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SUCROSE METABOLISM FOR CELLULOSE BIOSYNTHESIS IN COLORED COTTON FIBERS

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Assays were conducted to examine the contents of cellulose and callose, and the activities of enzymes related to sucrose metabolism at various stages of fiber development in colored cottons and white cotton. The results showed that the cellulose accumulation could be described with Richard curve equations, and the cellulose biosynthesis was reflected by the eigenvalues, especially the maximum biosynthesis rate (V_{max}) and the time taken for cellulose rapid biosynthesis (T). The period from 20 days post anthesis (DPA) to 40 DPA is the key stage for cellulose accumulation in colored cotton. During this period reduced activity acid invertase (AI) and β-1,3-glucanase, and decreased accumulation and transformation of callose in colored cotton might limit carbon supply and cellulose accumulation by affecting V_{max} and T, thus inhibiting sucrose metabolism during cellulose biosynthesis, then results in poor fiber quality.
Keywords: Colored cotton, cellulose biosynthesis, callose, sucrose metabolism, enzyme activity.

INTRODUCTION

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Colored cotton (*Gossypium hirsutum* L.) has received increasing attention in recent years because it reduces the cost for dying, creates less environmental pollution, and is beneficial to human health (Hua *et al.*, 2007; Yuan *et al*., 2012; Zhu *et al*., 2006). However, poor quality has limited the further development of colored cotton (Yuan *et al*., 2012; Zhang *et al*., 2010). Fiber quality is mainly determined by cellulose content because the secondary cell walls in cotton fibers are nearly pure cellulose (Haigler *et al*., 2005). Therefore, to better understand the physiological mechanisms that determine poor quality, it is essential to understand the pathway of sucrose metabolism during cellulose biosynthesis in colored cotton fibers.

The metabolic pathway for sucrose is regulated by sugars and related enzymes (Koch, 2004). Sucrose is the initial carbon source for cellulose biosynthesis in cotton fibers (Ma *et al*., 2008) and can be degraded by sucrose synthase (SS) and acid invertase (AI) (Alonso *et al*., 2007; Coleman *et al*., 2009;Koch, 2004). As previous reports, lower SS activity could hinder UDPG generation and affect the formation of quality fibers (Zhang *et al*., 2009). Similarly, higher AI activity could provide more abundant materials and energy for sugar metabolism during cellulose biosynthesis in cotton fibers (Feng *et al*., 2009). In addition, sucrose phosphate synthase (SPS) could provide a continuous substrate for SS and consequently cellulose biosynthesis from UDPG in cotton fiber (Haigler *et al*., 2005; Koch, 2004). Higher SPS activity can provide more abundant sucrose for sugar metabolism and subsequently maintain faster and more stable accumulation of cellulose for an extended period during cellulose biosynthesis (Feng *et al*., 2009).

Alternatively, the biosynthesis of cellulose in cotton fibers is accompanied by the biosynthesis of β-1,3-glucan (callose) which deposited naturally in cotton fibers during secondary wall development (Scheible and Pauly, 2004). Like sucrose, callose can be degraded to UDPG by β-1,3-glucanase (Delmer, 1999). The higher activity of β-1,3-glucanase could completely transform callose during late fiber development, provide more abundant UDPG for sucrose metabolism, and maintain rapid and stable accumulation of cellulose for an extended period during cellulose biosynthesis (Feng *et al*., 2009). In contrast to white cotton, cellulose biosynthesis in colored cotton fibers is accompanied by pigment biosynthesis (Zhang *et al*., 2011a,b). Many sugars, especially glucose, are used to produce pigment, which therefore affects cellulose biosynthesis (Hua *et al*., 2007; Zhang *et al*., 2012). Extensive investigations have been carried out on sucrose metabolism and the activities of related key enzymes in white cotton fibers during development (Brill *et al*., 2011; Ma *et al*., 2008; Ruan, 2012; Zhang *et al*., 2009), but knowledge of sucrose metabolism during cellulose biosynthesis in colored cotton remained limited.

In this study, two different colored cotton cultivars and one white cotton cultivar were employed to describe the characteristics of content of cellulose and callose, and the enzymatic activities of SS, SPS, AI, β-1,3-glucanase, then to further elucidate the physiological mechanisms contributing to poor quality in colored cotton.

MATERIALS AND METHODS

***Plant materials and experimental design*:** Experiments were conducted at the Experimental Station at the College of Agronomy, Shandong Agricultural University, Tai'an, China (117°08′ E, 36°11′ N), from 2010 to 2011. Soil at the experimental site contained 11.59 g kg^{-1} organic matter, 66.22 mg kg^{-1} alkali-hydrolyzable nitrogen, 33.34 mg kg^{-1} available phosphorus, and 79.03 mg kg^{-1} available potassium.

The cotton cultivars investigated includes a brown cotton cultivar (ZX-1), a green cotton cultivar (G-7), and a white cotton cultivar (LMY28) kept as the control. The cotton seeds were planted on 25 April in the field in a randomized block design with three biological replications. Each plot consisted of twelve rows, which were 25 m in length and 0.8 m apart from each other.

***Sampling and processing*:** Cotton flowers were labeled on the day of anthesis for harvesting the bolls at known ages in late July. Tagged bolls were harvested at 10-day intervals, from 5 days post anthesis (DPA) until 55 DPA. Four to eight bolls from each plot were collected at each harvest. Fibers were separated from the ovules of the bolls with a scalpel, and portions of the fibers collected from 5 DPA to 45 DPA were immediately put into liquid nitrogen for enzymatic activity measurements. Another portion of fibers collected from 5 DPA to 55 DPA were air-dried in the shade and then ground into powder to measure the contents of cellulose and callose.

***Cellulose biosynthesis and Callose biosynthesis assays*:** The contents of cellulose biosynthesized in cotton fibers were determined according to the method described by Zhang *et al*. (2012). Callose extraction and determination were determined using the method reported in Köhle *et al*. (1985).

***Enzyme extraction and assays*:** Crude enzyme extraction for SS and SPS were carried out according to King *et al.* (1997). SS activity was assayed using the method described by Doehlert *et al*. (1988). SPS activity was assayed using the method described by Hubbard *et al*. (1989). Crude enzyme of AI was extracted by the method of Bhowmik *et al*. (2001). AI activity was assayed using the method described by Hubbard *et al*. (1989). Crude enzyme extraction and assays for β-1,3-glucanase were performed according to Tang (1999).

***Statistical analyses*:** The Richard regression model was used to describe the accumulation of cellulose (Gu *et al*., 2001; Zhang *et al*., 2011):

$$W = A / (1+be^{-kt})^{m}$$

where t is the number of days post anthesis (independent variable, DPA), W is cellulose content (dependent variable, %), A is the maximum accumulation of cellulose, b is the initial parameter, k is the accumulative rate parameter and m is the form parameter.

RESULTS

***Patterns of cellulose accumulation*:** The characteristics of cellulose biosynthesis in cotton fibers of different cultivars were examined (Table 1) and were described as Richard equations with fitting coefficients (R^2) larger than 0.99 in all three cultivars. The maximum accumulation of cellulose (A), the date at which maximum biosynthesis rate was reached (T_{max}), the maximum biosynthesis rate (V_{max}), and the time taken for cellulose rapid biosynthesis (T) were lower in colored cotton than in white cotton. Among these parameters, A was significantly positive correlated with V_{max} of 0.9999 (P <0.01) and with T of 0.9985 (P <0.05) as shown in Table 2. In addition, the rapid biosynthesis period of cellulose occurs from approximately 20 DPA to 40 DPA in tested cultivars (Table 1), indicating that this time frame is a critical period for cellulose biosynthesis in colored cotton.

Table 2. Correlation coefficients among the eigenvalues of cellulose biosynthesis in cotton fibers.

	A	T_{max}	V_{max}	T
A	1.0000			
T_{max}	0.9921	1.0000		
V_{max}	0.9999**	0.9918	1.0000	
T	0.9985*	0.9974*	0.9984*	1.0000

* and **, Significant at $p < 0.05$ and $p < 0.01$, respectively. Abbreviations as in Table 1

***Patterns of callose biosynthesis*:** Callose contents are presented as single-peak curves in both colored cotton and the white cotton (Fig. 1). Callose levels rapidly increased and peaked at 25 DPA. Before 25 DPA, the callose content in colored cotton was significantly lower than white cotton (F = 104.76 – 438.65, $P \leq 0.0028$). In contrast, a sharp and continuous decline that lasted until 55 DPA was observed

Table 1. Parameters of Richard curve equations for cellulose biosynthesis in fibers of different cultivars.

Cultivars	Models	A (%)	R^2	T_{max} (d)	V_{max} (% d^{-1})	T (d)
LMY28	$W=84.9534/(1+0.4407e^{-0.1969t})^{14.4}$	84.9534	0.9915**	20.0	6.1271	20.4
ZX-1	$W=80.0270/(1+0.4269e^{-0.1998t})^{113.9}$	80.0270	0.9934**	19.6	5.8096	20.3
G-7	$W=75.0023/(1+0.4033e^{-0.1982t})^{111.0}$	75.0023	0.9927**	19.0	5.4881	20.1

A, the maximum accumulation of cellulose; R^2, fitting coefficient; T_{max}, the date reaching maximum biosynthesis rate; V_{max}, the maximum cellulose biosynthesis rate; T, the time taken for cellulose rapid biosynthesis. ** $p < 0.01$.

with significantly higher callose content in colored cotton compared to white cotton (F = 190.92– 1943.50, $P \leq 0.0001$). ***Sucrose synthase*:** The dynamic changes of SS activities peaked at 15 DPA (Fig. 2), when the SS activity levels were significantly higher in white cotton than colored cotton (ZX-1 > G-7) (F = 9.11, P = 0.0324). On the contrary, the SS activity was significantly higher in G-7 than LMY28 and ZX-1 at 25 DPA (F = 7.40, P = 0.0452). In addition, no differences were observed between the colored cotton and white cotton cultivars at 45 DPA (F = 0.12, P = 0.8913).

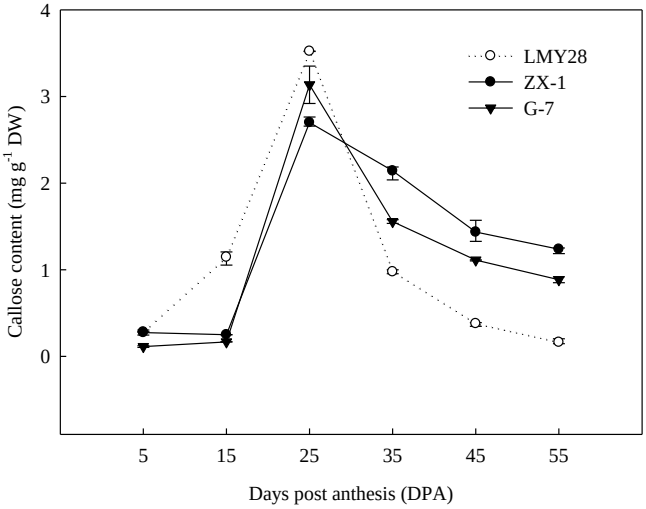

Figure 1. Callose biosynthesis in cotton fibers of different cultivars.

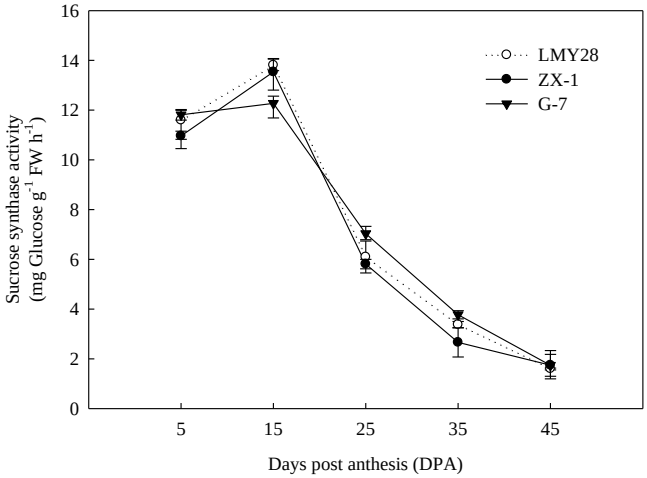

Figure 2. Sucrose synthase activity in cotton fibers of different cultivars.

***Sucrose phosphate synthase*:** The changing trends in SPS were similar in all three cotton cultivars declining at 15 DPA, and then increasing with peaks at 35 DPA (Fig. 3). SPS activity was significantly higher in ZX-1 than LMY28 and G-7 (F = 7.74 – 590.56, $P \leq 0.0422$).

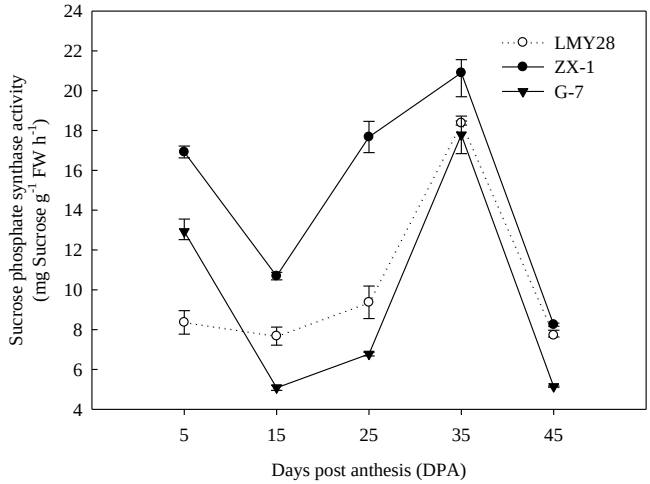

Figure 3. Sucrose phosphate synthase activity in cotton fibers of different cultivars.

***Acid invertase*:** The dynamic changesin AI activities are shown as single-peak curves with peaks at 15 DPA in all three cotton cultivars (Fig. 4). During fiber development, AI activity was significantly higher in LMY28 than ZX-1 and G-7, with the exception of 25 DPA (F = 20.71 – 977.47.56, $P \leq$ 0.0078).

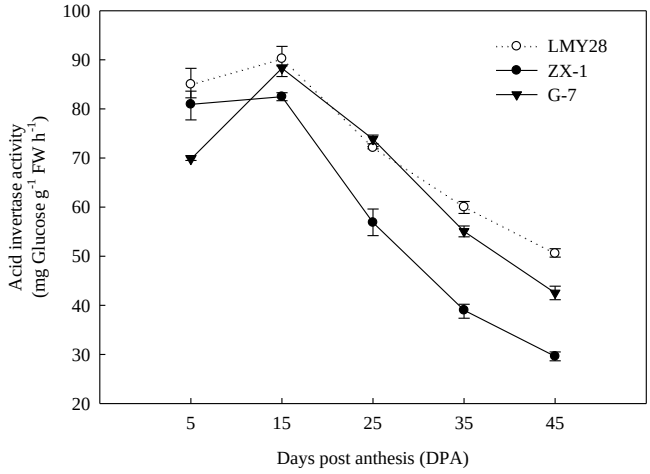

Figure 4. Acid invertase activity in cotton fibers of different cultivars.

***β-1,3-Glucanase*:** β-1,3-Glucanase activities are presented as single-peak curves with peaks occurring at 15 DPA in all three cotton cultivars (Fig. 5). During fiber development, β-1,3-glucanase activity was significantly higher in LMY28 than in ZX-1 and G-7 with exception at 15 DPA (F = 25.86 – 155.61, P = 0.0002 – 0.0052).

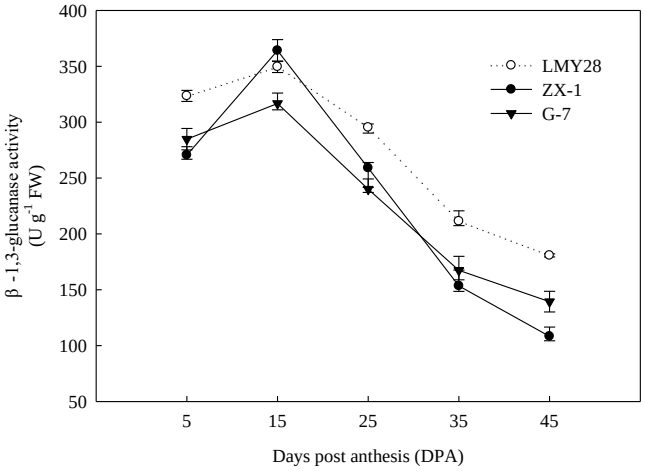

Figure 5. β-1, 3-Glucanase activity in cotton fibers of different cultivars.

DISCUSSION

Fiber quality is dependent upon fiber development in cotton, particularly the cellulose biosynthesis (Haigler *et al*., 2005). In previous study, less cellulose was accumulated in colored cotton than in white cotton, owing to the limited sugars (Zhang *et al*., 2012). Alternatively, sucrose is the major transport sugar and one of the initial signals for cellulose biosynthesis (Wind *et al*., 2010). Accordingly, sucrose metabolism is a pivotal process for cellulose biosynthesis in cotton fibers. In addition, cellulose biosynthesis also affected by a number of external factors including environmental conditions and agronomic practices (Dai and Dong, 2014; Dong *et al*., 2006), and is accompanied by the biosynthesis and deposition of pigments in colored cotton (Zhang *et al*., 2011a,b). This study was interested in exploring the physiological mechanisms behind poor fiber quality in colored cotton using sugars and related enzymes in sucrose metabolism during cellulose biosynthesis.

The model of cellulose biosynthesis is crucial for the formation of fiber quality (Haigler *et al*., 2005; Zhang *et al*., 2009), and the eigenvalues of Richard equation for cellulose biosynthesis were closely related to the cellulose content in cotton fibers (Zhang *et al*., 2011). In this study, we found that A, T_{max}, V_{max}, and T were lower in colored cotton than in white cotton, and the A had a significantly positive correlation with V_{max} and T. In addition, the rapid biosynthesis period for cellulose is from approximately 20 DPA to 40 DPA in the colored cotton, indicating that the time from 20 DPA to 40 DPA is a critical period for cellulose biosynthesis in colored cotton. Our previous study revealed that fiber quality of colored cotton was worse than white cotton (Zhang *et al*., 2010), and cellulose is the basis of cotton fiber quality (Zhang *et al*., 2011). During this time, the lower V_{max} and the shorter T might affect the biosynthesis of cellulose, resulting in the poor fiber quality observed in colored cotton.

Many enzymes are required for sucrose metabolism in cotton fibers during cellulose biosynthesis (Zhang *et al*., 2009). The activities of enzymes involved in sucrose metabolism (SS, SPS, AI, and β-1,3-glucanase) in cotton fibers were evaluated in our study. SS is a critical enzyme for cellulose biosynthesis (Coleman *et al*., 2009; Zhang *et al*., 2009) because it channels carbon directly from sucrose to glucose (Alonso *et al*., 2007; Coleman *et al*., 2009; Haigler *et al*., 2001). Hence, higher SS activity levels might be consistently correlated with the high rate of cellulose biosynthesis observed in white cotton fibers (Haigler *et al*., 2005). Similarly, in this study we found that brown cotton (ZX-1) displayed lower enzymatic activity of SS at 25 DPA and 35 DPA than white cotton. This result indicates that ZX-1 has less available glucose than white cotton during rapid biosynthesis of cellulose, thus affecting the rapid accumulation of cellulose in colored cotton. However, green cotton (G-7) had higher SS activity than LMY28 at the same stage. Theoretically, this result indicates that G-7 has more available carbon, resulting in more cellulose accumulation than in white cotton. Actually, this finding is in contrast with the theory, which indicates that the unstable pigments in G-7 require more carbon to form pigment (Zhang *et al.*, 2011b; Zhang *et al.*, 2012). Specifically, less carbon would be left for cellulose biosynthesis in green cotton.

Sucrose can be degraded by AI into glucose and fructose (Alonso *et al.*, 2007; Coleman *et al.*, 2009), and glucose and fructose are used subsequently as carbon sources for the biosynthesis of cellulose in cotton fibers (Alonso *et al.*, 2007). In this study, we found that the activity of AI was higher in LMY28 than ZX-1 and G-7 during cellulose biosynthesis. Specifically, the ability of AI to decompose sucrose was greater in white cotton compared to colored cotton. Our previous study noted that the consumption and transformation of sucrose was greater in white cotton than in colored cotton throughout fiber development (Zhang *et al.*, 2012). The study also found that the glucose content was significantly higher in white cotton than in colored cotton at 15 DPA (Zhang *et al.*, 2012). The higher activity of AI can hydrolyse sucrose to provide more energy for maintaining cellulose biosynthesis (Haigler *et al.*, 2001). The present study indicated that the ability of AI to decompose sucrose was lower in colored cotton than in white cotton, which affected the supply of carbon for cellulose biosynthesis.

SPS can provide a continuous substrate for SS and the biosynthesis of cellulose (Haigler *et al.*, 2005; Martin and Haigler, 2004). Meanwhile, the higher activity of SPS can provide a more abundant carbon source and maintain a more rapid and stable accumulation of cellulose over a long period of time (Feng *et al.*, 2009). Here, we found that the SPS activity was significantly higher in ZX-1 than LMY28 and G-7 during cellulose biosynthesis, theorizing that the higher

activity of SPS in ZX-1 could provide more abundant carbon source for the biosynthesis of cellulose than in LMY28 and G-7. However, the maximum biosynthesis rate of cellulose and the maximum cellulose content were lower in ZX-1 than in LMY28 and higher than G-7. The results of this study indicate that SPS is not the key enzyme affecting cellulose biosynthesis in colored cotton.

Callose deposition increases at the onset of secondary wall formation and then decreases until the end of fiber development (Scheible and Pauly, 2004). Indeed, low levels of callose in cotton cultivars were observed prior to 15 DPA, and then the levels quickly increased and peaked at 25 DPA in this study. Before 25 DPA, colored cotton had significantly lower callose content than white cotton, and after then callose content was significantly higher in colored cotton than white cotton. In other words, colored cotton has less accumulation and transformation of callose than does white cotton, indicating that the lower capacity for callose accumulation and transformation in colored cotton affected the supply of carbon for cellulose biosynthesis.

Callose is generally degraded by β-1,3-glucanase to provide more cellulose precursor (Delmer, 1999). In this study, we found that the activity of β-1,3-glucanase increased during primary cell wall elongation and continuously decreased during secondary wall thickening in cotton fibers. In addition, the activity of β-1,3-glucanase in white cotton was significantly higher than in colored cotton during fiber development except 15 DPA. Levels of β-1,3-glucanase activity is directly related to the degree at which callose is decomposed (Feng *et al.*, 2009), and higher activity of β-1,3-glucanase could completely transform callose in late fiber development, maintaining rapid and stable accumulation of cellulose over a long period during cellulose biosynthesis (Feng *et al.*, 2009). It is possible that the lower activity of β-1,3-glucanase in colored cotton resulted in lower transformation rates of callose relative to white cotton, which affected cellulose biosynthesis.

In contrast to white cotton, cellulose biosynthesis in colored cotton is accompanied by the biosynthesis and deposition of pigments (Zhang *et al.*, 2011a,b). Sucrose metabolism is also of paramount importance for pigment deposition (Haigler *et al.*, 2001; Lukaszewicz *et al.*, 2004) because sugars, especially glucose, are considered to be the direct precursors of pigments (Lukaszewicz *et al.*, 2004). Accordingly, sucrose metabolism is not only utilized for cellulose biosynthesis but also for pigment biosynthesis in colored cotton. As mentioned above, the stage of 20 - 40 DPA is the key stage for biosynthesis with maximum speed in colored cotton. Interestingly, pigment deposition in G-7 and ZX-1 started at 25 DPA and 35 DPA, respectively, while in white cotton there was no pigment deposition (Zhang *et al.*, 2011a,b). In summary, cellulose biosynthesis and pigment deposition will compete for sugars at the same stage. That is why LMY28 had more cellulose compared to ZX-1 and G-7 (Zhang *et al.*, 2012) and why poor fiber quality in colored cotton was observed.

***Conclusion*:** The period of 20 - 40 DPA is the key stage for cellulose accumulation in colored cotton. During this period reduced activity of AI and β-1,3-glucanase, and decreased accumulation and transformation of callose might limit carbon supply and cellulose accumulation. It is suggested that poor fiber quality in colored cotton was attributed to inhibited sucrose metabolism during cellulose biosynthesis in fiber development.

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