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Potassium application affects carbohydrate metabolism in the leaf subtending the cotton (*Gossypium hirsutum* L.) boll and its relationship with boll biomass

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ABSTRACT

Field experiments were conducted in 2012 and 2013 with two cotton (*Gossypium hirsutum* L.) cultivars (Simian 3, low-K tolerant; Siza 3, low-K sensitive) under three levels of potassium (K) fertilization (0, 150 and 300 kg K_2O ha^{-1}). Results showed that K application increased leaf K concentration, net photosynthetic rate (*Pn*), stomatal conductance (*Gs*), plant biomass and stimulated boll biomass (capsule wall, seed and lint biomass). K application increased the proportion of lint biomass, decreased the proportion of seed biomass, and did not affect the proportion of capsule wall biomass. Specific leaf weight (SLW), maximum/minimum sucrose contents and nonstructural carbohydrate (hexose, sucrose, starch) decreased, but sucrose transformation rate in LSCB increased in both cultivars after K application, the leaf critical K levels for hexose content, sucrose content and starch content were 1.1%, 1.3%, 1.2–1.4% in Simian 3 and were 1.6%, 1.7% and 1.7–1.8% in Siza 3, respectively. The activities of ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco), cytosolic fructose-1,6-bisphosphatase (cy-FBPase), sucrose phosphate synthase (SPS), sucrose synthase (SuSy) and amylase activities increased by K application, whereas soluble acid invertase (SAI) activity decreased. SPS and SuSy activities in Siza 3 were more sensitive than that in Simian 3. Correlation analysis revealed that higher *Pn*, sucrose transformation rate and SPS activity in LSCB were necessary to improve boll biomass, but the accumulation of sucrose in LSCB was not beneficial to boll biomass.

1. Introduction

Potassium (K) is one of the major mineral elements for normal plant growth and development, and plays a vital role in many physiological processes, including maintenance of charge balances, tissue turgor pressure, electrogenic transport processes and photosynthesis, regulation of stomata movement, activation of numerous enzymes and in protein synthesis (Dobermann, 2001; Oosterhuis et al., 2014). In recent years, K deficiencies have been increasing across 30 provinces in China, which will limit crop growth and development and represents a significant threat to China's future crop production. To rectify this deficiency of K will require an increase in K fertilizer use of more than 8% per year (Sheldrick et al., 2003).

Cotton (*Gossypium hirsutum* L.) has a large demand for K and appears to be more sensitive to low K availability than other crops (Cassman et al., 1989; Oosterhuis, 2001). K deficiency decreases seed cotton yield and lint yield (Pettigrew, 1999; Gormus and Yucel, 2002; Read et al., 2006), attributable to reduced boll weight (Gormus, 2002), lower boll number (Li et al., 2012) and lower lint percentage (Pettigrew, 1999). K deficiency negatively affects cotton fiber quality, by decreasing fiber length (Cassman et al., 1990), uniformity ratio (Pettigrew et al., 1996), fiber strength (Cassman et al., 1990; Minton and Ebelhar, 1991) and micronaire (Pettigrew et al., 2005). Some studies have shown that K deficiency also negatively affected cotton photosynthesis (Bednarz et al., 1998; Pervez et al., 2004), biomass production (Zhao et al., 2001), altered biomass

Abbreviations: CV(%), coefficient of variance; *Pn*, net photosynthetic rate; *Gs*, stomatal conductance; Rubisco, ribulose-1,5-bisphosphate carboxylase-oxygenase; cy-FBPase, cytosolic fructose-1,6-bisphosphatase; DPA, days post anthesis; LSCB, leaf subtending the cotton boll or the subtending leaf; SLW, specific leaf weight, mean the weight per cm^2 leaf; SPS, sucrose phosphate synthase; SuSy, sucrose synthase; SAI, soluble acid invertase.

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partitioning (Reddy and Zhao, 2005; Makhdum et al., 2007) and morphological indices (Gerardeaux et al., 2009*b*).

K deficiency significantly reduced dry matter partitioning to reproductive organs (Pettigrew et al., 2005; Makhdum et al., 2007) and increased dry matter partitioning to the leaf (Gerardeaux et al., 2009a; Wang et al., 2012). K deficiency increased carbohydrate concentrations in the cotton leaf (Bednarz and Oosterhuis, 1999), which may be associated with inhibition of phloem loading (Marschner et al., 1996; Zhao et al., 2001), such that the K disorder may cause an imbalance of source and sink (Wright, 1999). In cotton, the leaf subtending the cotton boll (LSCB) plays a vital role contributing to boll development as it is the main source of carbohydrate for the boll, supplying 60–87% of the total photoassimilate requirements (Constable and Rawson, 1980; Wullschleger and Oosterhuis, 1990; Liu et al., 2013).

Sucrose and starch are the main products of photosynthesis in most plants including cotton, although sucrose is the primary photosynthate transported from source to sink tissues and can be broken down into hexoses, which provide carbon and energy for plant growth. Starch as a temporarily stored carbohydrate can be converted into sucrose (Gandin et al., 2009). Previous studies have suggested that under K deficiency, soybean (*Glycine max*) (Huber, 1984) leaves had significantly higher hexose, sucrose and starch contents. In contrary, starch content in lemon (*Citrus volkameriana* Ten. & Pasq) leaves (Lavon et al., 1995) and sucrose content in maize (*Zea mays* L.) leaves (Pretorius et al., 1999) were reduced under K deficiency. There are many important enzymes involved in carbohydrate metabolism processes. Rubisco is the key and rate-limiting enzyme in the Calvin cycle, SPS (sucrose phosphate synthase, E.C. 2.4.1.14), SuSy (sucrose synthase, E.C. 2.4.1.13) and acid invertase are the main enzymes that control sucrose accumulation and degradation (Hendrix and Huber, 1986). The penultimate step in sucrose synthesis is catalyzed by SPS and the first committed step is catalyzed by cy-FBPase (cytosolicfructose-1,6-bisphosphatase, E.C. 3.1.3.11) (Liu et al., 2013). Amylase plays a important role in starch degradation (Hammond and Burton, 1983). Previous research has shown that all these enzymes were affected by K status. Rubisco activity decreased in alfalfa(*Medicago sativa* L.) (Peoples and Koch, 1979) leaves under K deficiency, but was hardly affected in mulberry (*Morus alba* L.) (Yamashita and Hikasa, 1988). SPS activity declined and acid invertase activity increased under K deficiency in soybean (Huber, 1984), but SPS activity was unaffected in maize (Pretorius et al., 1999). SuSy activity and amylase activity decreased in potato (*Solanum tuberosum*) under K deficiency (Lindhauer and De Fekete, 1990). In contrast, amylase activity was significantly higher in K-deficient leaves of lemon (Lavon et al., 1995). Therefore, carbohydrate metabolism of different plants has different responses to K deficiency. K deficiency has been shown to affect carbohydrate content in main-stem leaf of cotton (Bednarz and Oosterhuis, 1999) and partitioning to the reproductive components of cotton (Pettigrew et al., 2005), but the explanation of this is lacking.

The objectives of our research were (1) to study the effect of K on changes of plant and boll biomass partitioning during boll forming stage on the basis of carbohydrate metabolism in LSCB; (2) to understand the relationships between boll biomass and carbohydrate metabolism of cotton in relation to K fertility; and (3) to identify sensitive enzymes to K in carbohydrate metabolism for the two cultivars with different low-k sensitivity.

2. Materials and methods

2.1. Plant material

Two cotton cultivars, Simian 3 (low-K tolerant) and Siza 3 (low-K sensitive) were selected in this study based on the variance of yield and fiber quality of 12 diverse cultivars, predominantly grown in the lower Yangtze region in China (Yang et al., 2014). Simian 3, was developed by the Siyang Original Seed Farm of Jiangsu Province, and Siza 3, was developed by the Cotton Research Group, Suqian Academy of Agricultural Sciences.

2.2. Experimental design

Field experiments were conducted in the summer seasons of 2012 and 2013 at the Pailou experimental station of Nanjing Agricultural University, located at Nanjing, China (118°50′E, 32°02′N). The 2012 and 2013 field sites were located adjacently. The soil type was clay, mixed, thermic, Typic alfisols (udalfs; FAO luvisol) with a slightly acid pH of 6.7, the soil samples were collected at a 20 cm depth before sowing cotton, and the soil nutrient contents are listed in Table 1. Seeds were planted in a nursery bed on 23 April 2012 and 30 April 2013, and transplanted into the field when the cotton seedling had three true leaves. The experiment was performed in a randomized complete design with three replications. Plot size was 13 m long and 6.6 m wide, with 0.85 m between rows and 0.35 m between plants in the row. A uniform fertilizer application of 120 kg P_2O_5 ha^{-1} (at transplanting stage) and 240 kg N ha^{-1} (40% at transplanting and 60% at the flowering stage) was applied. The treatments consisted of three K fertilizer rates: (i) 0 kg K_2O ha^{-1}, as a control, (ii) 150 kg K_2O ha^{-1} (the recommended quantity of K under the soil available K in this experiment) (Xia et al., 2010), and (iii) 300 kg K_2O ha^{-1} using potassium sulphate.

2.3. Sampling and processing

White flowers at the first node of fruiting branches 7–8th of all plant were tagged with plastic tags that were used for noting the flowering date. The total time for tagging all treatments was not more than three days, to ensure that the labeled flowers had equivalent metabolic and developmental ages for all treatments. These tagged bolls and their subtending leaves were sampled every 7 days from 10 to 45 days post anthesis (DPA) at 9:00–10:00 A.M. local time. The samples of leaves were washed with distilled water, and divided into two halves by cutting the main vein; one half was immediately placed in liquid nitrogen and stored in an ultra-low temperature freezer (−80 °C) until enzymatic measurement, and the other half was used to measure leaf area and dry weight for calculating specific leaf weight (SLW), and the dried leaf tissues were then used to determine carbohydrate metabolism and leaf K concentration using an atomic absorption spectrophotometer (SpectAA-50/55, Varian, Australia). When the bolls opened, 50 tagged bolls in each treatment were harvested for the measurements of boll biomass accumulation and partitioning in to capsule wall, seed and lint biomass.

Table 1
Soil organic matter, nitrogen, phosphorus and potassium contents at the experimental sites in 2012 and 2013.

Year	Organic matter content (g kg^{-1})	Total N content (g kg^{-1})	Available N content (mg kg^{-1})	Available P content (mg kg^{-1})	Available K content (mg kg^{-1})
2012	15.9	0.9	69.8	23.6	86.3
2013	17.1	1.1	77.3	18.1	91.8