Pak. J. Bot., 54(1): 105-112, 2022. DOI: http://dx.doi.org/10.30848/PJB2022-1(19)

OSMOTIC COMPONENTS IN COTTON (*GOSSYPIUM HIRSUTUM* L.) FIBERS IN RESPONSE TO SOIL MOISTURE DEFICIT DURING FIBER EXPANSION

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Abstract

The present study aimed to determine how main osmotic active substances (malate, potassium and soluble sugars) in cotton fibers respond to soil drought. A pot study with two water regimes was performed in 2015 and 2016 using two cotton lines A001 and A705. The irrigated plants (control) were watered at 1-d interval with the optimum quantity of underground water determined on the basis of a gravimetric method. Drought treatment was defined as withdrawing water from pots until the leaf wilting symptom was visible, and water stressed plants were exposed to limited water supply for 25 days receiving 50% of the control irrigation at 2-d interval. Following 25 days of water deficit treatment, those plants were re-watered with the same quantity as the control. Drought induction caused a significant reduction in fiber length and strength in A001. Net photosynthetic rate (P_n), stomatal conductance (g_s), and transpiration rate (E) in A001 and A705 were reduced significantly by soil drought indicating the present water deficit design did generate a photosynthetically physiological difference. The depressed leaf photosynthesis led to the deficient accumulation of soluble sugars, malate and potassium in water stressed fibers, and in turn to the reduced fiber length.

Key words: *Gossypium hirsutum*; Drought stress; Potassium; Osmotically active solutes; Fiber length.

Introduction

Fiber length is an important determinant of cotton fiber quality due to its close association with yarn quality properties, such as strength, elongation, evenness and hairiness. The first 25 days after flowering is characterized by rapid cell elongation in cotton fibers and division in embryos. Cell elongation is driven by internal turgor pressure and irreversible cell wall extension. The generation and **maintenance** of turgor pressure are attributed to the relatively high concentration of osmotically active solutes driving the influx of water. The main osmotic active solutes in elongating fibers consist of malate, potassium (K^+), and soluble sugars together being responsible for approximately 80% of fiber sap osmolality (Dhindsa *et al*., 1975).

K^+ is a crucial macronutrient for cotton plants and exerts a key role in a multiple of physiological and metabolic processes, such as osmotic regulation, enzyme activation, photosynthesis and assimilate transport (Pettigrew, 2008). Soil potassium deficiency decreased fiber length as a result of decreased K^+ concentration and turgor pressure in cotton fibers (Bauer *et al.,* 1998; Yang *et al*., 2016). Different from K^+ imported into cotton fibers from the vascular tissue of the seed coat, malate was produced locally in fiber cell cytoplasm as triggered by phosphoenolpyruvate carboxylase (PEPC) (Li *et al*., 2010), which functions in fixing HCO_3^- emitted from dark respiration to generate oxaloacetate (OAA) and inorganic phosphate. OAA conversion into malate is catalyzed by malate dehydrogenase. Malate was likely contributed to the increased accumulation of K^+ in cotton fibers by serving as a major **counterion** to equilibrate K^+ in the development of the osmotic potential (Talbot *et al.*, 1998; Yang *et al*., 2016). In addition, malate could be used as the substrate for biosynthesis of membrane lipids during fiber cell expansion in which the tonoplast and plasma membrane were extended at an exceptional rate (Ruan *et al*., 2001). Although malate, acetate and pyruvate all are served as substrates to synthesize fatty acids, the rate of fatty acid synthesis due to malate was about 4.5 and 120 folds higher than those due to pyruvate and acetate, respectively (Smith *et al*., 1992). Consequently, malate may exert an important role in the development of the tonoplast and plasma membrane during fiber expansion by serving as the substrate for the biosynthesis of lipid (Li *et al*., 2010). Soluble sugars in cotton fibers contain mainly glucose, fructose and sucrose. Among them, hexose (glucose plus fructose) existed in cotton fibers in greater quantity (Li *et al*., 2010; Tang *et al*., 2014). Sucrose is the main form of soluble sugars transferred into fibers. When unloaded from the phloem of the seed coat, sucrose can be moved into the fiber cell in a **symplastic** way through the plasmodesmata (PD). Inside the fiber cell, sucrose can be cleaved by either vacuolar **invertase** (VIN) or sucrose synthase (Sus). VIN hydrolyzes sucrose into glucose and fructose, thus doubles the osmotic contribution of sucrose. **Sus** degrades sucrose into uridine diphosphate glucose (UDPG) and fructose in the presence of uridine diphosphate (UDP). UDPG is served as the substrate for the deposition of cellulose into the secondary cell wall of fiber cells (Amor *et al*., 1995).

Moisture deficit stress is a major abiotic factor compromising fiber growth. The stress occurring shortly post-**anthesis** significantly reduced fiber length (Marani & Amirav, 1971; Loka *et al*., 2011). Water deficit adversely affects leaf photosynthesis at both stomatal and non-stomatal levels (Loka *et al*., 2011). Considerable information is available on water deficit effects on carbohydrates dynamics in the leaf or young boll of cotton (Guinn, 1976; Ackerson, 1981; Timpa *et al*., 1986; Pline *et al*., 2003; Parida *et al*., 2007; Loka &

Oosterhuis, 2013). However, those osmotically active solutes in elongating fibers response to drought stress and its association with final fiber length still remain obscure. In the present study, we hypothesize that moisture deficit decreases the accumulation of three osmotic active solutes in cotton fibers, and thus increases osmotic potential (less negative), and further leads to decreased fiber length. The aim of this study was to examine the changes of soluble sugars, malate and potassium ion in fibers exposed to soil drought stress during fiber elongation, and ascertain osmolytes availability association with fiber length.

Materials and Methods

Experimental design: A pot study was carried out during 2015 to 2016 at the agricultural experiment station of Jiangxi Agricultural University (JXAU), Nanchang China. Seeds of two upland cotton lines (A001and A705) were planted into 40 cm diameter 35 cm height pots on May 16 and 14 in 2015 and 2016, respectively, and grown in a rainout shelter. A001 has better fiber quality performance over A705. Two hundreds sixty four pots were equally divided into four groups as follows: control with A001, water deficit with A001, control with A705, and water deficit with A705. The experiment was arranged in a completely randomized design with three replications. Thirty five kilogram of soil was added to each pot. The soil was taken from the top 20 cm of soil layer from a cotton field nearby, air dried and screened through a sieve for eradicating stones and grass roots with a slightly acid pH of 6.0, 25.1 g kg^{-1} organic matter, 0.19% total N, 159.21 mg kg^{-1} alkali-hydrolyzable N and available P-K at 34.23 and 180.93 mg kg^{-1}, respectively. Seven gram of 15-15-15 N-P-K was applied to each pot, pre-plant and **side-dress** incorporated at peak squaring stage, respectively. Plants were grown well until early flowering stage when they were divided into two groups exposed to different two soil moisture regimes. In the irrigated treatment (control), each pot was watered at 1-d interval with four liter of underground water pumped from a well. The 4L of water quantity was determined by a gravimetric method. The water stress treatment was initiated as obvious leaf wilting symptom occurred by withdrawing water, and followed by deficient water supply for 25 days with 50% of the control irrigation (2 L each pot) over water-stressed plants at 2-d interval. The combination of the irrigation quantity (4 L each pot) and frequency (at 1-d interval) was previously determined to be optimum for the growth of control plants, which could maintain the relative soil water content (RSWC) ranged from 70% to 80% of field capacity throughout the experiment period. The water deficit treatment, *i.e.*, two liter water each pot at 2-d interval, produced a RSWC of 50% - 60%, which was deemed as a mild water stress (Luo *et al*., 2016). Further, A LI-6400 photosynthesis system (LI-COR Inc., NE, USA) was used to help monitor the water status of the water stressed plants and the controls during the water stress period. Photosynthetic measurements were taken on the fourth leaf from the apex under 1,600 μmol (photo) $m^{-2}s^{-1}$ light intensity between 10:30 and 12:00 h on cloudless days. Four parameter measurements were made including net photosynthetic rate (P_n), internal CO_2 concentration (C_i), transpiration rate (E) and stomatal conductance (g_s), and following 25 days of drought treatment, the water stressed plants were re-irrigated with the same quantity as did the control. On the commencement of limited water supply white flowers from the **adaxial** positions on middle sympodials (7^{th} to 9^{th} fruiting branch) were labeled. The bolls and leaves subtending to the bolls were collected between 9:00 and 10:00 a.m. at 5-days interval over a period of 10-25 days post-anthesis (DPA), and brought back to the Lab on ice, where fibers were separated from seeds using a scalpel in an ice bath, and then oven-dried at 40°C to an invariable weight for malate, potassium and carbohydrate analyses. The remaining tagged bolls were harvested at the boll maturation phase. Lint samples were analyzed for five fiber quality parameters at Supervision Inspection and Testing Center of Cotton Quality, Ministry of Agriculture, Anyang, Henan province by high volume instrumentation testing, including upper half mean fiber length (UHM), length uniformity index (UI), micronaire (Mic), elongation at break (EI) and fiber bundle strength (Str).

Soluble sugars analysis: Soluble sugars containing glucose, fructose, sucrose were extracted in terms of the method of Tang *et al*., (2014). In brief, samples of 50 mg dry fiber were incubated three times in 3 mL of 80% ethanol (v/v) in an 80°C water bath with half an hour for each extraction, and sample tubes were centrifuged at 4200 rpm for 15 min to isolate the soluble from insoluble fractions after each extraction. The three supernatants were merged and brought to a final volume of 10 mL with 80% ethanol (v/v), and a 1.5 mL aliquot was purified with 20 mg of finely ground activated charcoal (Sigma SA-3) and centrifuged at 4200 rpm for 15 min to obtain a clear alcohol extract. The concentrations of glucose, fructose and sucrose were quantified using enzyme-coupled colorimetric reactions according to Hendrix (1993).

Malate extraction and assay: Malate extraction followed the method mentioned above. Malate concentration was determined using the enzyme-coupled method according to Li *et al*., (2010) with modifications. The reaction solution consisted of 40 mM Hepes-KOH (pH 7.1), 8 mM $MgCl_2$, 20 mM 2-amino-2-methylpropanol, 16 mM glutamate, and 0.4 mM NAD^+, and 500 μL of extract in a total volume of 2.5 mL. The reaction was initiated by the addition of 10 U of glutamate oxalacetate transaminase and 1 U of malate dehydrogenase to the assay mixture. Malate concentration was calculated from a standard curve measured at 340 nm.

Potassium extraction and assay: The potassium extraction was adopted according to the method of Lu (2000) with minor modifications. Two hundred milligrams of dry fiber sample was placed into a polystyrene tube and 9 mL 1 M ammonium acetate was added and homogenized thoroughly for 15 min at room

temperature with a homogenizer. Each sample was extracted twice and sample tubes were centrifuged at 4200 rpm for 15 min after each extraction. The two supernatants were combined in a volumetric flask and brought to a 50 mL final volume with 1 M ammonium acetate. Potassium concentrations were determined by flame photometry. Potassium standards were used in the range 0-100 mg/L potassium.

Statistical analysis

Paired *t*-tests were used to compare the water stressed plants and the control plants at each sampling date. Means were separated at the 5% probability level. The figures were plotted by using Sigma Plot version 14.0.

Results

Fiber quality performance: The 2 yr during this study indicated that a significant reduction in fiber length and strength was induced by soil drought in A001 but not for A705 (Table 1). Water stress reduced micronaire significantly in A001 relative to the control, but increased micronaire in A705 in 2015. Fiber elongation and length unity remained constant under water deficit stress for the two genotypes except length unity in A705 in 2016. The results showed that drought stress adversely affected both fiber length and fiber strength. The reduction degree was higher in A001 than in A705.

Leaf photosynthesis: P_n, E and g_s were significantly decreased by soil drought during a period of 5 to 23 DPA for the two genotypes except P_n with A705 at 5 DPA (Fig. 1a, 1b, 1c). A001 exhibited a significant reduction in internal CO_2 concentration (C_i) at 5 DPA under water deficit, but no difference for A705 (Fig. 1d). Less and insignificant reductions at the four photosynthesis parameters were observed at 30 DPA between two soil moisture regimes for A001 and A705. These results indicated that the water deficit method employed in this study did introduce a significant reduction at leaf photosynthesis level which may in turn lead to the decreased import into and/or biosynthesis of osmotically active solutes inside cotton fibers. No significant difference in photosynthetic parameters at 30 DPA could be attributed to the sufficient water recovery on the water stressed plants from 25 DPA onwards.

Soluble sugars in cotton fibers response to water stress: Soil moisture deficit significantly decreased the glucose concentration of the cotton fiber for A001 during 10 DPA to 25 DPA in 2015, but no difference in 2016 (Fig. 2a). The glucose concentration was decreased significantly for A705 from 5 through 20 DPA in 2015, and at 25 DPA in 2016 (Fig. 2b). However, the glucose concentration in A705 fibers was increased on 10 DPA and 15 DPA by water stress in 2016. There was a significant reduction in the fructose concentration for A001 at 10, 20 and 25 DPA in 2015, and at 10 and 15 DPA in 2016 (Fig. 3a). The significant reduction in fructose concentration for A705 was documented at 10, 20 and 25 DPA in 2015, and during a period of 10 to 20 DPA in 2016 (Fig. 3b). A001 expressed a significant reduction in sucrose concentration under water stress at 20 and 25 DPA in 2015, and 10 DPA in 2016 (Fig. 4a). Similarly, the sucrose concentration was decreased in A705 fibers during 10 DPA to 25 DPA in 2015, and at 25 DPA in 2016 under water stress (Fig. 4b). Soluble sugars exhibited a similar dynamics as fructose under either of two soil water regimes due to fructose being a dominant component of soluble sugars in cotton fibers (Fig. 5a, 5b).

Malate and potassium in cotton fibers response to water stress: A significant decrease in the malate concentration was found in stressed fibers of A001 compared to the control during a period of 10 to 20 DPA in 2015, and at 10 DPA in 2016 (Fig. 6a). A705 was documented a delayed decrease in the malate concentration for stressed fibers at 15 and 25 DPA in 2015, and at 20 DPA in 2016 (Fig. 6b). The potassium concentration was characterized by a sharp decline at 15 DPA onwards (Fig. 7a, 7b). Water deficit stress reduced significantly potassium levels in A001 fibers at 15 DPA in 2015, and 25 DPA in 2016, respectively (Fig. 7a). Potassium levels in the stressed fibers of A705 were significantly decreased by drought induction during a period of 10 to 20 DPA in 2015, and at 25 DPA in 2016 (Fig. 7b). The malate and potassium in the fibers of the two genotypes seem to be more severely influenced by water stress in 2015 than in 2016, as shown by more sampling dates with significant differences between two water regimes in 2015 than in 2016.

Table 1.Cotton fiber quality parameters as affected by two soil moisture regimes (dryland and irrigated) in 2015 and 2016.

Year	Genotype	Treatment	UHM (mm)	UI (%)	Mic	Elong (%)	Str (cN·tex^{-1})
2015	A001	Irrigated	30.0 a	85.3	5.4 a	6.9	29.7 a
		Dry land	25.9 b	83.8	4.4b	6.6	25.9 b
	A705	Irrigated	28.7	85.7	4.4 b	6.8	28.8
		Dry land	27.3	84.5	5.2 a	6.6	26.6
2016	A001	Irrigated	30.6 a	84.4	4.3	6.9	34.9 a
		Dry land	28.3 b	82.0	4.4	6.8	30.9 b
	A705	Irrigated	29.2	84.1 a	4.9	6.8	32.7
		Dry land	28.5	81.0 b	4.5	6.7	30.5

Within respective columns, values followed by the different letters are significantly different at p≤0.05. Letters omitted where p>0.05
UHM: upper half mean fiber length, UI: unity index, Mic: micronaire, Elong: elongation at break, Str: fiber strength

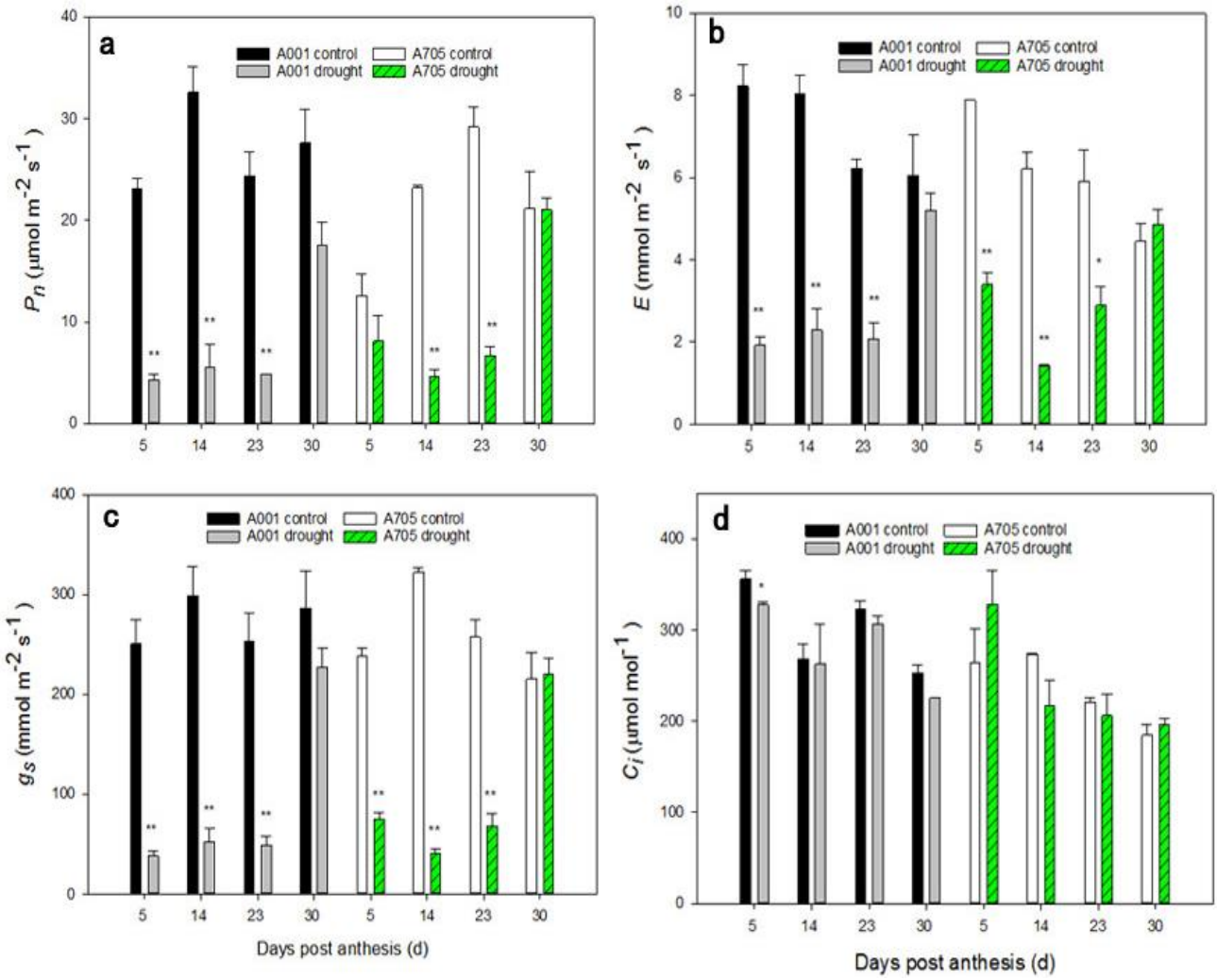

Fig. 1. Effects of water deficit stress on photosynthetic rate (P_n)(a), transpiration rate (E)(b), stomatal conductance (g_s)(c) and CO_2 concentration (C_i)(d) with the fourth stem leaf from the apex.

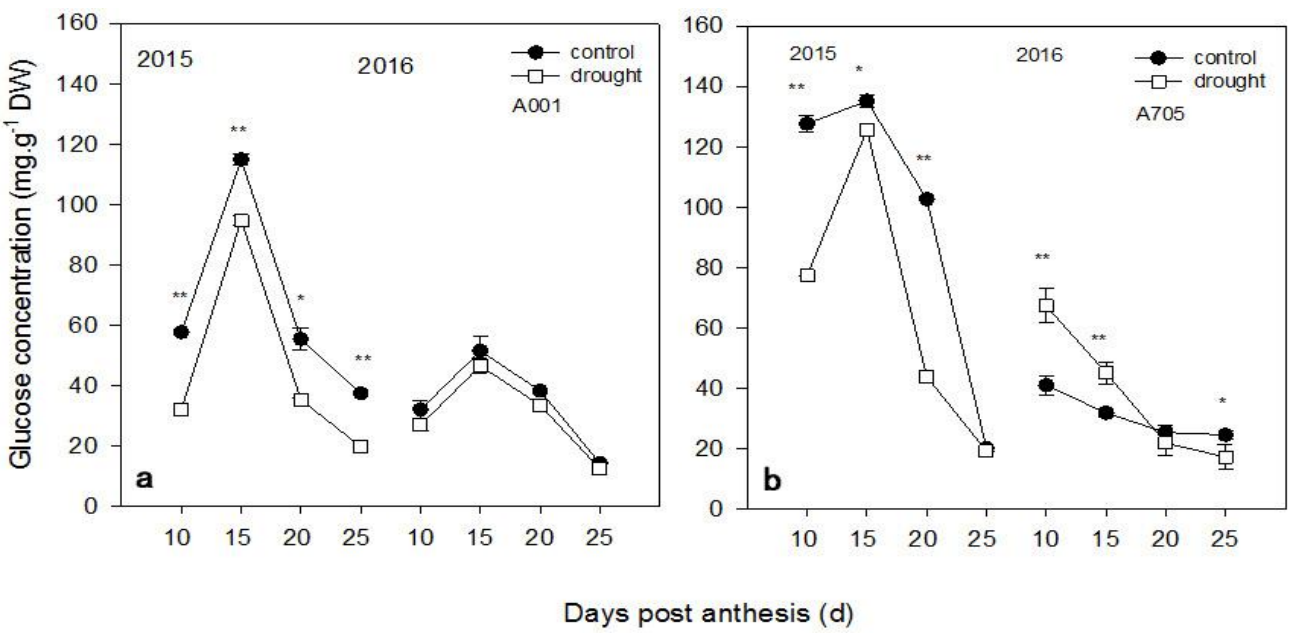

Fig. 2. Effects of water deficit stress on glucose concentrations in cotton fibers of A001 (a) and A705 (b) at various stages of boll development in 2015 and 2016. Each data point represents the mean ± SE (n=3). * and ** significant at $p \leq 0.05$ and 0.01 probability levels, respectively.

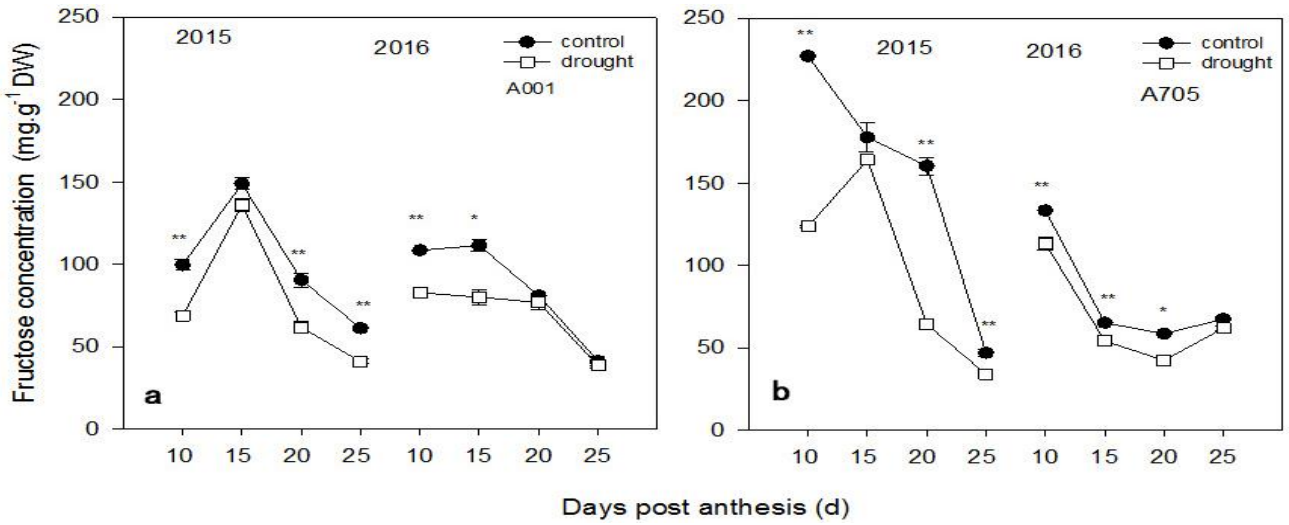

Fig. 3. Effects of water deficit stress on fructose concentrations in cotton fibers of A001 (a) and A705 (b) at various stages of boll development in 2015 and 2016. Each data point represents the mean ± SE (n=3). * and ** significant at p≤0.05 and 0.01 probability levels, respectively.

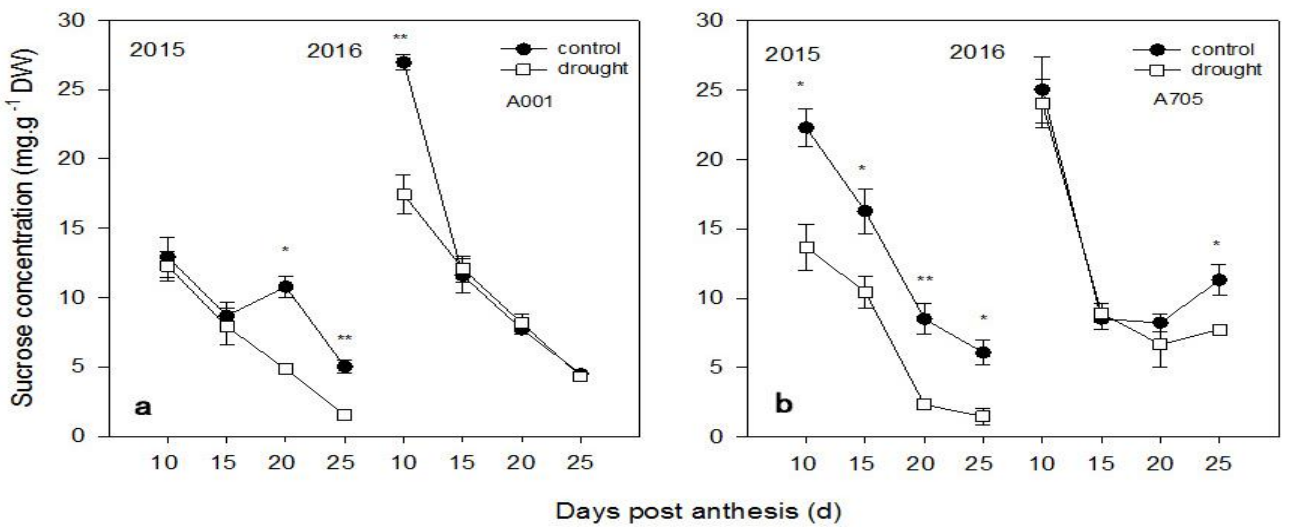

Fig. 4. Effects of water deficit stress on sucrose concentrations in cotton fibers of A001 (a) and A705 (b) at various stages of boll development in 2015 and 2016. Each data point represents the mean ± SE (n=3). * and ** significant at p≤0.05 and 0.01 probability levels, respectively.

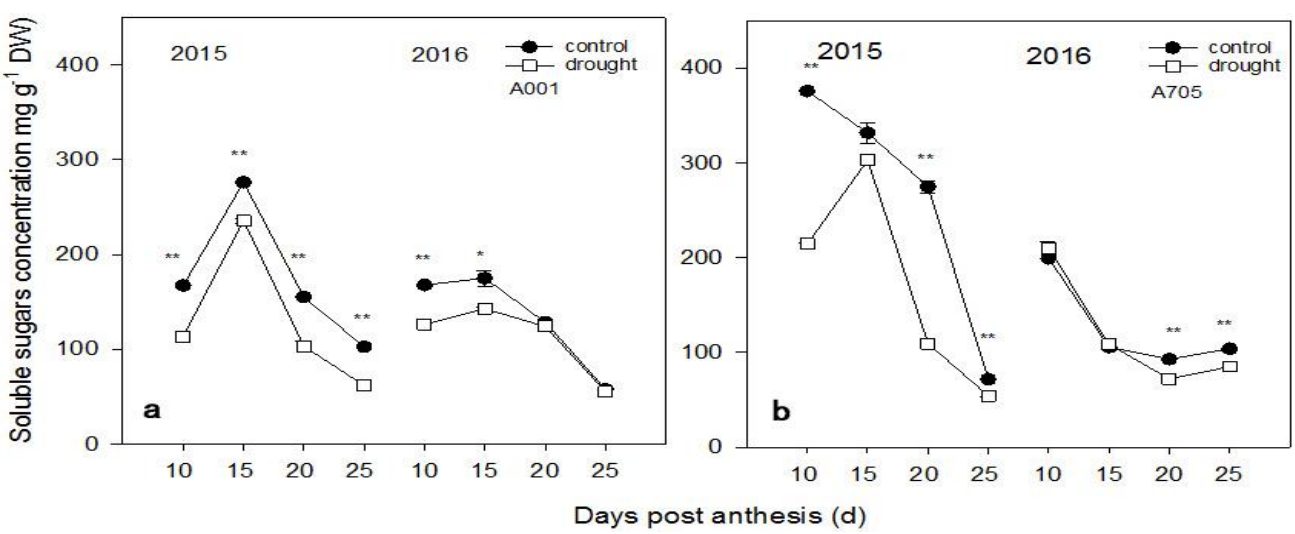

Fig. 5. Effects of water deficit stress on soluble sugar concentrations in cotton fibers of A001 (a) and A705 (b) at various stages of boll development in 2015 and 2016. Each data point represents the mean ± SE (n=3). * and ** significant at p≤0.05 and 0.01 probability levels, respectively.

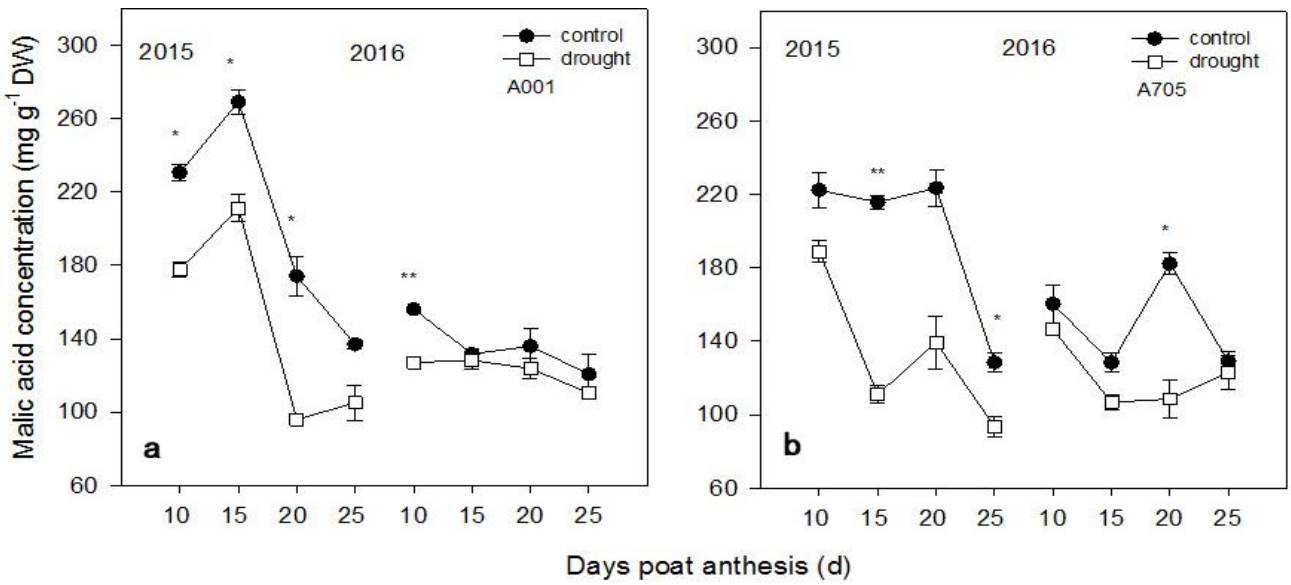

Fig. 6. Effects of water deficit stress on malate concentrations in cotton fibers of A001 (a) and A705 (b) at various stages of boll development in 2015 and 2016. Each data point represents the mean ± SE (n=3). * and ** significant at p≤0.05 and 0.01 probability levels, respectively.

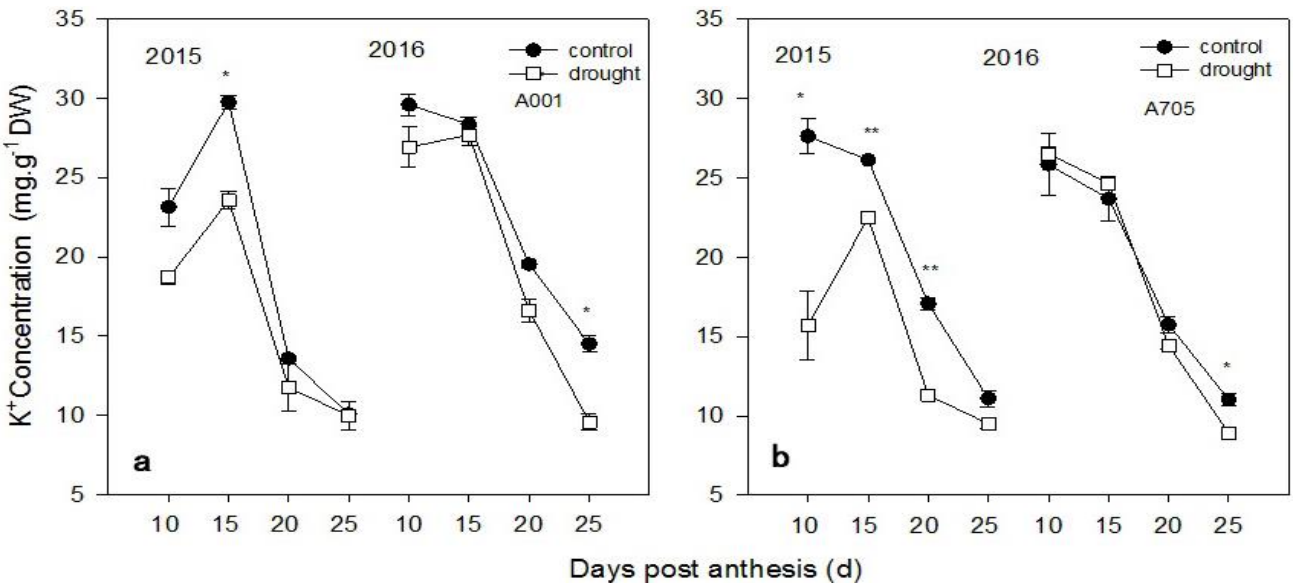

Fig. 7. Effects of water deficit stress on K^+ concentrations in cotton fibers of A001 (a) and A705 (b) at various stages of boll development in 2015 and 2016. Each data point represents the mean ± SE (n=3). * and ** significant at p≤0.05 and 0.01 probability levels, respectively.

Discussion

Solute sugars, potassium and malate are considered as three main active osmotica together accounting for around 80% of the fiber osmotic potential (Dhindsa *et al*., 1975). It has been established that soil drought can lead to a decreased fiber length in cotton (Marani & Amirav, 1971; Loka *et al*., 2011). This reduction may be due to the concurrent decline in the osmotica levels in fibers. Thus, we hypothesize that water deficit stress may limit the accumulation of soluble sugars, potassium and malate in fibers and in turn decrease fiber elongation.

Final fiber length depends on both the duration of fiber fast growth and its elongation rate. The duration of fast growth is controlled by the closure duration of plasmodesmata between the fiber cell and the epidermal cell (Ruan, 2007). Fiber expansion rate is governed by the turgor pressure against the fiber cell wall which is heavily dependent on the content of soluble osmolytes inside the vacuole (Ruan, 2007). Furthermore, fiber cell wall extensibility is also an important contributor to fiber elongation, together with turgor pressure allowing fiber elongation to proceed readily. As expected, soluble sugars, potassium and malate levels with cotton fibers were reduced by water deprivation during fiber elongation. Soluble sugars and K^+ ions inside the fiber cell are influxed from the vascular tissue of the seed coat where photoassimilates and inorganic minerals are unloaded. Thus, the decreased soluble sugars and K^+ accumulations in water stressed fibers may be caused by impaired phloem

loading and/or reduced sink activities under water deficit (Makela *et al*., 2005). Among soluble sugars, hexose (glucose plus fructose) is predominant over other soluble sugar components in fibers (Tang *et al*., 2014), while sucrose is the lead form transferred from source leaf to sink boll. Sucrose unloaded in the phloem of the outer seed coat must flow either outwards to fibers or inwards to embryos (Ruan, 2007). Upon entering the fiber cell, sucrose can be potentially hydrolyzed into glucose and fructose by vacuolar invertase, which doubles the osmotic contribution of sucrose requested for fast fiber cell expansion. Cassman *et al*., (1990) reported that positive correlations between fiber length and fiber potassium concentration at maturity, leaf potassium concentration at early bloom and soil potassium availability. Fiber length decreased linearly with the decline in leaf potassium content (Lokhande & Reddy, 2015). The application of potassium fertilizer contributed to long fibers (Girma *et al*., 2007). Besides function as a major osmoticum for the turgor regulation, K^+ ion can influence leaf photosynthesis including CO_2 assimilation rate and stomatal conductance and consequent photoassimilates allocation (Tsialtas *et al*., 2016). K^+ deficiency possibly induced a carbohydrate acquisition difficulty and in turn accelerated fiber maturity (Tsialtas *et al*., 2016; Yang *et al*., 2016), which may be another cause for decreased fiber length occasioned by potassium deprivation. Malate and Cl^- are regarded as main **counterions** to balance K^+ in building turgor pressure and osmotic potential (Talbott *et al*., 1998). Malate is locally synthesized in the fiber cell cytoplasm by the initial activity of PEPC. Water stress might deteriorate the enzyme activity of PEPC, and thus lead to a diminished malate content in fibers. On the other hand, the possibility of malate imported from the source leaf could not be excluded. Water stress increased the sum of citric and malic acids in cotton leaves 1.7 to 2.7 times greater than that in the control (Timpa *et al*., 1986), but malate concentration was decreased in cotton fibers under water stress relative to full irrigation in this study. The reason may be attributable to a reduction in the translocation of photoassimilates out of source leaves (Sung & Krieg, 1979). Yang *et al*., (2016) recorded that malate was involved in osmoregulation by facilitating K^+ accumulation in cotton fibers. Soluble osmolytes (sucrose, malate and K^+) were involved in shortening fiber length mediated by either of soil waterlogging and elevated temperature stresses (Chen *et al*., 2017; Dai *et al*., 2017).

Water deficit decreases leaf photosynthesis at both stomatal and non-stomatal levels (Lock *et al*., 2011). However, there has been some discrepancy in the comparative contributions of stomatal and non-stomatal factors to the decline of leaf photosynthesis in water-deprived plants. Faver *et al*., (1996) stated that non-stomatal factors were the dominant regulating factors under mild moisture deficit stress, while stomatal factors predominated when the moisture deficit stress is severe. In contrast, non-stomatal factors were deemed as primary components regulating photosynthesis under severe soil drought stress (Lock *et al*., 2011). A third viewpoint is that leaf stomatal resistance was significantly increased under moderate and severe soil drought stress (Wullschleger & Oosterhuis, 1990). In the present study, P_n, E and g_s were all reduced in the water stressed plants for each of the two genotypes except P_n with A705 at 5 DPA, but C_i remained unaffected except A001 with a significant decrease at 5 DPA. This result suggested that A001 might be more sensitive to soil drought stress than A705, as further supported by fiber quality data with A001 having a marked reduction with fiber length under water stress but not for A705. The decreased P_n and g_s in water stressed plants may be in part ascribable to the deficient level of leaf K^+, which in turn was caused by moisture deficit stress. The reasons are as follows: (1) the turgor pressure forcing the **stomates** open is developed through the influx of water powered by potassium accumulation in the guard cell: (2) ATPase, a key enzyme regulating photophosphorylation needs a sufficient level of K^+ to maintain an efficient and optimal activity level (Shingles & McCarty, 1994); (3) insufficient level of leaf K^+ resulted in limited photoassimilates transfer out of source leaves due to impaired phloem loading of sucrose (Gajdanowicz *et al*., 2011). Feedback inhibition from the excessive accumulation of leaf photoassimilates might compromise the photosynthetic process (Nafziger & Koller, 1976; Pee t& Kramer, 1980). The enhanced soluble sugar levels in the leaf subtending the boll were observed under drought stress in this study (data not list), which might lead to the decreased soluble sugar levels in the water stressed fibers. It is worthwhile to point out that no difference between A001 and A705 occurred in the fiber osmotica response to moisture deficit stress, but they responded inconsistently to water stress in fiber length, suggesting other factors such as the duration of fiber fast growth and cell wall extensibility (expansin, xyloglucan endotransglycosylases/ hydrolases XTH, etc.) might contribute to the inconsistency. This issue should deserve further research.

Conclusions

Moisture deficit stress depressed the photosynthetic process and led to the significant decrease of P_n, E, and g_s during the cotton fiber elongation, but no difference occurred for C_i except A001 with a significant reduction at 5DPA under soil drought stress. The decreased leaf photosynthesis contributed to the limited accumulation of active osmotica, such as soluble sugars, K^+ and malate in cotton fibers, and thus to reduced fiber length with the two genotypes A001 and A705.

Acknowledgments

This research was financially supported by the National Natural Science Foundation of China (Grant number: 31260302).

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(Received for publication 22 August 2019)