



Do genotypic differences in thermotolerance plasticity correspond with water-induced differences in yield and photosynthetic stability for field-grown upland cotton?



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ABSTRACT

To determine if cultivar differences in thermotolerance plasticity of photosystem II promote yield or photosynthetic stability when variability in both parameters is water-induced, the temperature response of maximum quantum yield of photosystem II (F_v/F_m) was evaluated for two cotton cultivars (FM 1944 GLB2 and PHY 499 WRF), at three times (squaring, first flower, and peak bloom) during the 2014 growing season, under five different irrigation regimes. The temperature inducing a 15% decline in F_v/F_m from the optimum (T_{15}) served as a measure of thermotolerance. Furthermore, during 2014 net photosynthesis (A_N) measurements coincided with T_{15} measurements; predawn water potential (Ψ_{PD}) was measured three days per week; and canopy temperature (T_C) was measured continuously. Yield was determined for both cultivars and all five irrigation regimes in 2013 and 2014 although significant irrigation effects were only observed during 2014. Thermotolerance, photosynthetic, and yield stability were determined using a regression approach to assess genotype \times environment interaction. Irrigation treatments significantly affected Ψ_{PD} and T_C , and large variability in thermotolerance (although all T_{15} values were well-above the observed air and canopy temperatures), A_N , and lint yield were observed. The most thermotolerance-stable cultivar was also the most photosynthetically stable and yield stable, suggesting that greater thermotolerance plasticity of PSII does not necessarily promote yield stability when yield variability is water-induced. Also, the methods described here provide an approach to rapidly assess thermotolerance plasticity of field grown cotton that could be adopted on a large scale and that does not require extensive knowledge of site-specific conditions.

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1. Introduction

Leaf temperatures in excess of 35 °C are known to negatively impact net photosynthesis (A_N) in *Gossypium hirsutum* (Crafts-Brandner and Salvucci, 2000; Snider et al., 2010; Wise et al., 2004). Because ambient temperatures are often well-above this threshold in many cotton-growing regions of the world, a substantial amount of effort has been expended to identify the “weak link” in the photosynthetic response to temperature (Crafts-Brandner and Salvucci, 2000; Salvucci and Crafts-Brandner, 2004a; Wise et al., 2004). Photosystem II was initially regarded as the most heat-

sensitive component of the photosynthetic apparatus (Berry and Bjorkman, 1980) and because chlorophyll *a* fluorescence methods are rapid (require approximately 1 s per measurement) and accurately quantify PSII efficiencies in vivo (Maxwell and Johnson, 2000), a relatively large volume of work has been devoted to assessing genotypic differences in heat tolerance using maximum quantum yield of PSII (F_v/F_m) or some other derivation of the maximum (F_m) and minimum (F_0) values obtained from the chlorophyll fluorescence trace (Burke, 1990; Froux et al., 2004; Knight and Ackerly, 2002; Snider et al., 2013). However, extending the findings of PSII temperature response experiments (either from controlled environment studies or from investigations conducted on excised leaf segments from field-grown plants) to real-world cotton production scenarios has been difficult for three primary reasons. (1) F_v/F_m , a very accurate measure of photosystem II

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quantum efficiency, in dark-adapted leaves shows no appreciable decline at moderately high temperatures that limit A_N (35–40 °C; Salvucci and Crafts-Brandner, 2004b; Snider et al., 2013), often showing no decline until leaf temperatures reach or exceed 45 °C. (2) PSII heat tolerance acclimates to prevailing environmental conditions such that high temperature thresholds are often well-above air temperatures observed in the field (Froux et al., 2004; Snider et al., 2013). (3) *G. hirsutum* exhibits limited homeothermy due to evaporative cooling, allowing leaf temperatures to be maintained well-below the 35 °C threshold noted previously, even when air temperatures reach 40 °C (Upchurch and Mahan, 1988). Thus, measuring the efficiency of an extremely heat-tolerant component of the photosynthetic apparatus on a crop like cotton that exhibits exceptional ability to cool well-below air temperature has cast doubt on the utility of using chlorophyll *a* fluorescence to detect heat stress at biologically relevant temperatures (Sharkey, 2005; Wise et al., 2004).

However, one situation in which genotypic differences in PSII heat tolerance might become relevant is under water deficit conditions. For example, under drought stress, stomatal closure limits transpiration and evaporative cooling, thereby causing increases in foliage temperature; If water deficit stress is severe enough, leaf temperatures can even exceed air temperatures (Idso et al., 1981), and a leaf exposed to $T_{\text{air}}=40$ °C would have $T_{\text{leaf}}>40$ °C, temperatures that more closely approximate PSII high temperature thresholds. Although A_N becomes nearly abolished under these conditions, likely due to the combined effects of drought (Carmo-Silva et al., 2012; Ennahli and Earl, 2005; Snider et al., 2014b) and high temperature (Carmo-Silva et al., 2012) stress, maintenance of PSII function and electron flow in cotton are thought to be important for mitigating damage caused by reactive oxygen species (ROS) production under abiotic stress conditions (Kitao and Lei, 2007). Furthermore, it has been proposed that certain genotypes that exhibit greater phenotypic plasticity to environment or cultural practices should also exhibit greater yield stability (Gingle et al., 2006). Heat tolerance of photosystem II can be influenced by a number of factors (Froux et al., 2004; Havaux, 1992; Snider et al., 2013, 2014a) including genotype, water availability, prior ambient temperature exposure, plant developmental stage, and likely other unexplored factors. Thus, even in intensively managed and monitored research plots under field conditions, it is not possible to account for all factors that influence thermotolerance acclimation. As a result, the authors propose applying the regression approach that has been described elsewhere (Eberhart and Russell, 1966) for quantifying yield stability. With this approach, one does not need to know everything about the environment the plant has been exposed to. Rather, an environmental index is developed by subtracting the environment mean (the average yield of all varieties grown in the same environment) from the grand mean (the overall average yield for all varieties in all yield-environments tested), and the average yield of each cultivar in a given environment is regressed against the environmental index. Differences in slope indicate differences in environmental responsiveness. A similar approach could be used to assess PSII thermotolerance plasticity, provided a

standardized measure of heat tolerance is universally applied to all plants. Studies assessing genotypic differences in thermotolerance in this manner for field-grown plants are, to our knowledge, non-existent. The same can be said of simultaneous studies of thermotolerance plasticity and yield stability for crops under water-limited conditions (conditions where extremely high leaf temperatures might be observed).

Consequently, it was hypothesized that a *G. hirsutum* cultivar with greater heat tolerance plasticity would also exhibit the greatest photosynthetic and yield stability when the crop was exposed to a range of water availability. Thus, the objectives of the current study were (1) to characterize water-induced yield variability for two commercially-available cotton genotypes (FM 1944 GLB2 and PHY 499 WRF), (2) to assess heat tolerance for both cultivars at three phenological stages during the growing season (squaring, first flower, and peak bloom) as the temperature causing a 15% decline in F_v/F_m from the value observed at the optimum temperature (T_{15}), and (3) to assess yield, photosynthetic, and thermotolerance plasticity for each cultivar.

2. Materials and methods

2.1. Plant material, study site, and irrigation treatments

A field site was established at the C.M. Stripling Irrigation Research Park near Camilla, GA (USA) (31°16'48"N, 84°17'29"W) in 2013 and 2014. Seeds of *G. hirsutum* cv. PHY 499 WRF (Dow AgroSciences) and FM 1944 GLB2 (Bayer CropScience) were sown at a 2.5 cm depth on May 6, 2013 and June 3, 2014. A 0.91 m inter-row spacing was used and a seeding rate of 11 seeds m^{-1} row. Plots were six rows wide and 12.2 m long with 2.4 m bare-soil alleys. The soil at the Camilla study site is classified as Lucy loamy sand (loamy, kaolinitic, thermic Arenic Kandiodults). Seedbed preparation, fertilization, and pest management practices were carried out in accordance with University of Georgia Cooperative Extension Service recommendations (Collins et al., 2013). Prior to imposing irrigation treatments at the appearance of the first floral bud (square), a healthy, uniform stand was obtained by supplementing rainfall with overhead sprinkler irrigation (14.9 cm of total water in 2013 and 18.5 cm total water in 2014 prior to squaring). Average plant densities were 10.0 and 10.2 plants per row meter for PHY 499 WRF in 2013 and 2014 and 10.1 plants per row meter for FM 1944 GLB2 in 2013 and 2014; all of these plant densities are known to produce maximal yields in cotton (Collins et al., 2013).

At squaring, five different irrigation treatments were initiated. (1) 100% Checkbook: this is a water balance method recommended by the University of Georgia Cooperative Extension Service (Collins et al., 2013). Using this approach, irrigation water supplements rainfall to provide a predetermined weekly water requirement for a given stage of plant development (not based on evapotranspiration calculations). (2) –0.5 MPa: Irrigation triggered when the average predawn leaf water potential (Ψ_{PD} ; measured three times per week) for this treatment declined below –0.5 MPa. (3) –0.7 MPa: irrigation triggered when the average Ψ_{PD} for this treatment declined below –0.7 MPa. (4) –0.9 MPa: irrigation

Table 1
Cumulative amount of water supplied to the cotton crop during the 2013 and 2014 growing seasons as irrigation, rainfall, and total water for each irrigation treatment from the start of irrigation treatment initiation until irrigation termination. Data are expressed in cm.

Treatment	Irrigation 2013	Irrigation 2014	Rainfall 2013	Rainfall 2014	Total 2013	Total 2014
100% Checkbook	17.4	29.9	66.9	34.9	84.3	64.8
–0.5 MPa	11.5	23.7	66.9	34.9	78.4	58.6
–0.7 MPa	2.5	14.2	66.9	34.9	69.4	49.1
–0.9 MPa	0	10.0	66.9	34.9	66.9	44.9
Dryland	0	0	66.9	34.9	66.9	34.9

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