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Potassium (K) supply affects K accumulation and photosynthetic physiology in two cotton (*Gossypium hirsutum* L.) cultivars with different K sensitivities

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ABSTRACT

A two-year field experiment was established to investigate the differences in the process of potassium (K) accumulation and photosynthetic physiology of functional leaves of two cotton (*Gossypium hirsutum* L.) cultivars with contrasting K sensitivity (Simian 3, low-K-tolerant cultivar and Siza 3, low-K-sensitive cultivar) under three K levels (0,150 and 300 kg K_2O ha^{-1}). Results in 2012 and 2013 indicated that the maximum theoretical accumulation of K, the maximum and average accumulation rate of K increased in the K-supply treatments (150 and 300 kg K_2O ha^{-1}), and the K accumulation in reproductive and reproductive organs was increased by K application. Decreased net photosynthetic rate (P_n) in the 0 kg K_2O ha^{-1} treatment was attributed to stomatal limitation at the boll setting stage for Simian 3 and at the peak flowering stage for Siza 3. After which, non-stomatal factors (low chlorophyll content, unbalanced chlorophyll a to chlorophyll *b* ratio, negative chlorophyll fluorescence parameters and decreased carboxylation efficiency) dominated the reduction in P_n under K deficiency. High total and initial Rubisco, sucrose phosphate synthase and sucrose synthase (SuSy) (except SuSy in Simian 3) activities did not result in high hexose, sucrose and starch contents in the K-supply treatments, because of a higher rate of sucrose export. Compared with Simian 3, the sensitivity of Siza 3 to low-K was showed in the following aspects: (1) the duration of K rapid-accumulation was increased by K application; (2) P_n, chl a + b and chlorophyll fluorescence parameters, especially *q*N, under K deficiency were more negative; (3) the occurring time of non-stomatal limitation under K deficiency was earlier; (4) the net photosynthetic rate of unit chlorophyll was significantly promoted by K application; (5) Siza 3 needed higher leaf K content to maintain Rubisco activation state; and (6) SuSy activity was increased by K application.

1. Introduction

Potassium (K) is the main inorganic cation in plants and plays a significant role in many physiological and metabolic processes, such as activation of numerous enzymes, maintenance of charge balance, cytoplasmic pH homeostasis, osmotic potential and water uptake, regulation of stomatal activity and photosynthate translocation (Oosterhuis et al., 2014). In recent years, K deficiency has become a very common problem around the world, and has occurred in many provinces of China (Wang et al., 2012). Moreover, severe K deficiency has been observed in cotton (*Gossypium hirsutum* L.) production, even when the K fertilizer was applied. This phenomenon is considered to occur because that some new cotton cultivars seem to be more sensitive to K than conventional cultivars (Dong et al., 2010; Zhang et al., 2007). Hence, there is a need to understand the differences between the two types of cotton cultivars in response to K application.

Abbreviations: CV(%), coefficient of variance; W_m, the maximum theoretical accumulation of potassium; V_m, the maximum accumulation rate of potassium; V_T, the average accumulation rate of potassium; t_1, the start time of the potassium rapid-accumulation period; t_2, the termination time of the potassium rapid-accumulation period; T, the duration of the potassium rapid-accumulation period; t_m, the occurrence time of maximum accumulation rate of potassium; P_n, net photosynthetic rate; g_s, stomatal conductance; C_i, intercellular CO_2 concentration; P_{max}, the maximum net photosynthetic rate; *CE*, carboxylation efficiency; *Ls*, relative stomatal limitation to photosynthesis; *Fv*/*Fm*, the maximal photochemical efficiency of PSII; Φ_{PSII}, the actual PS II efficiency; *q*P, the coefficient of photochemical quenching; *q*N, the coefficient of non-photochemical quenching; DAT, days after transplanting; PFS, the peak flowering stage; BSS, the boll setting stage; BOS, the boll opening stage; Rubisco, ribulose-1,5-bisphosphate carboxylase-oxygenase; SPS, sucrose phosphate synthase; SuSy, sucrose synthase.

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Cotton is more sensitive to low-K stress than other crops (Cassman et al., 1989), and K deficiency inhibits cotton growth and physiological processes, such as carbon assimilation (Wang et al., 2012), nitrogen assimilation (Hu et al., 2016a) and maturity (Pettigrew, 2003). Net photosynthetic rate (P_n) decreased significantly under low-K stress (Oosterhuis and Bednarz, 1997). Although the physiological basis for the decreased P_n under K deficiency has been investigated since 1960s, inconsistent conceptions still exist (Dong et al., 2004). Moss and Peaslee (1965) stated that the reduction in P_n was attributed to the increased stomatal diffusion resistance, but Longstreth and Nobel (1980) indicated that the reduction in P_n might be caused by increased mesophyll resistance. Zhao et al. (2001) reported that the decrease in P_n was related to poor chloroplast ultrasctruture, decreased chlorophyll content and low transport rate of saccharide, rather than the decreased stomatal conductance in K-deficient leaves. Similarly, Wang et al. (2012) also reported that biochemical factors might be the main causes of decreased photosynthesis. von Caemmerer et al. (1997) shared that low Rubisco activity could result in a reduced rate of photosynthesis. Sucrose phosphate synthase (SPS) and sucrose synthase (SuSy) could determine the allocation of photosynthate within the leaf (Galtier et al., 1993; Liu et al., 2013). In addition, previous studies reported that K application influenced SPS activity in the leaves of soybean (Huber, 1984) and SuSy activity in the tubers of potato (*Solanum tuberosum*) (Lindhauer and De Fekete, 1990). Therefore, the effects of K deficiency on photosynthesis might be interrelated with stomatal conductance and biochemical factors. Dong et al. (2004) suggested that the reasons causing the reduction in P_n should depend on the growth stage and the degree of K stress, and there was a need to study the main cause for the reduction in P_n under K deficiency at different growth periods of cotton.

Genotypic differences in K sensitivity have been reported in various crops including rice (*Oryza sativa* L.) (Jia et al., 2008), soybean (*Glycias max* L.) (Li et al., 2011) and cotton (Tian et al., 2008). Low-K-tolerant and low-K-sensitive cotton cultivars were screened in pot and field experiments according to yield, fiber quality and K^+ assimilation (Zhang et al., 2007; Yang et al., 2014). The cultivars with different K sensitivities had different K efficiencies, and the mechanisms of K efficiency included uptake efficiency and use efficiency (Tian et al., 2008). High-efficient K uptake could maintain a higher K content to ensure plant growth and development despite low K availability in the soil. Moreover, those cultivars with high K-uptake efficiency usually had well-developed root morphology and efficient physiological uptake characteristics (Rengel and Damon, 2008). Previous studies have reported that wheat and cotton genotypes differed in V_{max} (the capacity of root absorbing K^+) and K_m (the K^+ concentration when K uptake rate is half of V_{max}) (Glass and Perley, 1980; Tian et al., 2008). However, the differences in dynamic accumulation process after K absorption among different types of cotton are still not well documented. The crops with high utilization efficiency could achieve higher yield and quality with lower K concentration in the dry matter, which was defined as high K-use efficiency in plants (Brouder and Cassman, 1990). Wang et al. (2012) indicated that the different K utilization efficiencies among genotypes were due to certain biophysical functions, but the differences in biophysical functions in response to K among different types of cotton were not fully understood. Therefore, this study was designed to explore the effects of K supply on the physiological mechanisms in two cotton cultivars with different K sensitivities. The objectives of this study were (1) to determine the effects of K application on the dynamic process of K accumulation for the two types of cotton cultivars with contrasting K sensitivity, and (2) to investigate the effects of K application on photosynthesis and the associated physiological mechanism at different growth periods for the two types of cotton cultivars.

2. Materials and methods

2.1. Experimental design

Two cultivars with different K sensitivities have been screened according to cotton yield and quality using pot and field experiments (Yang et al., 2014). Simian 3 (low-K-tolerant cultivar) was developed by the Original Seed Farm of Siyang and widely planted in the Yangtze River Valley cotton belt in 1990s, and Siza 3 (low-K-sensitive cultivar) was developed by the Suqian Academy of Agricultural Sciences and was the main cotton cultivar planted in the Yangtze River Valley cotton belt since the early 21st century. Field experiment was established in the experimental station of Nanjing agricultural university, China (118°50′E, 32°02′N) in 2012 and 2013. In order to avoid residual effects of K fertilizer from previous year's experiment, the 2012 and 2013 sites were in two adjacent parts of the same field. The soil in the depth of 0–20 cm was clay, mixed, thermic, Typic alfisols (udalfs; FAO luvisol) with a pH of 6.7. The nutrient characteristics of the soil before sowing were 15.9 and 17.1 $g\,kg^{-1}$ organic matter, 0.9 and 1.1 $g\,kg^{-1}$ total nitrogen (N), 69.8 and 77.3 $mg\,kg^{-1}$ mineral N ($NH_4{}^+$-N and $NO_3{}^-$-N), 23.6 and 18.1 $mg\,kg^{-1}$ Olsen phosphorus (P), and 86.3 and 91.8 $mg\,kg^{-1}$ exchangeable K in 2012 and 2013, respectively, and the exchangeable sulfur was 29.9 $mg\,kg^{-1}$ in 2012. Seedlings were raised in nutrient bowls in a nursery bed covered by plastic film and were transplanted into the field at three true leaves stage on 23 May 2012 and on 30 May 2013. The experiment was arranged in a split-plot design with three replications. Main plots were varieties (Simian 3 and Siza 3) and subplots were K levels. Each main plot was 26 m long and 8 m wide, and each subplot was composed of 10 cotton rows with row spacing of 0.85 m, row length of 8 m and inter-plant spacing of 0.35 m. Three K levels were used: (I) 0 $kg\,K_2O\,ha^{-1}$, (II) 150 $kg\,K_2O\,ha^{-1}$ (the most economic quantity of K based on the exchangeable K in soil) (Xia et al., 2010), and (III) 300 $kg\,K_2O\,ha^{-1}$ using potassium sulfate (50% K_2O and 18% sulfur) at the transplanting stage. In order to avoid the effects of different sulfur levels on cotton growth and development, ordinary superphosphate (12% P_2O_5 and 12% sulfur) was applied at the transplanting stage to provide P fertilizer of 120 $kg\,ha^{-1}$. Nitrogen fertilizer was applied at the rate of 240 $kg\,N\,ha^{-1}$ using urea (46% N), with 96 $kg\,N\,ha^{-1}$ applied at the transplanting stage and 144 $kg\,N\,ha^{-1}$ applied at the flowering stage.

2.2. Photosynthetic parameters, chlorophyll fluorescence parameters and carbohydrates contents

Photosynthetic parameters (P_n, net photosynthetic rate; g_s, stomatal conductance; C_i, intercellular CO_2 concentration) were measured on the fourth main-stem leaf from the terminal of the plant as three replications between 9:00 and 11:00 at the peak flowering stage (PFS, the stage when more than 50% of all plants have white flowers on the first node of 4th fruiting branches) on 16 July 2012 and 20 July 2013, the boll setting stage (BSS, the period between the time the first white flower appears in the field and the time the boll begin to open) on 4 August 2012 and 5 August 2013, and the boll opening stage (BOS, the period between the time the boll begin to open and the time all the bolls are harvested) on 26 August 2012 and 28 August 2013 with a Portable Photosynthesis System Li-6400 (Li-COR, Lincoln, NE, USA) at 1500 $\mu mol\,m^{-2}\,s^{-1}$ quantum flux, 32 ± 2 °C leaf temperature, 380 ± 5 $\mu mol\,mol^{-1}$ CO_2 concentration and 65 ± 5% relative humidity. P_n vs. C_i curves were measured at BSS and BOS in 2013. Relative stomatal limitation to photosynthesis (L_S) was calculated as $L_S = 1\text{-}P_n/P_o$ according to Farquhar and Sharkey (1982), where P_o is the expected photosynthetic rate when intercellular CO_2 concentration is equal to ambient CO_2 concentration.