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Review Article

Research Advance of Sucrose Phosphate Synthase (SPS) in Higher Plant

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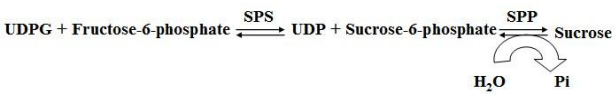
Abstract

Sucrose phosphate synthase (SPS) is considered to be a primary regulator for controlling biosynthesis and accumulation of sucrose and plays an important role in translocation and distribution of photoassimilate in higher plant. The review focused particularly on the SPS structure and family members, the biological functions of SPS, change regularity of SPS activity and environmental impact factors on SPS activity. Besides, the transgenic application and plant phenotype was introduced in this review. © 2013 Friends Science Publishers

Keywords: Sucrose phosphate synthase (SPS); Sucrose metabolism; Activity; Higher plant

Introduction

Sucrose is synthesized in the source tissue and then transported to the sink tissue for utilizing or storing, and as a specific signaling molecule (Wind *et al.*, 2010) to determine the altered gene expression and physiological adaptation. Sucrose served an integral role as a source of carbon and energy for non-photosynthetic tissues (Basson *et al.*, 2010). Reducing the rate of sucrose synthesis or increasing the degradation of sucrose would affect the plant physiology and fruit quanlity. Sucrose metabolism was a complex physiological and biochemical process throughout the whole plant growth process (Kühn and Grof, 2010). Until now, attempts to elucidate the sucrose metabolism have focused on sucrose-metabolizing enzymes including invertase (Inv), which catalyzed sucrose conversation into fructose and glucose, sucrose synthase (SS), which could catalyze the mutual conversion between sucrose and hexose, and sucrose phosphate synthase (SPS), catalyzing the conversion of Fructose-6-Phosphate and UDP-glucose into Sucrose-6-Phosphate (Winter and Huber, 2000; Yativ *et al.*, 2009). Besides, sucrose phosphatase (SPP) could convert Sucrose-6-Phosphate into sucrose irreversibly and using RNA interference technology to inhibit the expression of *spp* gene could factually lead to an obstacle to sucrose synthesis (Chen *et al.*, 2005). Catalytic reaction of SPS-SPP as follows:



As a key rate-limiting enzyme of sucrose synthesis, sucrose phosphate synthase (SPS) is the chief contributor for sucrose entering into the processes of various physiological metabolisms. As reported by many researchers, sucrose accumulation in a great many crops was largely the results of increased SPS activity or (and) decreased Inv activity (Hirotsu *et al.*, 2007; Ishimaru *et al.*, 2008; Zhang *et al.*, 2010). Huber (1983) reported that SPS activity was negatively correlated with starch accumulation and positively with sucrose accumulation, indicating that SPS was one of the pivotal regulatory factors for the carbon distribution of photosynthetic product. In addition, with the wide utilization of transgenic technology and the expansion of experimental materials, researchers found that SPS activity could be regulated by 14-3-3 protein phosphorylation (Winter and Huber, 2000) and inhibiting 14-3-3 protein expression would lead to the improvement of SPS activity and the sucrose accumulation (Szopa, 2002).

Recent years, the functions of SPS in sucrose metabolism and plant growth have been more comprehensively understood. In this review, we summarized the family members and structure of SPS and its main roles on sucrose metabolism, change regularity of SPS activity and *sps* transgenic application. In addition, the future research direction of SPS was put forward at the end of this review.

The Family Members and Structure of SPS

Family members: Due to the large-scale genomic sequencing of gramineae crops and EST project fulfilling, Castleden *et al.* (2004) made phylogenetic analysis on the all known SPS sequences based on strict criteria and revealed that 3 *sps* gene families (namely A-, B- and C-family) that existed in both dicotyledonous and monocotyledons plants, yet 1 special family (D-family) was only found in gramineous plants. For the present research

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and analysis, the functions of different SPS family members were largly diferent. For example, the content of starch in potato (*Solanum tuberosum*) could not be degraded effectively and sucrose synthesis was blocked seriously if the expression of C-family, not A-family, was suppressed by RNAi, suggesting that C-family was special to sucrose synthesis and starch degradation. However, the situation was apparently different in *Arabidopsis* leaf that sucrose synthesis was faced with great reduction without A-family expression (Chen *et al.*, 2005). Yet for all that, we have very little data to help us understand the detailed functions of the different family-types of SPS in the same plant.

Three Sites on SPS: Generally, there were 3 regulatory sites on SPS (A-, B-, C-family), namely light regulatory site, osmotic stress activation site and 14-3-3 protein specific site. But the special D-family actually had only light regulatory site, and its linker domain between the N-terminal catalytic glucosyltransferase domain and the C-terminal suc-phosphatase-like domain included 80 to 90 amino acid residues, which was shorter than that in A-, B- or C-type. It was unclear whether D-family could be phosphorylated or not, but the same conservative properties of amino acids with other SPS family genes at least could explain other phosphorylation sites ever existed on D-family genes. From gene structure perspective and the analysis of computer system evolution, D-family was much closer to A-family. Interestingly, A-family existed both in monocotyledons and dicotyledons but D-family was only found in gramineous plants (Castleden *et al.*, 2004). The most immediate explanation was probably that D-family was separated from A-family at once upon a time.

Two Domains on SPS: Recently, researchers have made it clear that SPS had two domains (Chua *et al.*, 2008), glucosyltransferase domain (N-domain), which was related to glucosyl transference and SPP-like domain (C-domain) that perhaps bound SPP to form SPS-SPP complexity. The donor substrate, for example, nucleotide diphosphate glucose (UDP-Glc), would bind to N-domain and the substrate D-fructose-6-phosphate (F-6-P) and the product D-sucrose-6-phosphate (S-6-P) would bind to the C-domain. According to current database, SPS and SPP possibly originated from the ancient *SPP-like* gene, but their structures and functions, respectively changed during the process of genetic evolution (Cumino *et al.*, 2002; Lunn, 2003).

Main Roles of SPS in Sucrose Metabolism

Influence on plant growth and fruit development: A fair amount of experiments have demonstrated that over-expression of *sps* would increase the carbohydrate accumulation and obtain high or super-high yield (Hirotsu *et al.*, 2007; Ishimaru *et al.*, 2008; Zhang *et al.*, 2010). Using antisense approach to inhibit *sps* expression in muskmelon (*Cucumis melo* L.), Tian *et al.* (2010) found that both the sucrose concentration and SPS activity in antisense plants markedly reduced in mature fruit, and the size of the plant was much smaller compared with the normal group. According to the plant growth and the variation of environment, *sps* transcript level presented differences in temporal and spatial expression. For example, in apples (*Malus pumila*), the transcript level of *sps* at the early stage was much lower than other enzyme genes, but during the period of fruit maturity sucrose accumulation and SPS activity guradully enhanced (Li *et al.*, 2012). In sugarcane (*Saccharum officinarum*), *sps* transcript expression level was higher in mature internodes than that in immature internodes (Verma *et al.*, 2010). In addition, Micallef *et al.* (1995) reported that *sps* overexpression resulted in flowering earlier and increasing the total fruit weight in tomato (*Solanum lycopersicum*), and *sps* overexpression in *Arabidopsis* led to high sucrose concentration and total dry weight (Park *et al*., 2008).

Regulation of distribution of photosynthetic products: The final forms of photosynthetic carbon fixation were sucrose and starch. The former was the main long-distance transport carbohydrate and the latter stored in the chloroplasts temporarily. Previous studies have showed that SPS activity was negatively correlated with starch accumulation but positively with sucrose accumulation (Huber, 1983). Verma *et al*. (2011) showed that the sucrose content increased because of the rise of SPS actvity. Similarly, the ratio of sucrose/starch and SPS activity had a significant positive correlation in tomato (Galtier *et al.*, 1993, 1995). Researchers inserted *sps* gene into rice (*Oryza sativa*) and sugarcane respectively to obtain over-expressed transgenic plants and the resulted indicated that the SPS activity, sucrose content and sucrose/starch ration were obvious higher comparing with the non-transgenic control plants (Ono *et al.*, 1999; Miswar *et al.*, 2007).

Although from above we have known that SPS could regulate carbohydrate allocation between sucrose and starch, there was no systematical theory of physiological regulatory mechanisms to put forward for expounding the detailed process of the regulatory function.

Involved in Cell Differentiation and Fiber Cell Wall Synthesis

Babb and Haigler (2001) reported that in transgenic cotton (*Gossypium Spp.*), the enhancement of SPS activity stimulated an increase in the precipitation capacity of fiber cell wall. UDP-glucose was considered to be channeled to cellulose synthase in the plasma membrane, implying that sucrose availability would affect the rate of the cellulose synthesis. In other words, increasing the conversion of sucrose to fructose and UDP-glucose would support the secondary wall cellulose synthesis on cotton fibers. Therefore, as the key enzyme of catalyzing sucrose synthesis, SPS played an important role in the process of the cellulose synthesis and fiber sedimentation cell synthesis. Park *et al.* (2008) reported that over-expression of A-family

sps gene in *Arabidopsis* had a crucial potential to improve plants growth rate and fiber elongation. The latest research showed that altering sucrose metabolism through UDP-glucose pyrophosphorylase (UGPase), SPS did not have an end affect on cellulose production (Heather *et al.*, 2010). Combined with Fig. 1, we concluded that the reversible reaction between UDP-glucose (free pool) and glucose-1-phosphate by UGPase could not change sucrose accumulation by SPS-SPP catalysis, then sucrose was degraded to UDP-glucose (no pool), which was conversed to cellulose under the catalysis of cellulose synthase (CesA).

Interact with 14-3-3 Proteins

Toroser *et al.* (1988) found a regulatory interaction of 14-3-3 proteins with Ser-229 on SPS in spinach (*Spinacia oleracea*) leaf. Likewise, Bornke (2005) and Zuk *et al.* (2005) reported that 14-3-3 proteins could down-regulated SPS activity in tobacco (*Nicotiana tabacum*) and potato, respectively. In tomato, there were 12 isoforms of 14-3-3 proteins named TFT1~TFT12. Yu *et al.* (2010) inferred that 2 members (TFT1 and TFT10) were more likely to interact with SPS through bioinformatics method.

Except for the regulation on SPS, in fact the interaction between 14-3-3 proteins and SPS had significance. Cotelle *et al.* (2000) found that the interaction could protect SPS from the attack of proteinase. However, not one or all 14-3-3 protein(s) in higher plant could interact with SPS, suggesting that the effects of different 14-3-3 protein isoforms on SPS had great difference (Bornke, 2005).

Change Regularity of SPS Activity

Hussain *et al.* (1999) found that SPS activity in rice leaves was lower at night and then increased with the enhancement of light intensity: the maximum value of SPS activity appeared at 8:00 under the enough moisture condition or 12:00 under water limited condition. Sinha *et al.* (1998) reported that there was a significant similarity in the diurnal patterns of SPS activity and the net photosynthetic rate (PN) in *Prosopis juliflora*, increasing after irradiation, reaching a maximum at 8:00 and then declining during midday. Diurnal fluctuations of SPS activity could be due to the amount of protein (V_{max}) as well as to the changes in kinetic properties (V_{lim}).

Wang *et al.* (2003) reported that the change of SPS activity was similar to the change of sucrose content in wheat (*Triticum aestivum*) flag leaf, decreasing until the 7th day after anthesis and then rising, appearing a consecutive drop until fruits mature from 14th day after anthesis. However, Li *et al.* (2005) argued that SPS activity in wheat flag leaf showed a rising trend within 7 days after anthesis and kept high activity until to 21th day and then declined sharply. At present, the studies about the dynamic changes of SPS activity were mainly served to carbohydrate metabolism process. However, till now, none of the research achievements could explain clearly the change mechanisms of SPS activity at different growth periods.

Environmental Factors Affecting SPS Activity

Light intensity: The study of diurnal variation of SPS activity in the early leaves of potatoes showed that the highest SPS activity appeared at 14:00 with the moment of the strongest light intensity, and the lowest SPS activity appeared at 18:00 with the moment of the weakest light intensity (Pattanayak, 1998). The result was consistent with the studies in rice, maize (*Zea mays*) and wheat leaves (Lunn and Hatch, 1997; Hussain *et al.*, 1999; Tevanion *et al.*, 2004)

Water: SPS activity in rice leaves was higher under saturated irrigation condition than that under the condition of water shortage (Hassain, 1999). Wang *et al.* (2004) also reported that the SPS activities and sucrose contents in soil water stress treatment obviously increased both in rice leaves and stems.

CO_2: Rice plants were transferred into low CO_2 concentration environment from the normal, SPS activity would markedly decrease but increase under the condition of higher CO_2 concentration (Gesch *et al.*, 2002), indicating that the appropriate enrichment of CO_2 concentration was beneficial to induce the rise of SPS activity.

Temperature: The content of sucrose and the activity of SPS, not SS and Inv, in two evergreen trees, *Sabina. przewalskii* Kom. and *Sabina. chinensis* Ant., were higher in the winter than in the summer, suggesting that only SPS played positive role in freezing tolerance for increasing soluble sugar concentration (Chen *et al*., 2012). In addition, potatoes were stored at 3, 5, 7, 9 and 11℃ for 10 days to determine the SPS activity. The result showed that SPS activity increased slightly at 7℃, obviously increased 3~4 times at 5℃ and 5~6 times at 3℃. More interesting, the increased SPS activity at low temperature completely disappeared when the potatoes were back to room temperature (about 20℃) (Deiting *et al.*, 1998).

Except for the above influencing factors, new evidences have indicated that sugar-metabolizing enzymes including SPS largely reduced by root hypoxia in diving tomato fruit (Horchani *et al.*, 2011), ethylene and white light treatments could strongly increase the accumulation of *sps* transcript, and auxin marginally regulated *sps* gene expression during fruit ripening (Choudhury *et al.*, 2008).

A large number of experimental results have indicated that SPS activity and the quantity of *sps* transcript would be regulated accordingly under different environment effect factors. However, the regulatory mechanism, especially at transcriptional level, has not been clarified. Therefore, research and analysis the change rules of SPS activity and *sps* expression in different environments in different environments at physiological and molecular levels will be beneficial to increase the yield and fruit quality.

Table 1: Transgenic research with SPS genes in plants

Gene Source	Family	Promoter	Receptor	Main Result	Reference
ZmSPS1 (gi401114/P31927)	Family B	rbcS	*Lycopersicon esculentum*	Sucrose content and SPS activity significantly increased.	Quoc *et al.* (1998)
ZmSPS1 (gi401114/P31927)	Family B	35S	*Solanum tuberosum*	SPS activity was 4 times as control group.	Ishimaru *et al.* (1999)
ZmSPS1 (gi401114/P31927)	Family B	rbcS	*Arabidopsis thaliana*	Sucrose/starch ratio obviously increased.	Signora *et al.* (1997)
ZmSPS1 (gi401114/P31927)	Family B	rbcS	*Nicotiana tabacum*	Enhanced sucrose synthesis and carbon sequestration.	Baxter *et al.* (2003)
AtSPS1 (gil5241313/NP_197528)	Family A	35S	*N. tabacum*	Sucrose content, dry matter and fiber length increased;	Park *et al.* (2008)
ZmSPS1 (gi401114/P31927)	Family B	35S	*Oryza sativa*	SPS activity was 3 times as control group; Plant height higher.	Ishimaru *et al.* (2004)
SolSPS (gil70147/AAA20092)	Family A	35S	*Gossypium hirsutum*	Sucrose/starch ratio and cotton quality obviously increased.	Haigler *et al.* (2007)

rbcS: The small subunit of ribulose-1,5-bisphosphate carboxylase oxygenase promoter;
35S: The cauliflower mosaic virus (CaMV) 35S promoter

Transgenic Application and Plant Phenotype

Sps gene has been cloned from a variety of crops, such as spinach, maize, sugar cane, apples and rice, and researchers transferred cloned *sps* gene into another crops to investigate the expression level of *sps* and the phenotypes of the transgenic plants (Table 1). For example, Baxter (2003) transferred maize *sps* gene into tobacco and found that the transgenic lines bloomed earlier, the quantity of flowers and sucrose accumulation were much more than non-transgenic group. Moreover, transgenic *sps* over-expressing plants lines had higher sucrose/starch ratios in leaves and ^{14}C preferred to flow to sucrose rather than starch (Haigler *et al.*, 2007). However, *synechocystis* SPS was transferred into *Arabidopsis* plants, the SPS activities in transgenic plants and the wild type plants were not significantly different, but sucrose and starch contents decreased and the hexose content significantly increased in transgenic plant leaves, indicating that high acid invertase activity, but not the over-expression of *sps* (Voon *et al.*, 2004), played an important role.

Conclusion

With the deepening and development of plants transgenic technology, transgene over-expression has attracted more attention. Analysis of existing studies on over-expression of transgenic *sps* gene was mostly about its activity, physiological index, phosphorylation and isomerization after the protein translation. Numerous studies indicated that *sps* gene could start expression in special tissues at certain developmental stage(s). However, it has not been clear about the process of the transcription of *sps* so far, especially the situation of lacking *sps* gene promoters information. So we believe that the future research fields should focus on the cloning of relevant promoter sequences, analyzing the effect of cis-acting elements on the promoter and trans-acting factors binding with promoter to the gene transcription. In addition, the present transgenic research of

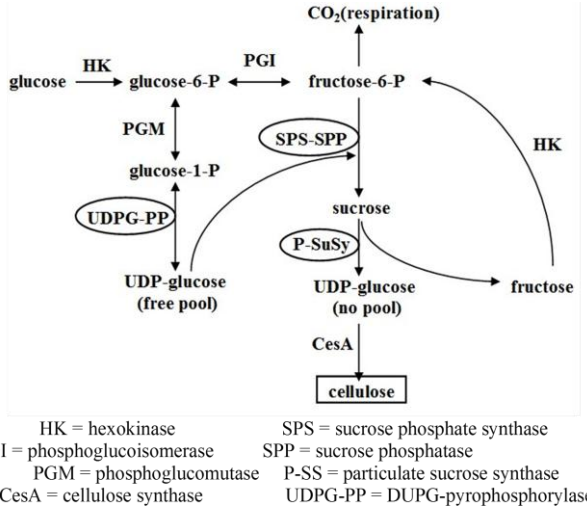

Fig. 1: The Process of cellulose synthesis (Babb and Haigler, 2001)

SPS is aimed at the functions of A- and B-family, such as *ZmSPS1* (B-family) in maize, *AtSPS1* (A-family) in Arabidopsis thaliana and *SolSPS* (A-family) in spinach, but C- and D-family *sps* genes haven't been reported into transgenic plants. It deserves further study to affirm whether their effects are same as A- and B-family or not.

On the other side, although the roles of the activity of three critical enzymes during the process of sucrose metabolism are clear, the signal transduction in signal network systems is not perfectly clear, when the signal starts and what's the form of the signal to work need more experimental results to make public. Therefore, to reveal these issues is beneficial to regulate the accumulation of sugar on signal transduction level.

Last, SPS and SPP (sucrose phosphatase) existed in the form of SPS-SPP complex in higher plant. Sucrose synthesis would be blocked if the expression of *spp* was inhibited. Since it was cloned in 2000, the detailed

biological functions and the binding pattern of SPS-SPP should be paid more attention.

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