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Changes of sucrose metabolism in leaf subtending to cotton boll under cool temperature due to late planting

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ABSTRACT

Because reproductive growth could be influenced by sucrose metabolism of major source leaf (leaf subtending to cotton boll, LSCB), we hypothesized that decreased temperatures under field conditions would limit morphology and biomass distributions of the whole cotton plant by decreasing photosynthesis of LSCB and inhibiting sucrose metabolism in LSCB. To address this hypothesis, two cotton cultivars, Kemian 1 and Sumian 15, were grown at three planting dates (25 April, 25 May and 10 June) in 2009–2011 to obtain LSCB and bolls exposed to contrasting ambient temperatures while at the same developmental stage (white flowers on the first position of 6–7th fruiting branches). Sample collection and measurement were conducted during boll development at MDTmin of 25.9 °C and 24.0 °C for the early planting date of 25 April (optimal planting date in the Yangtze River Valley), 20.4 °C and 18.4 °C for the 25 May planting date, and 16.5 °C and 16.0 °C for the 10 June planting date in 2010 and 2011, respectively. Microclimate measurements included photosynthetic active radiation, relative humidity and air temperature. Late planting decreased boll number, boll weight, LAI, total biomass and harvest index ($P < 0.05$), but increased leaf to shoot, leaf to stem and leaf to boll ratios. Cool temperature increased SLW and carbohydrate contents in LSCB, but decreased *Pn* and sucrose transformation rate in LSCB ($P < 0.05$). Under cool temperatures (MDTmin of 20.4 °C and 16.5 °C in 2010, and 18.4 °C and 16.0 °C in 2011 during boll development) in the late planting dates (25 May and/or 10 June), the activities of Rubisco and cytosolic fructose-1,6-bisphosphatase (cy-FBPase) increased, whereas sucrose phosphate synthase (SPS) and sucrose synthase (SuSy) activities decreased, and their peak values were delayed. The variability of *Pn*, SPS activity, sucrose transformation rate in LSCB and boll weight under cool temperature for Sumian 15 was greater than those of Kemian 1. In addition, there was a significantly positive correlation between *Pn* and SPS in LSCB, as well as SPS and boll weight in 2010 and 2011 ($P < 0.05$). It is concluded that, of the measured physiological and reproductive processes, the difference of sucrose metabolizing enzymes in LSCB for the two cotton cultivars under cool temperature due to late planting were mainly determined by SPS activity, while higher *Pn* and SPS in LSCB were necessary to improve boll weight. However, greater boll weight does not necessarily need high *Pn*, SPS and SuSy activities, and great sucrose transformation rate in LSCB.

1. Introduction

Cool temperature is one of the most important environmental constraints for crop growth in agriculture (Janas et al., 2002). The periods of flowering and boll development of cotton in many cotton growing areas are restricted partly because of cool temperature in late season in many cotton-growing areas (Gormus and Yucel, 2002). The ideal temperature range for cotton optimal metabolic activities (also known as the thermal kinetic window) is 23.3–32.2 °C (Burke et al., 1988), and fruiting and yield decrease with a low minimum temperature of 22 °C (Liakatas et al., 1998). Furthermore, the synthesis and export of photosynthate were greatly hindered and bolls failed to develop normally at

Abbreviations: CV(%), coefficient of variance; cy-FBPase, cytosolic fructose-1,6-bisphosphatase; DPA, days post anthesis; FAPAR, fractional interception of absorbed photosynthetic active radiation; LAI, leaf area index; LSCB, leaf subtending to cotton boll or the subtending leaf; MDT, mean daily temperature; MDTmax, mean daily maximum temperature; MDTmin, mean daily minimum temperature; MDTdif, mean diurnal temperature difference; PAR, photosynthetic active radiation; RH, relative humidity; Rubisco, ribulose-1,5-bisphosphate carboxylase-oxygenase; SLW, specific leaf weight, mean the weight per cm^2 leaf; SPS, sucrose phosphate synthase; SuSy, sucrose synthase; T_{air}, canopy air temperature.

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temperatures lower than 15 °C (Guo et al., 1991; Martin and Haigler, 2004). Previous studies compared the weather data (maximum and minimum daily air temperature and photonflux density) and microclimate measurements including photosynthetic active radiation (PAR), relative humidity (RH) and canopy air temperature (T_{air}) in the different planting dates. These studies reported that in different planting dates, temperature was the main factor affecting diurnal pollen tube growth rate, biomass distributions, cotton yield and quality (Yeates et al., 2010a,b,c; Snider et al., 2011), although cool temperature reduced radiation use efficiency (Cirilo and Andrade, 1994; Yeates et al., 2010b). Therefore, to more realistically reflect the effect of cool temperature on cotton growth and physiological metabolism, planting date studies have been used instead of controlled environment chamber studies (Dong et al., 2006; Yeates et al., 2010a,b,c; Snider et al., 2011; Zheng et al., 2012).

Cool temperature due to late planting decreased crop growth rate and leaf area index (LAI) in the reproductive stage, and strongly decreased dry matter partitioning to reproductive organs (Cirilo and Andrade, 1994; Bange and Milroy, 2004). Some studies have suggested that physiological metabolism in the major source leaves may correlate with reproductive metabolism to ensure sufficient assimilate allocation to developing reproductive units (i.e., flowers and bolls) under temperature stress (Guinn, 1985; Kurek et al., 2007), although the involvement of mineral nutrition or plant hormones cannot be excluded (Guinn and Brummett, 1989). In cotton (*Gossypium hirsutum* L.), the leaf subtending to cotton boll (LSCB) is the primary source of carbohydrate for a boll, supplying 60–87% of the total requirement (Ashley, 1972; Constable and Rawson, 1980; Wullschleger and Oosterhuis, 1990). Therefore, LSCB plays a crucial role in contributing to cotton yield, particularly to boll weight during boll development.

Sucrose and starch are the principal end products of photosynthesis in most plants including cotton. Moreover, sucrose is the principal carbohydrate translocated from source to sink tissues (Lunn and Hatch, 1995), and is sensitive to abiotic stress. Sucrose metabolizing enzymes have been studied extensively. Rubisco is the key and rate-limiting enzyme in the Calvin cycle. SPS, a key regulatory enzyme involved in carbon partitioning between sucrose and starch in leaves (Huber and Huber, 1996), is often closely correlated with the rate of sucrose export in source tissues (Huber and Huber, 1992). It catalyzes the penultimate step in sucrose synthesis, and shares control of this pathway with the first committed step catalyzed by cytosolic FBPase. A recent study about SuSy with orchid (*Oncidium goldiana*) suggested that its crucial function in plant metabolism was mainly sucrose breakdown and energy provision (Li et al., 2002). All of these enzymes are affected by cool temperature, but the response of these enzyme activities to temperature varies in different plants and/or organs. Rubisco and SPS activities might increase (Bascuñán-Godoy et al., 2006) or decline (Van Heerden et al., 2004) at cool temperature in some species. Moreover, cytosolic FBPase activity may either increase (Guy et al., 1992) or remain constant (Du and Nose, 2002) under cool temperature. Previous studies have focused on carbohydrate contents or sucrose metabolizing enzymes of expanding leaf in cotton under suitable environmental conditions. They also focused on cotton seedling in artificial growth chambers imitating natural cool temperature conditions (Perera et al., 1995; Zhao and Oosterhuis, 2000). However, little is known about the effects of natural cool temperature caused by late planting on biomass partitioning or the dynamic changes in carbohydrate contents and their corresponding key enzymes in LSCB during boll development under field conditions.

The study aimed (1) to study the effect of cool temperature on changes of morphology and biomass partitioning of the whole cotton plant; (2) to find sensitive enzymes to temperature in sucrose metabolism for the two cultivars; and (3) to clarify the relationship between sucrose metabolism, *Pn* and boll weight, under cool temperature due to late planting. These results might elucidate the physiological and biochemical mechanism of LSCB under cool temperature, to help breeding and selection of new cotton cultivars with enhanced tolerance to cool temperature.

2. Materials and methods

2.1. Experimental design

A pot experiment in 2009 and field experiments in 2010 and 2011 were conducted at the Pailou experimental station, Nanjing, Jiangsu, China (118°50′E, 32°02′N). The soil at the experimental site was clay, mixed, thermic, Typic alfisols (udalfs; FAO luvisol) in 20 cm depth of the soil profile, and the soil nutrient contents before sowing cotton are listed in Table 1.

Cotton cultivars were different sensitive to cool temperature (Martin and Haigler, 2004). Based on the variance of fiber strength, 14 diverse cultivars, widely grown in the Yangtze River Valley in China, were studied with different flowering dates (Wang et al., 2008). Cotton cultivars were clustered into three groups as a temperature-sensitive group (typical for Sumian 15), a moderately sensitive group (typical for NuCOTN 33B) and a temperature-tolerance group (typical for Kemian 1). Therefore, Kemian 1 (temperature-tolerate) and Sumian 15 (temperature-sensitive) were selected in this study. Furthermore, Shu et al. (2009) found that Sumian 15 was more sensitive than Kemian 1 in cellulose synthesis under cool temperature due to late planting.

To ensure that bolls and their subtending leaves selected for morphology and physiological measurements would be in the same developmental stage, i.e., the first-position of 6–7th fruiting branches, but exposed to different ambient temperature conditions during boll development, three planting dates, 25 April, 25 May and 10 June, were used in the 3 yrs. The optimal planting date was the middle- and late-ten day period of April, whereas 25 May and 10 June were the late planting dates in the Yangtze River Valley (Jiang et al., 2006). Cotton seeds were planted in nutrition pots in a nursery bed, and seedlings with three true leaves were transplanted into the plastic pots or into the field. In the pot experiment, each treatment had 33 pots (diameter 60 cm, height 55 cm) with 40 kg soil. In the field experiment, each treatment plot was 6 m wide and 10.5 m long, and three replications for each treatment were assigned randomly. Furrow-irrigation was applied as needed to minimize the moisture stress during each season. Conventional weed and insect control measures were utilized as needed.

2.2. Sampling and processing

For both pot and field experiments, white flowers on the first node of 6–7th fruiting branches of all plants were tagged with small plastic tags, and the flowering date was noted on the tags. White flowers were tagged for each planting date on the same day, no more than 3 days after the start of tagging, to ensure that the tagged flowers were of equivalent metabolic and developmental ages for each treatment. These labeled bolls and their subtending leaves were collected once every 7 days from 10 days post anthesis (DPA) until the boll opening dates. The bolls samples and their subtending leaves were collected at 9:00–10:00 am, and transported from the field to the lab in an ice box. The leaves were washed with distilled water, and divided into two halves each side of the main vein, one half was immediately placed in liquid N_2 and stored in an ultra-low temperature freezer (−80 °C) until enzymatic measurement. The remainder of the leaves was used for leaf area and biomass measurements for calculating specific leaf weight (weight per cm^2 leaf, SLW). Next, the dried leaves were used in carbohydrate