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Potato starch synthases: Functions and relationships

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ABSTRACT

Starch, a very compact form of glucose units, is the most abundant form of storage polyglucan in nature. The starch synthesis pathway is among the central biochemical pathways, however, our understanding of this important pathway regarding genetic elements controlling this pathway, is still insufficient. Starch biosynthesis requires the action of several enzymes. Soluble starch synthases (SSs) are a group of key players in starch biosynthesis which have proven their impact on different aspects of the starch biosynthesis and functionalities. These enzymes have been studied in different plant species and organs in detail, however, there seem to be key differences among species regarding their contributions to the starch synthesis. In this review, we consider an update on various SSs with an emphasis on potato SSs as a model for storage organs. The genetics and regulatory mechanisms of potato starch synthases will be highlighted. Different aspects of various isoforms of SSs are also discussed.

1. Introduction

Starch, a megadalton-size glucose polymer is a prominent storage carbohydrate in many higher plants. With many genes encoding starch biosynthesis enzymes known, starch has become very amenable for (bio) engineering *in planta*. Moreover, bacterial and other foreign genes involved in glycogen biosynthesis and other glucose polymers such as mutan, dextran, and alternan have also been applied to alter starch characteristics with varying success [1–4].

Starch synthesis involves a number of enzymes, including soluble starch synthases (SSs; EC 2.4.1.21), starch branching enzymes (SBEs; EC 2.4.1.18), starch debranching enzymes (DBE; EC 3.2.1.68) and disproportionating enzymes (EC 2.4.1.25) [5]. Various SSs are involved in the elongation of the glucan chains by transferring glucose residues from ADP-glucose to the non-reducing end of the growing glucan chains. SBEs introduce the α−1,6 linkages by simultaneous cleavage of some short α−1,4 linked glucan chains and connecting them to other chains, thus providing amylopectin molecules as well as increasing the number of non-reducing ends for further elongation by various SSs isoforms. DBEs seem to trim the irregularly arranged glucan chains to maintain glucan branches in amylopectin molecules in a regular order, thus enabling formation of semi-crystalline structures. Disproportionating enzymes cleave short malto-oligosaccharides (MOS) producing glucose units which can either be used for the ADP-glucose synthesis or as an energy source for plant metabolism.

Higher plant SSs possess multiple isoforms which are grouped based on their amino acid sequence similarities [6]. All the SSs appear to share the same overall structure, consisting of a glass domain (substrate-binding site), a typical transit peptide [7] and different motifs [8]. SSs are further classified into three distinctly localised groups in the plastids, i.e., exclusively granule-bounded (Granular-Bound Starch synthase, GBSS) exclusive or nearly exclusive activity in the soluble phase; and those present in both the granule and soluble phase. Moreover, in potato SSs are further subdivided into four subclasses based upon cDNA and amino acid sequence similarities, i.e. GBSS (~60 kDa), SSI (~57 kDa), SSII (~77 kDa), and SSIII (~110–140 kDa). Nevertheless, pea GBSSI has been further subdivided into GBSSIa and GBSSIb isoforms [9]. Since different SSs contribute to starch biosynthesis, a better knowledge of the relationships among SSs enzymes involved will definitely provide guidelines for plant geneticists, biotechnologists, and breeders to modify starch properties as demanded by various sections. In this review, the function and contributions of different SSs isoforms with an emphasis on potato SSs are discussed.

2. Sucrose to starch conversion in storage organs

The polyglucan starch is made up of two glucose polymers, amylose and the more highly branched amylopectin. Amylose is a linear polymer of glucose units held together entirely by α−1,4 glucosidic bonds, whereas amylopectin is a highly-branched polysaccharide consisting of α−1,4 linked glucose with α−1.6 linkages at the branch points (Fig. 1). Sucrose to starch conversion is a relatively complicated

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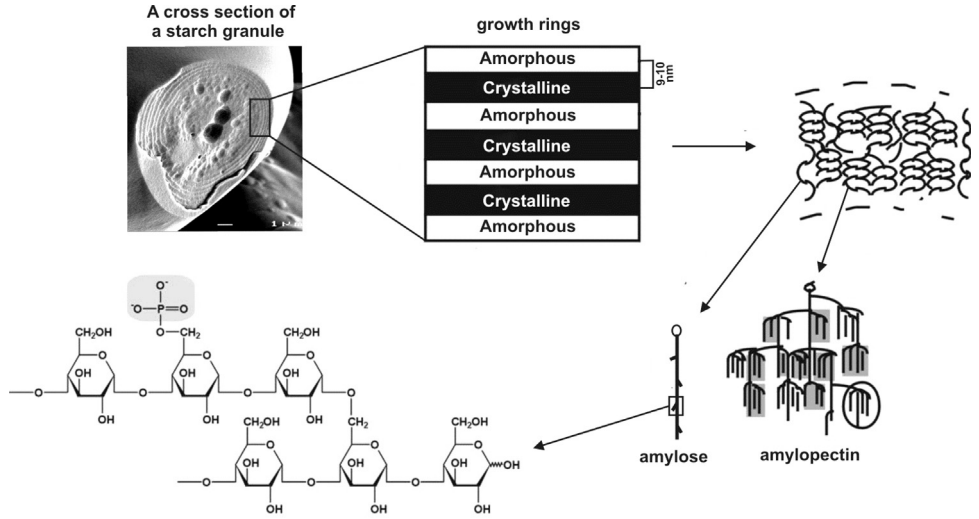

Fig. 1. Schematic representation of the structure of a starch granule, with alternating amorphous and semi-crystalline regions constituting the growth rings. The glucose residues are connected through α − 1,4 and α − 1,6 linkages. In potato starch one out of 200–300 glucose units of amylopectin is phosphorylated. Phosphate groups can be attached to the C-3 or the C-6 of a glucose residue. The position of the phosphate group with respect to the α − 1,6 branch point is arbitrary (Figure reproduced with minor modifications from [98]).

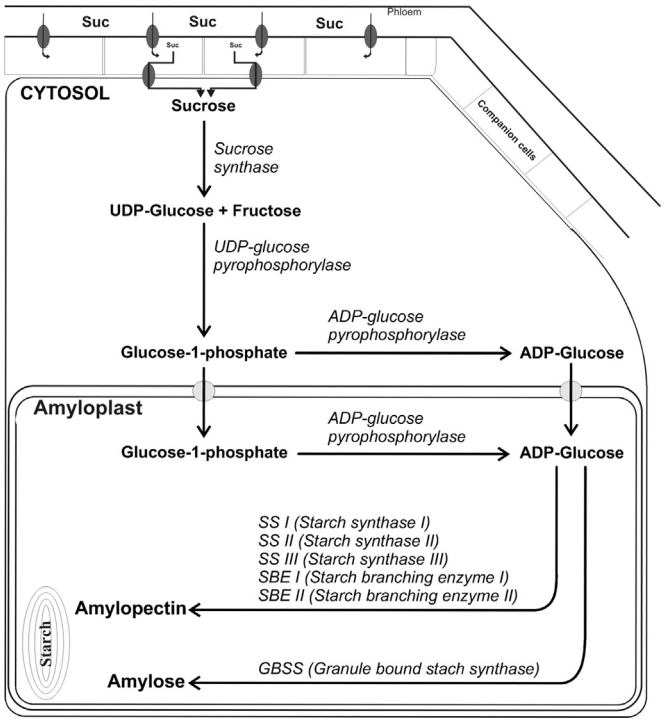

Fig. 2. Illustration of the starch biosynthesis pathway in potato tubers. ● and ○ represent putative transporters.

pathway involving many known SSs as well as a number of sugar transporters (Fig. 2). Plasmalemma-bound transporters and/or diffusion not only transport hexose sugars but also translocate apoplastic sucrose directly to the cytosol [10]. In developing storage organs (e.g., potato tubers) sucrose present in the phloem is metabolised in different ways. Apoplastic or cytosolic invertases convert sucrose molecules to glucose and fructose. Alternatively, sucrose is converted to UDP-glucose (UDP-Glc) and fructose by a sucrose synthase (Susy, EC 2.4.1.13). A part of apoplastic sucrose, upon entry into the cytosol, is transported to vacuoles by endocytosis. The starch biosynthesis in higher plants takes place in a specialized compartment, plastids, which relies on translocation of precursors from the cytosol through the plastid envelop. Glucose-6-phosphate (Glc-6P) and ADP-glucose (ADP-Glc) transporters are actively involved in transferring these important nucleotide precursor molecules into plastids [11,12]. In potato tubers and once inside the amyloplasts, Glc-6P is subsequently converted to glucose-1-phosphate (Glc-1P) and ADP-Glc by phosphoglucomutases (PGM, EC 2.7.5.1) and ADP-glucose pyrophosphorylase (AGPase, EC 2.7.7.27), respectively. In plants, at least five independent-conserved classes of genes encode SSs [13]. These SSs use ADP-Glc produced by AGPase as a substrate to catalyse the formation of new glycosidic linkages by transferring glucose moieties of ADP-Glc to the non-reducing end of an existing α − 1,4 glucan chain.

The semi-crystalline structure of amylose-free starches in potato (*amf*) and cereal crops (*waxy*) suggest that amylose is synthesized downstream of amylopectin, using either amylopectin or small soluble glucans as a primer [14,15]. In principle, two mechanisms proposed for the amylose synthesis can occur side-by-side. Within the crystalline matrix, GBSSI is responsible for the amylose biosynthesis. It seems that once MOS molecules have been elongated to a certain extent, they may become too large to escape from the growing starch granules. After further extension, these moderate molecular weight (10^5–10^6) chains form amylose. It has also been shown that this mechanism appears to be at work in the starches extracted from higher plants [16]. Moreover, the GBSSI activity seems to be stimulated by MOS molecules in the course of starch synthesis [17]. In the small glucan-primed amylose biosynthesis, DBEs could also play an important role in generating small molecules which diffuse into the granule to serve as a preferred substrate for GBSSI. Apart from being exclusive granule-bounded, GBSSI elongates a growing α − 1,4 linkage processively, suggesting that the enzyme does not dissociate from the growing granule right after each glucose unit is added. Very recently, a plastidial protein named Protein targeting to starch (PTST) has been identified which seems to be specifically required for amylose synthesis and targeting GBSSI to starch granules in *Arabidopsis* [18]. *Arabidopsis ptst* mutants did not produce amylose and they were phenotypically similar to GBSSI mutants.

3. Reaction catalyzed by SSs

Potato contains four different SSs isoforms (SSI, SSII, SSIII and GBSSI). Contrary to other SSs, SSI does not have multiple isoforms in plants, suggesting a presumably unique and important role in starch biosynthesis [19]. However, its precise role is not yet clear. For instance, although the activity of SSI enzyme was repressed to non-detectable levels in potato transgenic plants, neither amylopectin structure nor starch granule morphology was changed. The reason for

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