

## Biosynthesis of waxy starch – a review

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### ABSTRACT

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Starch comprises nearly linear amylose and branched amylopectin, whilst waxy starches are a special form, containing almost exclusively amylopectin. Modern techniques in plant breeding together with new data from starch biosynthesis research have enabled new food and non-food uses of waxy starches. This paper describes the basic ways of glucose conversion to waxy starch in plants. The recent evidence of ADP-Glc accumulation in cytosol of photosynthetically competent cells proposes a more complex pathway of starch biosynthesis based on a tight interconnection of sucrose and starch metabolic pathways. Also many studies indicate the existence of different pathways for the sucrose-starch conversion process in heterotrophic organs of dicotyledonous and monocotyledonous plants. At least six classes of starch synthases (SS) have been recognised in plants including soluble SS1, SS2, SS3, SS4, SS5, and granule bound SS (GBSS), required for the synthesis of short and long chains of amylopectin, till now. As to amylose (not-present in waxy starches), GBSS is the only starch synthase isoform encoded by the waxy genes situated at independent loci.

**Keywords:** waxy protein; Calvin-Benson cycle; sucrose-starch conversion; starch-branching enzyme; adenosine diphosphoglucose

Starch is the main component of digestible carbohydrates; it consists of amylose and amylopectin. The so-called waxy starch consists almost exclusively of branched chains typical for amylopectin. A macromolecule of amylopectin composed of  $\alpha$ -(1 → 4)-D-glucopyranose chains connected with  $\alpha$ -(1 → 6)-linkages is arranged in a clustered structure forming crystalline regions of the starch.

The internal organisation of the chains within the building blocks of starch granules is unique to each plant and manifests the shape and size of the granules. E.g. Zhou et al. (2014) found that waxy wheat starch has a more spherical disc-like morphology compared to regular wheat starch, a smaller proportion of (smaller) B-type granules, and a higher degree of crystallinity (Zhang et al. 2013).

Regular native starches form a solid gel after gelatinization. The follow-up retrogradation is a

crystallization process typical for the reassociation of solubilized starch polymers. Amylose retrogrades in these gels within a day of ageing. Waxy starch (without amylose) is therefore applied in food technologies (e.g. confectionary or bakery) where it minimises retrogradation. On the other hand, amylopectin forms very weak gels that break down on shear (Murray and Phisarnchananan 2014).

Starch can be debranched at 1, 6 linkages by debranching enzymes (e.g. isoamylase and pullulanase) under specific conditions. For waxy starches, only short linear chains are released in this process, and therefore these chains have a relatively narrower molecular weight (MW) distribution which is important for the preparation of nanoparticles. They may be used as fillers and reinforcing agents in polymer composites or carriers for drug delivery, barrier coating materials and stabilisers in

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Table 1. Numbers of enzymes

1, 1'	fructose-1,6-bisphosphate aldolase
2, 2'	fructose 1,6-bisphosphatase
3	PP <sub>i</sub> : fructose-6-P 1-phosphotransferase
4, 4'	phosphoglucose isomerase (PGI)
5, 5'	phosphoglucomutase (PGM)
6	UDP-Glc pyrophosphorylase (UGP)
7	sucrose-phosphate-synthase
8	sucrose phosphate phosphatase
9	adenosine diphosphoglucose pyrophosphorylase (AGPase)
10	starch synthase (SS)
12	plastidial hexokinase
13	plastidial UGP
14	plastidial ADP-Glc pyrophosphatase
15	plastidial starch phosphorylase
16	sucrose synthase (SuSy)

X and X' distinguish isoenzymes in the cytosol and the plastidial ones

oil-in-water emulsions. Waxy starch can also be applied as a raw material in further technologies, as a part of biocomposites and other polymers or co-polymers, for pharmaceutical uses, and in many others (Šárka and Dvořáček 2017).

**Biosynthesis of adenosine diphosphoglucose**

Starch biosynthesis proceeds in leaves as well as in heterotrophic plant tissues. A part of the photosynthetically fixed carbon is retained within the chloroplasts during the day to synthesize starch, which is then remobilized during the night to support non-photosynthetic metabolism and growth by continued export of carbon to the rest of the plant (Bahaji et al. 2014). In tubers or seeds, starch serves as a longer-term carbon store (Geigenberger et al. 2004).

The common step of starch biosynthesis (Figures 1–3) is based on the conversion of glucose 6-phosphate (Glc-6-P) to glucose 1-phosphate (Glc-1-P) by phosphoglucomutase (PGM; 5). ADPglucose (ADP-Glc – adenosine diphospho-

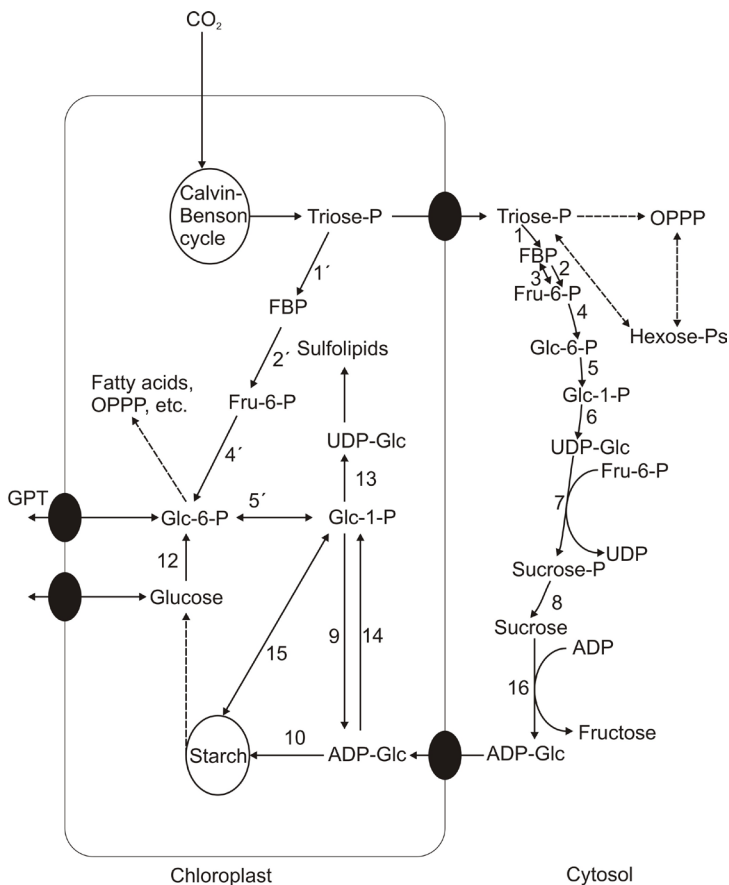


Figure 1. Starch biosynthesis in leaves (complex pathways) according to Bahaji et al. (2014). ADP-Glc – adenosine diphosphoglucose; Fru-6-P – fructose 6-phosphate; FBP – fructose biphosphate; Glc-1-P – glucose 1-phosphate; Glc-6-P – glucose 6-phosphate; GPT – Glc-6-P/Pi translocator; OPPP – oxidative pentose-phosphate pathway; Triose-Ps – triose phosphates; UDP-Glc – uridine diphosphate glucose; numbers of enzymes see Table 1

glucose) is subsequently made from Glc-1-P and ATP (adenosine triphosphate) by ADPglucose pyrophosphorylase (AGPase – adenosine diphosphoglucose pyrophosphorylase; 9). ADP-Glc acts as the glucosyl donor for starch synthases (SS; 10) (Zeeman et al. 2010, Geigenberger 2011).

In illuminated leaves, Glc-6-P is synthesised from the Calvin-Benson cycle intermediates via plastidic PGI (phosphoglucose isomerase) (4') and PGM (5'), while ATP is provided by the photophosphorylation in the thylakoid membrane (Geigenberger 2011). Triose-Ps (triose phosphates) produced in the Calvin-Benson cycle are exported to the cytosol where they can be channelled into the regeneration sequence of pentose-P pathway (OPPP – oxidative pentose-phosphate pathway). This model supposes a plastidial sucrose as a precursor for starch biosynthesis. Additionally, a tight interconnection of sucrose and starch metabolic pathways is regulated by means of cytosolic ADP-Glc producing enzymes such as sucrose synthase (16; acting when cytosolic sucrose transiently accumulates during illumination), and by an ADP-Glc translocator located at the chloroplast envelope membranes, and both AGPase (9) and pPGM (plastidial phosphoglucomutase) (5') play an important role in the scavenging of glucose units derived from starch breakdown occurring during starch biosynthesis (Figure 1).

There are different pathways for the sucrose-starch conversion process in heterotrophic organs of dicotyledonous and monocotyledonous plants.

In non-photosynthetic tissues such as potato tubers (Figure 2), incoming sucrose is transferred by series of cytosolic reactions to the Glc-6-P, which is imported into amyloplast using antiport with inorganic phosphate ( $P_i$ ) by GPT (Glc-6-P/ $P_i$  translocator) (Kammerer et al. 1998) and subsequently converted to Glc-1-P via plastidial PGM (5'). The second substrate of AGPase (9), ATP, is obtained by mitochondrial respiration and imported into the plastid via a membrane ATP/ADP exchanger (Tjaden et al. 1998, Bahaji et al. 2014). The enzymes pPGM (5') and AGPase (9) located in the amyloplast further play an important role in the scavenging of the glucose units derived from a starch breakdown.

In contrast, AGPase (9) in cereal seed endosperm is mainly located in the cytosol (Figure 3). Recent transport studies confirmed that this enzyme exchanges ADP-Glc by antiport with ADP (Bowsher et al. 2007, Kirchberger et al. 2007). The starch biosynthesis further implies the additional pathways involving UDP-Glc (uridine diphosphate glucose) produced by SuSy (sucrose synthase) (16) and cytosolic hexose-6-P derived from the action of UGP (UDP-Glc pyrophosphorylase) (6) on UDP-Glc.

### Biosynthesis of amylopectin

At least six classes of SSs have been recognised in seed plants including soluble SS1, SS2, SS3, SS4

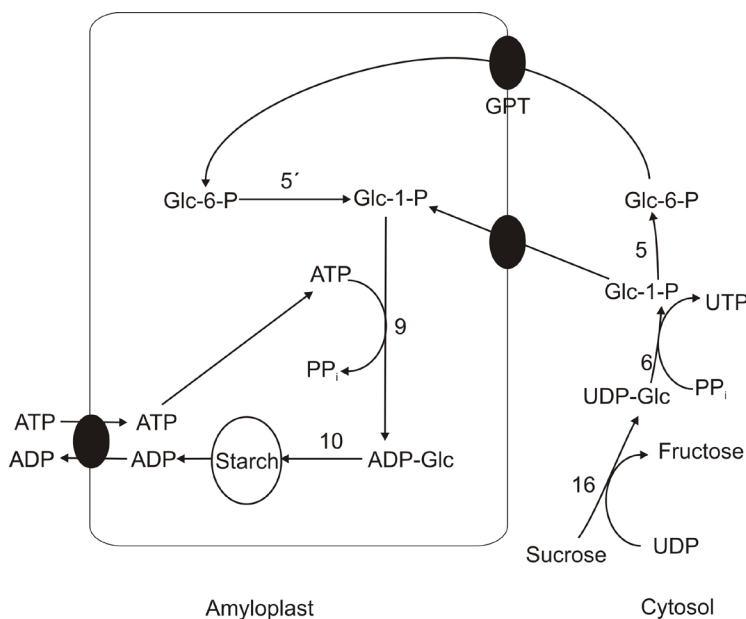


Figure 2. Basic mechanism of starch biosynthesis in the heterotrophic organs of Dicotyledons (e.g. potato) according to Bahaji et al. (2014). ADP-Glc – adenosine diphosphoglucose; ATP – adenosine triphosphate; Glc-1-P – glucose 1-phosphate; Glc-6-P – glucose 6-phosphate; UDP-Glc – uridine diphosphate glucose; numbers of enzymes see Table 1

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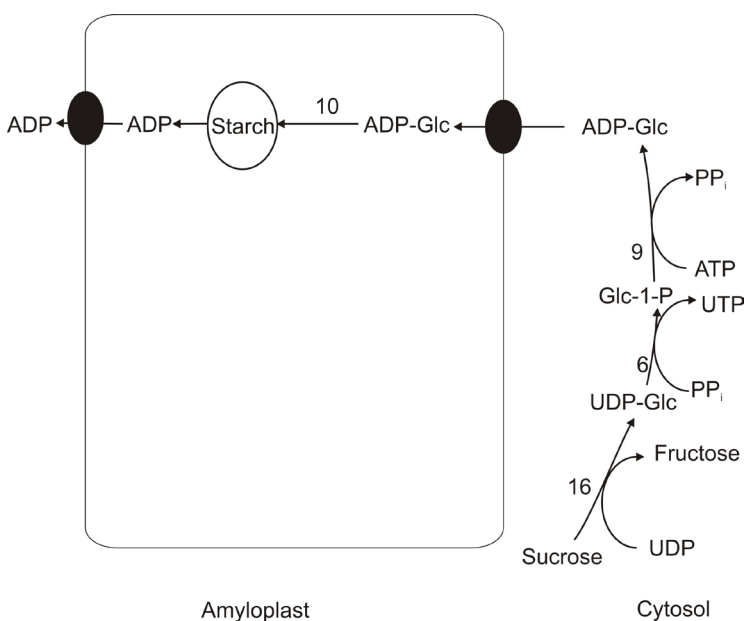


Figure 3. Basic mechanism of starch biosynthesis in the heterotrophic organs of Monocotyledons (cereals) according to Bahaji et al. (2014). ADP-Glc – adenosine diphosphoglucose; ATP – adenosine triphosphate; Glc-1-P – glucose 1-phosphate; UDP-Glc – uridine diphosphate glucose; numbers of enzymes see Table 1

and SS5, and granule bound SS (GBSS – granule bound starch synthase), till now (Yan et al. 2009, Liu et al. 2015). Starch synthase SS1 catalyses the synthesis of amylopectin chains with the degree of polymerization (DP) of approximately 6–7, to form chains of DP 8–12. SS2 catalyses the synthesis of chains of DP 6–10 to DP 12–25 (Chen et al. 2014). SS3 catalyses the synthesis of chains of DP 25–35 or greater. SS4 controls the initiation of starch granules (Roldán et al. 2007, Szydłowski et al. 2009). GBSS is an enzyme responsible for synthesis of the extra-long chain fraction of amylopectin (Wattebled et al. 2002, Ral et al. 2006, Ahuja et al. 2014). A novel SS isoform (SS5) has been recently identified by Liu et al. (2015) in maize seed. The action and concentration of the synthases in cereals depends on the day post-anthesis (Chen et al. 2014).

The starch-branching enzyme isoforms (SBEI and SBEII) and two groups of debranching en-

zymes (SDBEs) are involved in the amylopectin biosynthesis. The SBEI plays an important role in the synthesis of B1-, B2-, and B3-chains (Figure 4). SBEII-b performs a distinct function in the formation of A-chains. Whereas SBEI and SBEII generate 1, 6 linkages that form the branched structure of amylopectin, SDBEs presented in plants in two types: isoamylase and pullulanase efficiently hydrolyse 1, 6 linkages in amylopectin. They remove unnecessary or erroneous branches. Simultaneously, SDBEs are essential players in the formation of crystalline amylopectin (Chen et al. 2014).

**Elimination of the GBSS activity: molecular genetic approach**

GBSS (waxy protein) in two forms (GBSS-I and GBSS-II) is the only starch synthase isoform re-

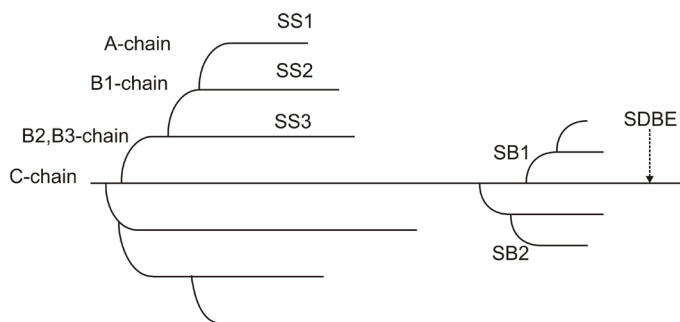


Figure 4. Core enzymes of the final step of starch biosynthesis. SS – starch synthase; SDBE – starch-debranching enzyme

quired for amylose synthesis. According to Wang et al. (2014) GBSS-I is mainly responsible for amylose synthesis in cereal endosperm, whereas the GBSS-II is responsible for amylose synthesis in leaves and other non-storage tissues which accumulate transient starch. Amylose is synthesized within the amylopectin matrix (Tatge et al. 1999, Denyer et al. 2001). GBSS is encoded by so called waxy genes situated at independent loci; plants lacking the waxy gene produce starch without amylose, known as waxy starch (Sano 1984, Shapter et al. 2009).

According to Biselli et al. (2014) the waxy gene in rice is located on chromosome 6 and consists of 13 exons and 12 introns. A single nucleotide polymorphism (AGGT or AGTT) at the first nucleotide of the first exon-intron junction of the waxy gene affects the expression of waxy gene. If the first nucleotide of intron 1 is G (AGGT), the intron is excised for external splicing normally and the expression level of the mature mRNA is high, resulting in high levels of amylose and thus, non-waxy starch. On the other hand, if the first nucleotide is T (AGTT), the intron is not spliced normally and gene expression is reduced, resulting in low amylose content and waxy starch (Pusadee et al. 2014). Rohde et al. (1988) found that barley waxy gene consists of 12 exons and 11 introns. Chao et al. (1989) found that wheat endosperm has three isoforms of GBSSI encoded by the Waxy (Wx) loci, Wx-A1, Wx-B1, Wx-D1, located on chromosomes 7AS, 4AL (translocated from 7BS), and 7DS, respectively. Yamamori (2009) and Yamamori and Yamamoto (2011) developed wheat lines with amylose content of 1–20%, which carried two null waxy alleles and one allele with reduced activity or expression.

Waxy genes were identified in many species, including maize (Shure et al. 1983), rice (Wang et al. 1995), cassava (Ceballos et al. 2007), wheat (Nakamura et al. 1995, Hung et al. 2007), potato (Hovenkamp-Hermelink et al. 1987), and *Arabidopsis* (Ovecka et al. 2012, Ortiz-Marchena et al. 2014). Several properties distinguish GBSS from other starch synthase isoforms. Firstly, it is tightly bound to starch granules and is the most abundant protein there (Grimaud et al. 2008). Secondly, unbound GBSS protein appears to be unstable, since it is not detectable in soluble protein fractions of leaves, even in the absence of starch granules (e.g., at the end of the night, when the starch has been fully degraded) (Smith et al. 2004).

Finally, unlike soluble starch synthase isoforms such as SS2, GBSS elongates malto-oligosaccharides processively and with higher efficiency (Denyer et al. 1999).

Recent research has further revealed another protein responsible for elongating amylose polymers in the *Arabidopsis* model plants: protein targeting to starch (PTST), which possesses an N-terminal coiled coil domain and a C-terminal carbohydrate binding module (CBM – carbohydrate binding module). *Arabidopsis* mutants bearing a functionless PTST synthesised similar amylose-free starch as in the case of the mutation in the enzyme GBSS. It was further revealed that GBSS non-covalently interacts with PTST via a coiled coil domain. Furthermore, the CBM domain of PTST, which mediates its interaction with starch granules, is also required for correct GBSS localisation. Thus, PTST represents a promising new gene target for the biotechnological modification of starch composition, as it is exclusively involved in amylose synthesis (Seung et al. 2015).

Although waxy alleles have a negative effect on the productivity and disease resistance several modern waxy wheat cultivars have already been registered in China (Zhang et al. 2013), France (<http://www.secobra.com/en/wheat.aspx>, 20.8. 2015) and USA (Graybosch et al. 2014).

## Conclusion

Waxy starch (without amylose) is applied in food technologies (e.g. confectionary or bakery) where it minimises retrogradation and consequently ageing of the products. Besides, when amylopectin is debranched at 1, 6 linkages by debranching enzymes (e.g. isoamylase and pullulanase) under specific conditions, only short linear chains having a relatively narrow MW distribution are released, and they may be applied for the preparation of nanoparticles.

Detailed studies focused on the pathway of starch biosynthesis and signals and mechanisms regulating starch synthesis in plants have been published by a number of authors. The precursor of starch is ADP-Glc which originates in different plants and tissues by different ways briefly described here.

Elongation and branching of amylopectin during its biosynthesis is a complex process and requires an array of enzymes viz. starch synthases, starch



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branching enzymes and debranching enzymes. However synthesis of amylose not present in waxy starches is brought about solely by the enzyme granule-bound starch synthase I or waxy protein.

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