Environmental and Experimental Botany 137 (2017) 73–83

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Research Paper

Potassium fertilizer improves drought stress alleviation potential in cotton by enhancing photosynthesis and carbohydrate metabolism

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ARTICLE INFO

Article history:
Received 2 December 2016
Accepted 3 February 2017
Available online 4 February 2017

Keywords:
Cotton
Soil drought stress
Photosynthesis
Ribulose-1,5-bisphosphate carboxylase
Dry matter partitioning
Sucrose phosphate synthase

ABSTRACT

Under drought, limited photo-assimilates synthesis and their poor partitioning is a main constraint to final yield production in cotton (*Gossypium hirsutum* L.). To study the potassium (K) role in photo-assimilation and carbohydrate metabolism in cotton under soil drought stress during flowering and boll formation stage, a two-year pot experiment was conducted in 2015 and 2016. Two cotton cultivars namely Simian 3 (low-K tolerant) and Siza 3 (low-K sensitive) were grown under three K rates (0, 150 and 300 kg K_2O ha^{-1}). Plants were exposed to well-watered [(75 ± 5%) soil relative water content (SRWC)] and water stress (35–40% SRWC) for 7 days followed by re-watering to SRWC (75 ± 5%). The results showed that water-stressed plants under K0 application exhibited significant decline in net photosynthesis, stomatal conductance, intercellular CO_2 concentration and ribulose-1,5-bisphosphate carboxylase (Rubisco) activity and resulting in reduced photo-assimilates synthesis and partitioning towards reproductive organs in both cultivars. Conversely, K application decreased the decline in photosynthesis, Rubisco activity and biomass accumulation and partitioning. The positive effects of K application increased as increasing K rates, and that was more pronounced in Siza 3 than Simian 3. Drought stress decreased starch content but increased sucrose content; whereas, K application maintained higher concentration of sucrose in leaves of water-stressed plants through the regulation of higher sucrose phosphate synthase (SPS), sucrose synthase (SuSy) and lower soluble acid invertase (SAI) activities. The results of the study concluded that K application regulated the photo-assimilation and translocation process along with the related enzymes activities in cotton. The study suggests that K nutrient management strategy has the potential to minimize the impacts of drought stress in cotton.

1. Introduction

Cotton (*Gossypium hirsutum* L.) is very sensitive to biotic and abiotic stresses. Moreover, modern cultivars are more affected by environmental stresses due to indeterminate growth behavior, which directs the stress mitigation mechanism (Quisenberry and Roark, 1976). Drought stress reduces plant growth by affecting photosynthesis and cell expansion processes. Photosynthesis is the most essential process in the plant for growth and biomass production, thus it is the driving force for final yield (Pettigrew and Gerik, 2007). Studies about changes and fluctuations in morphological and physiological processes in crops to alleviate drought stress can be used to identify resistant genotypes, design cotton production schemes or develop new varieties for better productivity under drought stress conditions (Nam et al., 2001).

Under drought, crop photosynthesis rate reduces due to stomatal and/or non-stomatal limitations that may occur concurrently under severe stress. Non-stomatal factors are more important in reducing photosynthesis under severe stress while in mild drought stomatal limitation is the major factor affecting net photosynthesis (Cornic, 2000; Bota et al., 2004). Drought stress can also reduce leaf area, transpiration rate and total dry matter accumulation due to shedding of leaves and fruiting structures that leads to diminished final yield (Pettigrew, 2004). Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase E.C. 4.1.1.39) is the key enzyme involved in CO_2 fixation in photosynthesis, and its activity is rapidly flactuated for regulating the photosynthetic carbon reduction cycle during stress conditions (Field et al., 1998). Degree of reduction in Rubisco activity depends on the severity and/or duration of the drought as well as the genotypic difference of the cultivars (Arquero et al., 2006; Flexas et al., 2006). Limited

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http://dx.doi.org/10.1016/j.envexpbot.2017.02.002

carbon fixation caused by stomatal closure and reduced photosynthesis under drought stress disrupts carbohydrate metabolism and dry matter partitioning processes (Chaves et al., 2002). Nontheless, inspite of this reduction, plants accumulate a lot of carbohydrates (Villadsen et al., 2005; Valliyodan and Nguyen, 2006); which act as osmolytes to mitigate drought stress, an acclimating response in plants under drought. Ultimately organic carbon has to be shifted to regulate osmoregulation which increases root-to-shoot ratio due to low availability of carbon for shoot growth.

In water-stressed plants, limited *Pn* results in reduced photo-assimilates synthesis, meanwhile, stored reserves i.e. starch is depleted due to continuous respiration in plants (Galmés et al., 2007). Hence, an imbalance occurrs between photo-assimilates accumulation and their utilization through photo-respiration resulting in reduction of photo-assimilates translocation towards reproductive organs (Abid et al., 2016b). Additionally, carbohydrate metabolizing enzymes are also down or upregulated by the sugar status of plant cell. Both SPS (Sucrose phosphate synthase E. C. 2.4.1.14) and SuSy (Sucrose synthase E.C. 2.4.1.13) are involved in sucrose synthesis and their combined effect under drought stress stimulate high sucrose production. Whereas, SAI (Soluble acidic invertase EC 3.2.1.26) catalyzes sucrose hydrolysis into glucose and fructose; low concentration of SAI also promotes osmoregulation by increasing sucrose accumulation in stressed leaves (Kaur et al., 2007).

Promising evidence is there, which states that mineral nutrients play a critical role to withstand the adverse environmental conditions (Kant and Kafkafi, 2002; Hawkesford et al., 2012). Potassium (K) is an essential nutrient and is the most abundant cation in plants, plays a pertinent role in plant growth and almost in all related functions. Previous studies show that sufficient K in plants enhanced *Pn*, plant growth, yield, and drought resistance in different crops under water stress conditions (Egilla et al., 2001; Pervez et al., 2004; Thalooth et al., 2006). K promoted solutes accumulation during drought in soybean (*Glycine max*) (Itoh and Kumura, 1987), maize (*Zea mays* L.) (Premachandra and Ogata, 1991) and cotton (Pervez et al., 2004). K application positively influenced the normal funtioning of stomata, biomass production (Zhao et al., 2001), biomass partitioning (Reddy and Zhao, 2005; Makhdum et al., 2007) and morphological indices (Gerardeaux et al., 2009) in cotton crop. Under drought stress, in K deficient plants, stomata cannot function properly and moisture is lost through transpiration, which results in decreased CO_2supply to chloroplasts and limited *Pn* (Flexas et al., 2004). K can play imperative role for improving photo-assimilates production by increasing *Pn* meanwhile, sucrose accumulation and translocation by regulating the carbohydrate metabolizing enzymes. Our previous study reported that SPS, SuSy and SAI, the main enzymes involved in sucrose synthesis, accumulation and degradation, are fluctuated by K level in cotton leaves (Hu et al., 2015). Carbohydrate metabolizing enzymes response to K application in drought stressed plants is needed further elucidation to fully understand the drought mitigation mechanism in cotton by K nutrient management.

Under drought stress conditions K uptake from soil is impeded because diffusion of K to roots is reduced due to low soil moisture (Mengel and Kirkby, 2001). So, sufficient availability of K may be better to maintain proper growth during stress period. Previous researchers observed higher *Pn* in drought stressed plants with higher dose of K than those under lower application (Pier and Berkowitz, 1987; Pervez et al., 2004). However, few studies provide complete information about the critical role of K in photosynthetic system and photo-assimilate partitioning in cotton cultivars possessing variable K use efficiency under drought stress. This study was aimed to investigate the effect of K in regulating the enzyme activities involved in carbohydrate metabolism and photo-assimilate partitioning in different cotton cultivars under drought stress conditions.

2. Materials and methods

2.1. Plant materials and growth conditions

The experiment was conducted at Pailou Experimental Station, Nanjing Agriculture University, Jiangsu Province, P. R. China. Two cotton cultivars, Simian 3 (low K-tolerant) and Siza 3 (low K-sensitive) (Hu et al., 2015), were sown in nursery on 5th of April 2015 and 7th of April in 2016. Individual healthy and uniform seedlings with three true leaves were transplanted in plastic pots. The pots (37 cm in diameter and 32 cm high) were filled with 25 kg of well-mixed fertile soil collected from the topsoil layer up to 30 cm depth from the experimental station. The soil type was clay, mixed, thermic, Typic Alfisols (Udalfs; FAO Luvisol) and contained 16.5 g kg^{-1} organic matter, 1.1 g kg^{-1} total nitrogen (N) content, 70.8 mg kg^{-1} available N, 23.6 mg kg^{-1}available Phosphorus (P) and 97.3 mg kg^{-1} exchangeable K content. All recommended cultural and plant protection practices were applied for normal cotton growth.

2.2. Experimental design and treatments

Experiment consisted three Potassium levels i.e., 0 (K0), 150 (K1) and 300 (K2) K_2O kg ha^{-1} with two water regimes control (WW) and drought (DS) imposed on two cotton cultivars Siza 3 (low K-sensitive) and Simian 3 (low K-tolerant). K fertilizer was applied in splits, 40% before transplanting and 60% at flower initiation stage using potassium sulphate. 120 kg P_2O_5 ha^{-1} before transplanting whereas, 240 kg N ha^{-1} in two splits 40% before transplanting and 60% at flowering stage were applied, respectively. Single plant was planted in each pot and every pot was considered as a replication. All plants were watered equally up to flower initiation on 6–7th fruiting branches. At flowering all pots were divided into two halves. One half pots continued to be watered as before and other half pots were stopped to be watered for 7 days till the moisture level reached to severe soil drought stress at 35–40% soil relative water content (SRWC) and then re-watered up to 75 ± 5% SRWC. Soil moisture level of all pots was maintained by following the method adapted by Liu et al. (2008). Soil samples from 0 to 25 cm depth were collected on daily basis during drought stress treatment at 18:00–19:00 local time with a punch (2 cm diameter) from different pots of each half and then composite samples were collected. 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 from control half would be watered to maintain 75 ± 5% SRWC in the early morning. Pots were placed under polythene shelter to avoid rain during treatment.

2.3. Plant sampling and measurements

The youngest fully expanded main stem leaves (fourth leaf from the top, functional cotton leaf) were selected at the flowering stage to minimize the confounding influence of location on measurements. Measurements were made on last day of drought stress and after 10 days of re-watering. After measurements, the leaf samples were taken to lab immediately in ice box for further analysis. Leaves were washed with distilled water and removed the midrib. Half part of each sampled leaf was stored in −40 °C for assay of enzyme activity for carbon metabolism (Rubisco, SPS, SuSy, SAI); whereas, other part of leaf was dried at 105 °C for 30 min and then to constant weight at 80 °C.