



Research article

Carbon allocation, osmotic adjustment, antioxidant capacity and growth in cotton under long-term soil drought during flowering and boll-forming period



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ABSTRACT

Responses of plant to drought largely depend on the intensity, duration and developmental stage at which water stress occurs. The purpose of this study was to analyze the dynamic of cotton physiology response to different levels sustained soil water deficit during reproductive growth stage at leaf basis. Three levels of steady-state water regimes [soil relative water content (SRWC) maintained at $(75 \pm 5)\%$, $(60 \pm 5)\%$ and $(45 \pm 5)\%$] were imposed when the white flowers had opened on the first fruiting position of the 6–7th fruiting branches (FB₆₋₇), which was the first day post anthesis (i.e. 1 DPA) and lasted to 50 DPA. Results showed decreasing SRWC slowed cotton growth on the base of biomass and leaf area. However, carbon metabolites levels were globally increased under drought despite of notably inhibited photosynthesis throughout the treatment period. Clear diurnal pattern of sucrose and starch concentrations was obtained and sucrose levels were evaluated while starch concentration was reduced with decreasing soil water content during a 24-h cycle. Osmotic adjustment (OA) was observed at most of the sampling dates throughout the drought period. K^+ was the main contributor to osmotic adjustment (OA) at 10 and 24 DPA then turned out to be amino acid at 38 and 50 DPA. The stressed cotton gradually failed to scavenge reactive oxygen species (ROS) with increasing days post anthesis, primarily due to the permanent decrease in SOD activity. Elevated carbohydrates levels suggest cotton growth was more inhibited by other factors than carbon assimilation. OA and antioxidant could be important protective mechanisms against soil water deficit in this species, and transition of these mechanisms was observed with drought intensity and duration increased.

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1. Introduction

Soil desiccation is one of the major environmental stresses that limit crop production worldwide. Limiting available soil water content severely altered plant morphological and physiological characters across a range of temporal and spatial scales, and lead to negative effects on plant growth (Tardieu et al., 2000; Chaves et al., 2002; Muller et al., 2011; Carmo-Silva et al., 2012; Deeba et al., 2012). Cotton is grown in a wide region around the world and is negatively affected by water stress (Gerik et al., 1996; Pettigrew, 2004; Lokhande and Reddy, 2014). What's worse, changes in

climate might lead to expanding of drought-affected areas and enhancement of drought intensity according to projected increase in global air temperature (Giorgi and Lionello, 2008). Therefore, understanding cotton physiological mechanisms in response to water stress is critical for cotton production improvement via stress-tolerant genotypes identification and management practices.

The balance between carbon assimilation, storage and use is important to plant growth (Smith and Stitt, 2007). Numerous studies have addressed the impact of water deficit on carbon (C) metabolism in various plant species. Most studies (Timpa et al., 1986; Pelleschi et al., 1997; Clifford et al., 1998; Praxedes et al., 2006; Hessini et al., 2009; Muller et al., 2011) demonstrated that drought most often induced carbohydrates accumulation in varying plant organs, even increased carbon availability in root (Hummel et al., 2010; Durand et al., 2016), indicating that carbon demand is decreased more than carbon supply under water stress. These

Abbreviations: DPA, days post anthesis; LWP, leaf water potential; OA, osmotic adjustment; ROS, reactive oxygen species; SRWC, soil relative water content.

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results were contrary to the hypothesis that plants under drought suffer from carbon shortage due to the down-regulation of photosynthesis (Chaves et al., 2002; McDowell et al., 2008). But supported results were obtained under some extreme scenarios like severe and prolonged water deficit or interaction with high temperature (McDowell and Sevanto, 2010).

The increase in carbohydrate concentration was usually considered to be in pace with an increased need for OA under drought (McCree et al., 1985; Chaves, 1991; Clifford et al., 1998). Some previous studies (Koppelaar et al., 1991; Wang and Stutte, 1992; Bajji et al., 2001; Hessini et al., 2009) supported this hypothesis: OA in *Picea glauca* shoots and *Pinus banksian* roots largely resulted from an increase in fructose and glucose (Koppelaar et al., 1991). Bajji et al. (2001) showed sugars were the main solutes that contributed to OA in wheat plants exposed to water deficit; OA was mainly due to the accumulation of sugars and proline in mild water deficit, while plants failed to develop active osmotic adjustment under severe water stress in *S. alterniflora* (Hessini et al., 2009). On the other hand, organic acids were the major constituents of the soluble carbon fraction involved in OA in *Fraxinus excelsior* L. and Hummel et al. (2010) reported that not sugars but K^+ was the main contributors to osmotic adjustment in drought stressed *Arabidopsis* plants.

Water stress promoted the production of reactive oxygen species (ROS) as the absorption of excess photons that could not be used by photosynthesis in leaves (Mittler, 2002). In order to keep the balance between ROS production and scavenging, plants developed scavenging systems against ROS, involving both enzymatic and non-enzymatic systems. Under mild short-term water deficit, activities of antioxidant enzymes like SOD, POD and CAT were increased to eliminate excess ROS, but MDA still showed a slight increasing trend, suggesting antioxidant capacity was not sufficient to contribute to resistance to water stress (Reddy et al., 2004; Ge et al., 2006). Zhang et al. (2000) reported that SOD activity was decreased, and CAT activity was enhanced first then declined as the duration of water stress increased, while POD activity was affected differently in various cultivars.

Thus, it was hard to assess the physiological response of plants under drought condition from fore-mentioned reports. This is not surprising, since the consequences of water deficit depend on species, mode of water stress imposed and interaction with other environmental factors (Bray, 2004; Liu et al., 2008; Loka and Oosterhuis, 2012; Tozzi et al., 2013). It was assumed that the adaptive mechanisms of plants change with the intensity or duration of water deficit. Future studies should impose reproducible levels of water deficit and pay attention to interaction with the possible accompanying stresses to explore the consequence of drought (Hummel et al., 2010; Lokhande and Reddy, 2014).

Cotton is sensitive to water stress, particularly during reproductive growth stage which is the most sensitive period to water shortage (Loka and Oosterhuis, 2012). Therefore, we imposed steady-state and reproducible levels of water deficit during the periods of flowering and boll-formation in cotton, aiming to evaluate the dynamic of carbohydrate profiles, OA, antioxidant capacity and their relationship with cotton growth.

2. Materials and methods

2.1. Plant materials and growth conditions

Pot experiment (32 cm high and 37 cm diameter, filled with 25 kg of soil) was conducted at the experimental station (32°02'N and 118°50'E) of Nanjing Agricultural University in Nanjing, Jiangsu Province, China in 2012 and 2013. Cotton seeds (cv. Siza 3) were sown on 25 April 2012 and 8 April 2013, respectively. Two rows of

pots were placed together, and then a 40-cm-wide aisle was left. The soil type was clay, mixed, thermic, Typic alfisols (udalfs; FAO luvisol) which was collected from topsoil layer to 30 cm depth from the experimental station. In 2012 and 2013, respectively, the soil averaged 16.4 and 17.7 g kg⁻¹ organic matter, 1.12 and 1.14 g kg⁻¹ total N, 65.9 and 70.0 mg kg⁻¹ mineral N (NH₄⁺-N and NO₃⁻-N), 18.1 and 20.4 mg kg⁻¹ Olsen P, and 122 and 135 mg kg⁻¹ exchangeable K (NH₄OAc-K). The pots were covered with a transparent waterproof material above the crop canopy when it rained. Other practices were conducted following the standard commonly performed in the area.

2.2. Experimental designs

Experiments were conducted in a randomized complete block design with three replications. Each plot consisted of 40 pots of cotton plants. Cotton was grown under three levels of soil water regimes: SRWC maintained at (75 ± 5)%, (60 ± 5)% and (45 ± 5)%, denoted as SRWC (75 ± 5)%, SRWC (60 ± 5)% and SRWC (45 ± 5)%, respectively. Soil water treatments were established when approximately 50% of white flowers had opened on the first fruiting position of the 6–7th fruiting branches (FB₆₋₇), which was the first day post anthesis (i.e. 1 DPA) and lasted to 50 DPA. Cotton plants were well-watered before the water deficit event.

2.3. Soil water content and leaf water potential

Soil water content was measured according to the method of Liu et al. (2008). Soil samples at 0–25 cm depth were collected about every 2 day at 18:00–19:00 local time with a punch (2 cm-diameter) from each plot. Fresh weight of the soil samples were determined and then these samples were oven-dried at 105 °C for 8 h. Soil water content was expressed as g water g⁻¹ dried soil. Cotton plants would be watered to the upper soil water limit in the early morning. Pre-dawn leaf water potential (LWP) was measured every three days during flowering and boll-forming period, on topmost fully expanded leaves with two samples per plot at 5:00–6:00 local time. Leaves were removed by cutting the petiole, then used the pressure chamber (3005 Pressure Extractor, Soilmoisture Equipment Corp., Goleta, CA, USA) to measure water potential.

2.4. Growth and morphological indices

Cotton plant biomass was measured after determining of leaf area with an area meter (Li-3000A, Li-COR Inc., NE, USA). Shoot and root of cotton plants were killed at 105 °C for half an hour and then maintained at 80 °C until constant weight. Measurements were done every 10 d with three plants per plot from 0 to 40 DPA. Number of bolls and boll sets were counted in ten targeted plants at the same time. Boll shedding rate was also calculated for these ten plants.

2.5. Gas exchange measurements

Gas exchange parameters were measured on the topmost fully expanded leaf on main stem on 10, 24, 38 and 50 DPA. These parameters were measured with a photosynthesis system (Li-6400, Li-COR, Lincoln, NE, USA) under 1500 μmol m⁻² s⁻² light intensity at 9:00–11:00 a.m.

The diurnal course of net photosynthesis of the topmost fully expanded leaf was determined at about 17 DPA using the same photosynthesis system but under ambient light intensity. Measurements were conducted on two leaves per plot at intervals of 2 h from 6:00 to 20:00. Light intensity, leaf and air temperatures were documented simultaneously.

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