (Cottee *et al.* 2010, Snider *et al.* 2010). These studies either used controlled environmental chambers (Snider *et al.* 2010) or tents made out of polyethylene UV-stabilized film with an 18% shade value but also increased the relative proportion of diffuse radiation entering the canopy (Cottee *et al.* 2010) to increase the exposure temperatures. However, these temperature elevation techniques could also arguably created an environment even more artificial than the one created by the techniques utilized in this current study.

Genetic differences in photosynthetic parameters: The cultivar photosynthetic differences were more consistent throughout the duration of the study. Some of the genotypic differences were similar to those reported earlier, such as the superior P_N for the okra leaf–type cultivar (Pettigrew *et al.* 1993, Pettigrew and Meredith 2012). The cultivar ST 559BR exhibited lower P_N relative to the other cultivars, despite its consistently higher F_v/F_m ratio, an estimate of the maximal quantum efficiency of PSII. These data indicate genetic variability in some of the components that make up the photosynthetic process. This level of variation in the photosynthetic components hints at the possibility of being able to achieve even better photosynthetic performance through a more optimal grouping of photosynthetic components *via* appropriate genetic manipulation. However, it remains to be seen what level of heritability is associated with the genetic variability in these photosynthetic components.

Conclusions: Genotypic variation was demonstrated in photosynthetic performance and to a limited basis for possible heat tolerance. Unfortunately, the inconsistency and small magnitude of the variations limits the usefulness of the findings. Nonetheless, the mere existence of these variations offer promise for the discovery of greater variations if a larger segment of the *Gossypium* germplasm pool is explored. If greater variations could be discovered, these might prove useful to a cotton breeding program.

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