A review of starch biosynthesis in cereal crops and its potential breeding applications in rice (*Oryza Sativa* L.)

Ruiqing Li[1,2], Wenyin Zheng[2], Meng Jiang[3] and Huali Zhang[1]

[1] State Key Laboratory of Rice Biology and Chinese National Center for Rice Improvement, China National Rice Research Institute, Hangzhou, China
[2] College of Agronomy, Anhui Agricultural University, Hefei, China
[3] State Key Laboratory of Rice Biology, Institute of Crop Sciences, Zhejiang University, Hangzhou, China

ABSTRACT

Starch provides primary storage of carbohydrates, accounting for approximately 85% of the dry weight of cereal endosperm. Cereal seeds contribute to maximum annual starch production and provide the primary food for humans and livestock worldwide. However, the growing demand for starch in food and industry and the increasing loss of arable land with urbanization emphasizes the urgency to understand starch biosynthesis and its regulation. Here, we first summarized the regulatory signaling pathways about leaf starch biosynthesis. Subsequently, we paid more attention to how transcriptional factors (TFs) systematically respond to various stimulants *via* the regulation of the enzymes during starch biosynthesis. Finally, some strategies to improve cereal yield and quality were put forward based on the previous reports. This review would collectively help to design future studies on starch biosynthesis in cereal crops.

INTRODUCTION

With the improvement of living standards, people have higher and higher requirements for food quality. As the main component of grain crops, especially cereal crops, the content, and quality of starch will directly affect the economic benefits of crops. The harvested heterotrophic parts of staple crop plants are usually starch-storing organs such as roots (cassava, taro, and sweet potato), tubers (potato), and cereal seeds (rice, maize, wheat, barley, and sorghum) (*Bahaji et al., 2014*). Among of these, cereal seeds contribute to maximum annual starch production (*Zeeman, Kossmann & Smith, 2010*; *Nuttall et al., 2017*) and provide primary food to humans and livestock worldwide. However, the growing demand for starch in the food industry and the increasing loss of arable land due to urbanization emphasized the need to uncover starch biosynthesis and its regulation. The detailed regulatory mechanisms of starch biosynthesis during seed formation are largely unknown, irrespective of most starch metabolic enzymes have been identified (*Thitisaksakul et al., 2012*).
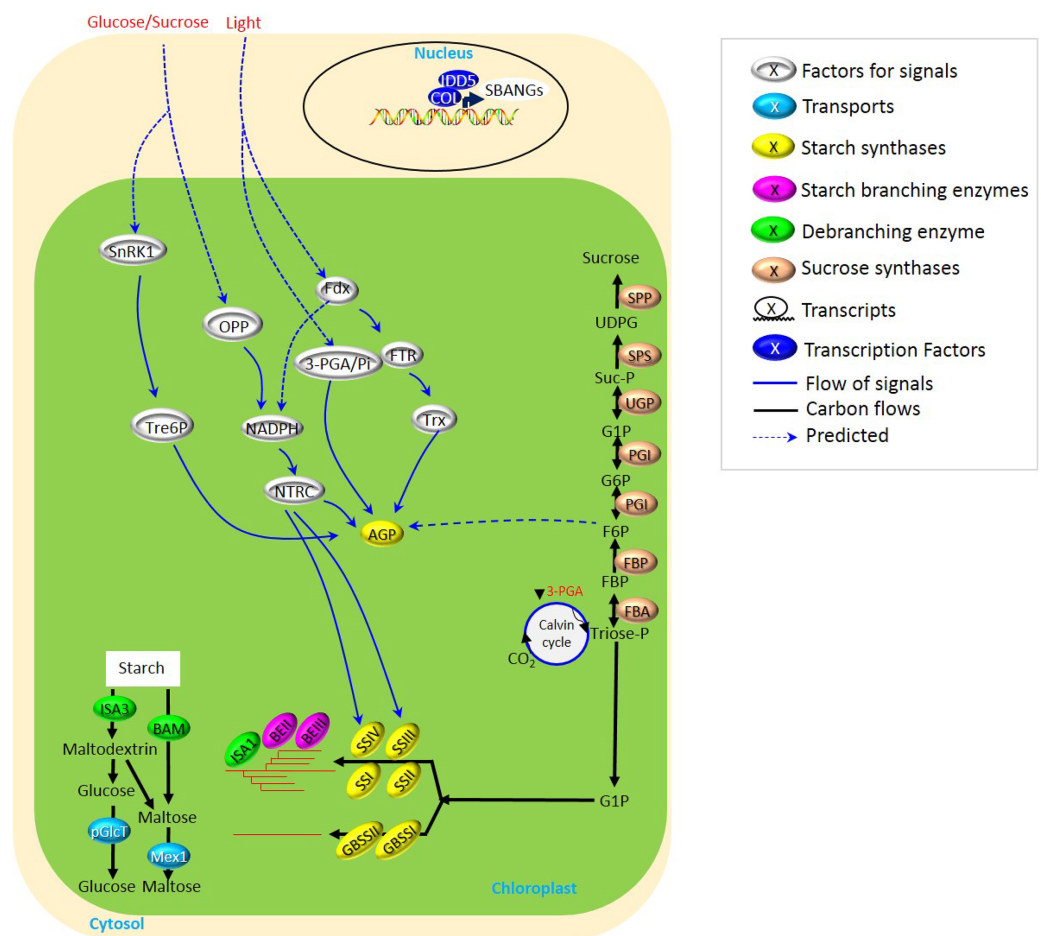
Figure 1 Biosynthesis of transient starch in cereal crops. Starch biosynthesis in cereal leaves displays the rhythmic turnover following the day and night oscillation of recurrent cycles of accumulation and degradation. This was largely related to the light- and glucose/sucrose-mediated signals for the regulation of starch synthases, *i.e.*, AGP, SSIII, and SSIV. NADPH seemed to be served as one of the common modules of the light- and glucose/sucrose-mediated signals, while SnRK1-Tre6P performed as an independent pathway to mediate AGP. All these determine a subtle and flexible mechanism of starch biosynthesis in leaves. Full-size ⬙ DOI: 10.7717/peerj.12678/fig-1

Starch is composed of amylose and amylopectin glucan polymers, which are packaged to form the insoluble semi-crystalline starch granules (*Sabelli & Larkins, 2009*; *Pfister & Zeeman, 2016*). There are at least two types of synthesized starch in plants (Fig. 1). Transitory starch usually exists in the plastids of photosynthetic organs and display circadian turnover regulation with diurnal cycles (*Pfister & Zeeman, 2016*; *Stitt & Zeeman, 2012*). More importantly, the non-photosynthetic amyloplasts usually serve as the synthetic places for storage starch, which require the supply of sucrose and ATP from leaves to realize the starch synthesis (*Bahaji et al., 2014*). Therefore, various transporters are also essential for storage starch synthesis through the delivery of sucrose and energy by using vascular system (*Geiger, 2011*).

Starch synthesis requires three sorts of enzymes (*Myers et al., 2000*), including starch synthase (SS), branching enzymes (BEs), and debranching enzymes (DBEs). Among them,

SSs are responsible for elongating glucan chains, and nowadays, six SS isoforms (SSI-SSV), granule-bound starch synthase I (GBSS/Wx) have been well characterized into the roles during starch synthesis, except for SSV (*Nougué et al., 2014*). SSI-SSIII are vital to establish proper amylopectin synthesis, while GBSS mainly functions in amylose synthesis (*Pfister & Zeeman, 2016*; *Delvallé et al., 2005*; *Fujita et al., 2007*). Besides, SSIV prefers to create branched glucans together with BEs and DBEs and to initiate granule formation (*Crumpton-Taylor et al., 2013*; *Pfister et al., 2016*; *Roldán et al., 2010*; *Malinova et al., 2017*; *Lu et al., 2018*). Moreover, BEs form an α-1,6-linkage *via* transferring linear glucan, and DBEs facilitate the formation of the crystalline amylopectin layers through removing α-1,6-linkages (*Pfister et al., 2014*; *Pfister & Zeeman, 2016*).

Starch accounts for 85% of the dry weight of cereal endosperm (*Bahaji et al., 2014*; *Geigenberger, 2011*) is a major storage carbohydrate formed in cereal seeds and contributes to crop yield. Starch biosynthesis in cereal crops requires coordination of starch biosynthetic enzymes and coordinates with other metabolic processes that utilize starch biosynthetic enzymes (Table S1). Thus, it is vital to engineer crops with desirable agronomic traits using biotechnological approaches (*Bahaji et al., 2014*) and marker-assistant breeding (*Rahim et al., 2020*) in crops. Based on the current references, little differences exist between several cereal crops. Nonetheless, more starch related references are reported in rice. Also, as the model plant of monocotyledonous, rice could provide referees for other species. Besides, the demand for rice quality has been getting higher and higher with the improvement of people's living standard (*Bahaji et al., 2014*). The rice qualities determine its commercial value in the economic market, and have attracted the focus of both consumers and rice breeders (*Bahaji et al., 2014*; *Geigenberger, 2011*; *Chen et al., 2012*). With the increasing demand for rice of good qualities, it is vital to explore starch biosynthesis and its regulatory mechanisms, which would be important for the oriented genetic improvement of rice qualities.

Nowadays, there are many published reviews about starch biosynthesis in plants (*Geigenberger, 2011*; *Bahaji et al., 2014*; *López-González et al., 2019*). Based on the timeliness of starch research, more recent works on starch biosynthesis have been focused on the transcriptional factors and the regulatory mechanisms. This review furthermore updated the works of starch metabolism in cereal crops on the basis of previous reviews. Since grain development is limited by the duration of flag leaf photosynthesis (*Borrill et al., 2015*) and associated with the sugar levels and activities of important starch-synthesizing enzymes (*Fahy et al., 2018*) during seed development in cereal crops, we initiated to summarize the regulatory signals in leaf starch biosynthesis. Subsequently, we paid more attention to how transcriptional factors (TFs) systematically respond to various stimulates *via* regulations of the enzymes during endosperm starch synthesis. Finally, the molecular mechanism of starch synthesis was summarized and strategies for rice yield and quality improvement were discussed, providing theoretical basis for improvement and breeding in rice. Some strategies were put forward to improve cereal yield and quality based on the previous reports. Our review provides a critical review of the studies on starch biosynthesis regulation and some potential starch-related strategies for applications in crops.

SURVEY METHODOLOGY

To complete this article, an electronic literature search was performed exhaustively on the databases of Web of Science, Google Scholar, Science Direct, Mendeley and EndNote using key words such as "starch metabolism", "cereal crops", "transcription factors", "transient starch", "endosperm starch", "rice", "maize", "wheat", "Barley", "sucrose-to-starch", integrated with the usage of "+", "or", "AND" for specific search returns. Works of the past 20 years (up until Aug 29th, 2021) were mostly focused here. More than eight hundred publications were retrieved, and article selection was conducted according to previous method (*Moher et al., 2009*). First of all, the duplicated articles were deleted. Subsequently, unrelated articles were then screened out after examining the titles and abstracts. Eventually, the most relevant articles in English were used to complete this review.

Biosynthesis of transient starch in cereal crops

Compared to many studies on the biosynthesis of transient starch in other plants, *i.e.*, *Arabidopsis*, few have focused on cereal crops. This is largely attributed to the phenotypical obscurity derived from the aberrant metabolism of transient starch in cereal leaves and the inedible traits of leaves. However, although sucrose-to-starch metabolism occurs with transport *via* phloem to sink tissues (*Macneill et al., 2017*), due to utilizing fructose phosphates to glucose phosphates to ADP-glucose, transient starch metabolism in leaves is vital for the formation of seeds, and nowadays, it is also helpful to explore the source of potential biofuels to relieve energy shortage. Several reviews (*Zeeman et al., 2002*; *Geigenberger, 2011*; *Stitt & Zeeman, 2012*) have focused on starch metabolism in plants. Our review highlights the possible signaling of starch biosynthesis explicitly upon starch metabolism under light/darkness alternation in crops, including glucose/sucrose signals (Fig. 1 and Table S1).

Light-dependent signaling pathway

The rhythmic turnover following the day and night oscillation of recurrent cycles of accumulation and degradation has been displayed through the biosynthesis of transient starch in cereal leaves (*Bahaji et al., 2014*; *Fernandez et al., 2017*). However, various types of light/darkness alternation and glucose/sucrose availability, as well as protein-protein interaction, determine a subtle and flexible mechanism of starch biosynthesis in leaves (Fig. 1 and Table S1).

Because light-dependent photosynthesis provides raw materials for starch synthesis, the synthetic rate of starch in leaves is regulated to encounter the fluctuating day length. However, fluctuation of day length usually temporarily generates a period of carbon shortage, which is mainly dependent on the light-dependent rebalance of the carbon budget. The rebalance of the carbon budget is usually realized by accelerating the starch synthesis while hindering the rate of starch degradation (*Graf & Smith, 2011*). Moreover, from a part of the newly fixed carbon during the light period, starch was synthesized and then degraded into glucan in the following night period, termed as starch turnover (*Bowsher et al., 2007*; *Lee et al., 2016*). This promotes starch turnover to

synchronize with the day length (*Fernandez et al., 2017*; *Davies et al., 2003*; *Pan, Strelow & Nelson, 1990*), which maximizes the efficiency of carbon use. Therefore, starch turnover is essential for plant development and biomass generation, and more importantly, is an effective and efficient response to light-dependent environment adaptation.

Light-dependent signaling usually realizes its regulation to starch synthesis through the control of starch biosynthetic enzymes. ADP-glucose pyrophosphorylase (AGPase) was supposed to be one of the most studied enzymes involved in the light-dependent signaling pathway, in which the regulation of AGPase was largely related to the modules of photosynthesis. For example, ferredoxin (Fdx), thioredoxins (Trx), and Fdx-dependent Trx reductase (FTR) participated in the regulation of AGPase in response to light (*Lunn et al., 2014*; *Davies et al., 2003*). Besides, through nicotinamide–adenine dinucleotide phosphate (NADPH) and NADP-thioredoxin reductase (NTRC), light-induced Fdx also regulated the expression of AGPase/starch synthase III (SSIII)/SSIV/β-amylase (BAM) (*Yadav et al., 2014*). 3-phosphoglycerate (3-PGA; *Guo et al., 2012*) and fructose-6-phosphate (F6P; *Koumoto et al., 2013*) were also involved in the regulation of AGPase, but the detailed mechanisms were not very clear. Collectively, for transient starch biosynthesis, light is vital to regulate the activities of various starch biosynthetic enzymes through (i) 3-PGA→AGPase, (ii) Fdx→FTR→Trx→AGPase, and (iii) Fdx→NADPH→NTRC→ AGPase/SSIII/SSIV/BAM (Fig. 1).

Glucose/sucrose-dependent signaling pathway

As important forms of carbon budget, glucose and sucrose also function in the regulation of carbon allocation during starch biosynthesis. Nonetheless, this is a very complex process. More than that, glucose and sucrose are also greatly related to the balancing of growth and reproduction using the available carbon, which involves trehalose 6-phosphate (Tre6P) in higher plants (Fig. 2).

Tre6P, an intermediate of trehalose (TRE) biosynthesis, functions in the sucrose-Tre6P sensor nexus (*Paul et al., 2010*; *Martins et al., 2013*). It involves the coordination of carbon and nitrogen metabolism in plants (*Bledsoe et al., 2017*; *Paul et al., 2008*). To optimize the intracellular sucrose concentrations for plants' growth and development, Tre6P usually acts as both a signal and a negatively retrograde regulator (*Yadav et al., 2014*). Although the contents of Tre6P and TRE are low, Tre6P is essential in making sucrose available to organs, correlating strongly with changes in available carbon (*Martínez-Barajas et al., 2011*). During sucrose and starch metabolism, the interaction of Tre6P with the sucrose nonfermenting1-related kinase 1 (SnRK1) system occurred (*Zhang et al., 2009*; *Nunes et al., 2013*). It provided new views on the allocation of carbon to the developing cereal grains.

In fact, in the endosperm of cereal crops, the deposition of starch grains is closely connected with Tre6P. In several cereal crops, a model for the role of Tre6P in carbon partitioning and yield was proposed and confirmed (*Langlois, Shulman & Arbesman, 2015*). Local sucrose availability played key roles in Tre6P/SnRK1 signaling to determine yield and grain quality (*Martínez-Barajas et al., 2011*; *Lawlor & Paul, 2014*). In Tre6P/ SnRK1 signaling, another key factor was trehalose-6-phosphate phosphatase 7 (TPP7),
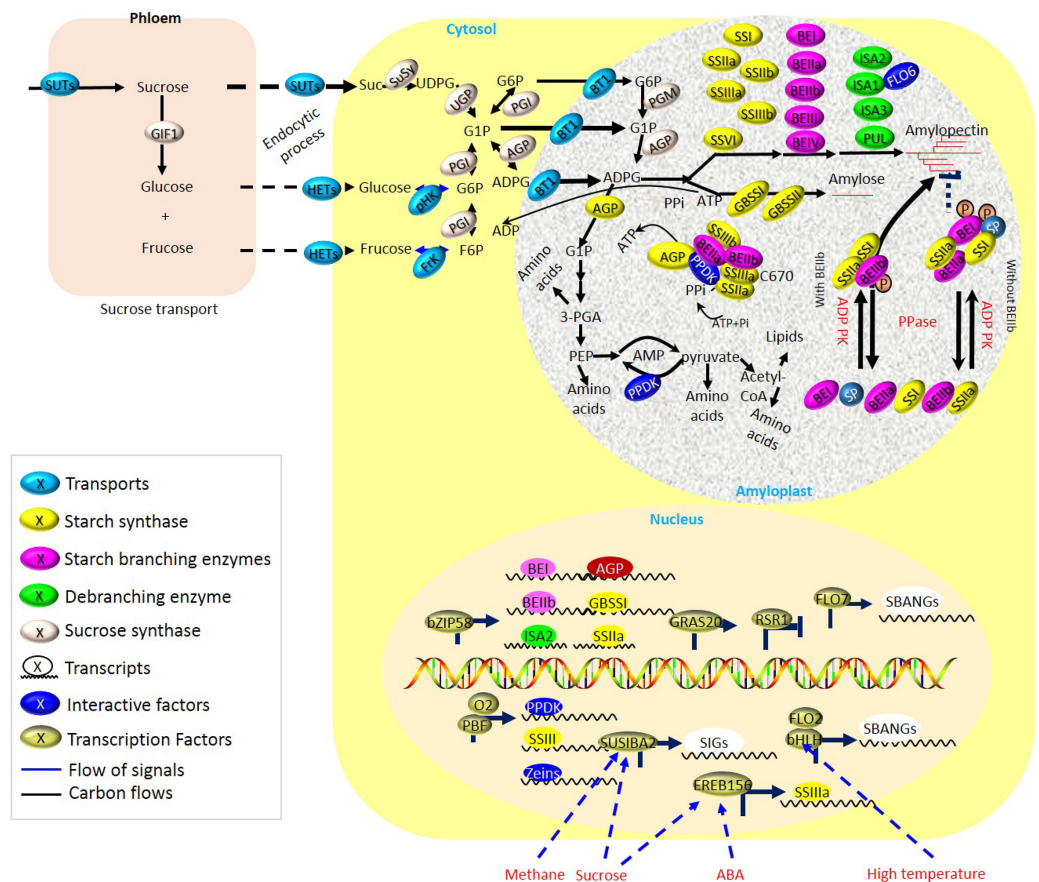
Figure 2 Biosynthesis of storage starch in cereal crops. During the grain filling period, sucrose localized in vegetative organs (*i.e.*, leaves) is intensively unloaded from the phloem and transported into the reproductive organs (*i.e.*, grains). Multiple starch biosynthetic enzymes co-operate to produce starch granules both in transient and storage starch biosynthesis. Grain-filling is associated with the normal development of amyloplasts, delivery of carbon precursors and energy from leaves to endosperm by sucrose transporters (SUTs), and enzymes of endosperm starch biosynthesis during grain-filling periods, which are greatly susceptible to fluctuated environments. Full-size ◩ DOI: 10.7717/peerj.12678/fig-2

which increased Tre6P turnover and served as an energy sensor (*Kretzschmar et al., 2015*). Also, TPP7 could measure anabolism or catabolism depending on the availability of local sucrose (*Nuccio et al., 2015*), thereby enhancing starch mobilization to trigger the growth dynamics of the germinated embryo and elongated coleoptile sheath. This consequently improved anaerobic germination tolerance in direct-seeded rice (*Kretzschmar et al., 2015*). Because of high sucrose concentration, the accumulation of Tre6P inhibited SnRK1 to promote growth. However, low sugar promoted the conversion from Tre6P to TRE, and therefore, phosphorylated SnRK1 to activate C/S1 basic leucine zipper (bZIP) transcription factors (TFs) for resource sequestration in sinks (*Langlois, Shulman & Arbesman, 2015*). The Tre6P-C/S1 bZIP-SnRK1 regulatory module existed in both monocotyledon (*i.e.*, rice; *Cho et al., 2012*) and dicotyledons (*i.e.*, *Arabidopsis*; *Lunn et al., 2014*; *ÓHara, Paul & Wingler, 2013*). The effective nutrient-sensing system served as a spatial-temporal regulator (*Langlois, Shulman & Arbesman, 2015*; *Cho et al., 2012*), which improved the yield stability of staple crops under adverse conditions.

Aside from light, sucrose or glucose also served as another factor in activating the signaling of NADPH-NTRC to regulate AGPase/SSIII/SSIV (*Guo et al., 2012*). Nonetheless, oxidative pentose phosphate (OPP) and SnRK1 (*Nunes et al., 2013*) were supposed to be the first sensors for sugar.

Collectively, the accumulation of sucrose was vital for plant growth through regulation of starch biosynthesis, and several sucrose-dependent signaling has been summarized here, including (i) sucrose→SnRK1→Tre6P→AGPase and (ii) sucrose→OPP→NADPH→NTRC→AGPase/SSIII/SSIV (Fig. 1).

Circadian rhythms for starch biosynthesis

Circadian rhythm is also an important regulator for starch biosynthesis. Starch biosynthesis followed the circadian rhythms (*Annunziata et al., 2017*) and relied on the duration and light intensity (*Fernandez et al., 2017*). Thus, based on the light-dependent activity of starch-degrading enzymes, starch was more susceptible to degradation. This was partly attributed to the transcript levels of β-amylase 3 (BAM3), the major starch degrading enzyme with a short half-life (*Li et al., 2017a*). However, many other starch degradation-related enzymes, including glucan water dikinase (GWD), α-amylase 3 (AMY3), and disproportionating enzyme 2 (DPE2), had long half-lives over the day/night cycle (*Skeffington et al., 2014*; *Baerenfaller et al., 2012*; *Nelson et al., 2014*; *Wu et al., 2002*). This also determined that their activities were probably not regulated at the gene expression level. For example, to activate enzymes' activities and initiate starch breakdown in light, the transcription levels of AMY3- and BAM1-encoded genes were greatly upregulated in the present osmotic stress. Nonetheless, these two enzymes were not essential for diel starch metabolism without abiotic stress conditions (*Fulton et al., 2008*; *Horrer et al., 2016*; *Thalmann et al., 2016*). Inversely, in the presence of light, a higher increased propensity of starch degradation with time largely depended on phosphorylation of BAM1 and AMY3 (*Fernandez et al., 2017*; *Thalmann et al., 2016*). The phosphorylation regulation was achieved by adding phosphate groups to glucose (Glc) residues with two GWDs and phosphoglucan water dikinase (PWD). This reduced the level of crystalline organization of the granule matrix and exposed the surface of BAMs to attack, thus causing an increased propensity for starch degradation with time during the light period (*Scialdone et al., 2013*; *Fernandez et al., 2017*). Therefore, the elaborate regulation of enzymatic activities is tightly related to environmental conditions.

Besides the light period, several starch biosynthetic enzymes were prone to function in dark conditions. For example, GBSS/Wx elongated the amylose polymers released from the starch granule and rapid degradation of starch granule at night (*Ortiz-Marchena et al., 2014*). Another was early starvation 1 (ESV1), a relatively novel starch degradation factor, which was essential for controlling the starch breakdown rate at night (*Feike et al., 2016*). Nonetheless, through phosphorylation/dephosphorylation enzymes, ESV1 performed a distinguished working mode and directly mediated starch-bound phosphate (*Feike et al., 2016*). Besides, for starch degradation, ESV1 and its homologs also displayed spatiotemporal specificity. In the absence of ESV1, for promoting the accumulation of maltose from starch degradation, starch granules in leaves appeared to be accessible to

hydrolytic enzymes during the day and night (*Weise, Weber & Sharkey, 2004*). However, starch storage may be prevented in other organs due to simultaneous biosynthesis and starch degradation (*Feike et al., 2016*).

The phenomenon of light alternating between day and night also made the metabolism of starch rhythmicity. It was mainly realized through the starch-degrading enzyme (Fig. 1). Compared with the regulation of starch synthase at the gene expression level, phosphorylation regulation of long half-life enzyme activities appeared to be more conducive to the biological adaptation of light rhythm and biological stress. Besides, some of the regulatory elements and enzymes displayed certain temporal and spatial expression specificity in the biosynthesis of starch. Therefore, there has been a certain difference between the synthesis of temporary starch and the synthesis of storage starch. It might help realize the effective regulation of seed formation to bring clarity in the commonness and difference.

Delivery of the carbon precursors from leaves to developing grains

For energy production and starch biosynthesis, sucrose synthesized in leaves must be transported from the leaves throughout a long-distance vascular pathway (phloem) to the developing grains (Fig. 2 and Table S1). Three types of sucrose transporters (SUTs or SUCs) have been identified in plants (*Reinders, Sivitz & Ward, 2012*; *Kühn & Grof, 2010*). Multiple SUTs have now been identified in cereal crops, including C3 grasses such as rice (*Sun et al., 2010*), wheat (*Aoki et al., 2004*), and barley (*Haupt et al., 2001*), and C4 grasses, including maize (*Baker et al., 2016*; *Guo et al., 2012*) and sweet sorghum (*Bihmidine et al., 2016*). The type I SUTs are unique to eudicots and play roles in loading and retrieval of Suc in the transport phloem (*Gould et al., 2012*). For type II SUTs, at least three functions have been proposed in cereals (*Aoki et al., 2003*; *Scofield et al., 2002, 2007*; *Sauer, 2007*; *Baker et al., 2016*), including (i) Suc phloem loading in leaves, (ii) phloem unloading of Suc in sink tissues, and (iii) retrieval of leaked Suc. Among of them, the type II SUTs in rice has been showed the likewise functions (*Ishimaru et al., 2001*; *Scofield et al., 2002, 2007*). Besides, the type III SUTs localizes at vacuolar membrane and functions in sucrose-uptake (*Schulz et al., 2011*). Besides, at least one Type III SUT exists in each plant species. By regulating the energy status and controlling flowering, sucrose supply to the filling grain was crucial for crop yield and quality (*Kühn & Grof, 2010*). SUTs were tightly regulated depending on fluctuating environments such as light and photoperiod, and internal stimuli such as phosphate (P) starvation, sucrose leakage, and H^+ leak (Fig. 2).

Sucrose transporters appear to be relatively conserved within the *Viridiplantae* plants, despite limited studies on the regulation of SUTs in cereal crops. The identification of sucrose transporters in cereal crops could be aided by the complete genome sequences of Arabidopsis and potato.

Biosynthesis of storage starch in cereal crops

Aside from sucrose and ATP from leaves, normal development of differential plastids, amyloplasts, are essential for the synthesis of endosperm starch, and thereby, there are
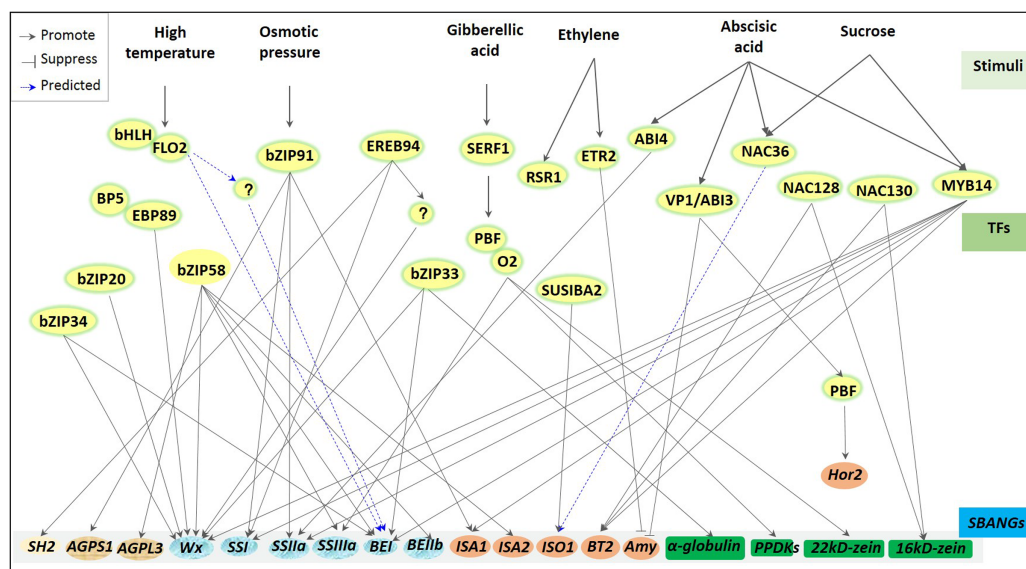
Figure 3 Regulators of transcriptional factors involved in starch biosynthesis of cereal crops. A great deal transcription factors (TFs), including bZIPs, bHLHs, NACs and MYBs, are involved in the regulation of starch biosynthesis, and functions with the different conditions, especially under the environmental stress (*i.e.*, high temperature, osmotic stress) and the stimulations of various phytohormones, including ABA, GA, and ethylene. Response of TFs to the stimulates usually showed systematic transcriptional regulation. Almost all TFs control multiple genes, including bZIP58, MYB14, bZIP91 and so on; in turn, one gene may also response to several TFs, *e.g.*, *Wx* (*GBSSI*), *BEI* et al. All these suggests that one complex and elaborate regulated network is existed during starch synthesis in cereal crops, despite showing many unknown mechanisms. Full-size ⬛ DOI: 10.7717/peerj.12678/fig-3

some common traits existing between chloroplasts and amyloplasts. During starch biosynthesis, expression of starch biosynthetic genes was proposed to be regulated by tetrapyrrole intermediates both in BY-2 cultured cells (*Enami et al., 2011*) and in rice (*Li et al., 2021*). The mutation of rice *genome uncoupled 4*, which was revealed as one predominant regulator of chlorophyll biosynthesis, performed negative effects on the starch synthetic genes, such as *GBSSI* and *AGPS1*, in endosperm during early seed development, partially through mediating the accumulation of heme (*Li et al., 2021*). Obviously, the well-functioning of starch biosynthetic enzymes also plays key roles during starch synthesis (Fig. 2), whereas mutations of the genes encoding starch biosynthetic enzymes usually lead to negative yield and/or quality of crops. Nonetheless, part of the mutation also contributes to some peculiar features of starchy endosperm, which could serve as excellent features in breeding applications (*i.e.*, floury; Table S1). Obviously, one complex regulatory network seems to be employed for the accumulation of storage substances and relies on coordination among different metabolic and cellular processes.

Regulators of transcriptional factors

Regulation of transcriptional factors for storage starch biosynthesis has been greatly reported in plants (*Mangelsen et al., 2010*; *Tiessen et al., 2012*; *Fu & Xue, 2010*) and greatly depends on varied environments (Fig. 3). For example, high temperature stress usually downregulated the expression of starch synthesis-related genes, including GBSS,

branching enzyme I (BEI; *Blauth et al., 2002*; *Satoh et al., 2003*), substandard starch grain (*Matsushima et al., 2014*; *2016*), and BEIIb (*Nishi et al., 2001*; *Regina et al., 2005*), whereas ABA and sucrose induced the ZmSSIIIa expression (*Huang et al., 2016*). Although diverse starch biosynthetic genes were subjected to be driven through different specific TFs, some regulations appeared to have pleiotropisms or multigenic effects. One ZmEREB156 specifically combined with ZmSSIIIa promoter to regulate starch synthesis in maize (*Huang et al., 2016*). However, to regulate starch synthesis in rice endosperm, one leucine zipper bZIP58 showed wide compatibility to regulate several genes (*Zhang et al., 2012*; *Hanashiro et al., 2008*; *Lee et al., 2007*; *Wei et al., 2017*), including *OsAGPL3*, *OsGBSSI* (*Wx*), *OsSSIIa*, *BEI*, *OsBEIIb*, and isoamylase-type debranching enzyme 2 (*ISA2*). Besides, *GBSSI* was reported to be regulated by several TFs, including bZIP33, bZIP34 (*Wang et al., 2013*), and bZIP58 (*Onodera et al., 2001*) in rice and ZmMYB14 (*Xiao et al., 2017*) and prolamin-box binding factor/opaque 2 (PBF/O2) (*Zhang et al., 2016a*) in maize. Nowadays, many TFs involved in endosperm starch biosynthesis have been reported, including GRAS20 (*Cai et al., 2017*), ethylene response 2 (ETR2; *Wuriyanghan et al., 2009*), bZIP91 (*Zhang et al., 2016b*), NAC36 (*Chen et al., 2016*), FLOURY ENDOSPERM7 (FLO7) (*Zhang et al., 2014*; *Li et al., 2014a*), and SUSIBA2 (*Sun et al., 2003*; *Su et al., 2015*) in rice, barley, and maize. However, most of them have not been explored in specific regulated genes with their given degree of studies.

Besides, transcriptional regulation on starch biosynthesis can also be realized through TF combination with other factors. Under high temperatures, starch biosynthesis-associated nuclear genes (SBANGs) were regulated by the interaction of FLO2 and bHLH (*She et al., 2010*). One novel FLO2-interacting protein was demonstrated to maintain fertility and seed quality in rice (*Suzuki et al., 2020*). Regulation of pyruvate orthophosphate dikinase (PPDK), SSIII, and zein during protein and starch synthesis were subjected to the co-interaction of O2 and PBF (*Zhang et al., 2016a*).

Additionally, in different cereal crops, transcriptional regulation on starch biosynthesis also showed a certain degree of conservation. The DOF transcription factors bound to GaMyb to mediate α-amylase (AMY) in rice (*Yamamoto et al., 2006*; *Kawakatsu et al., 2009*) and in barley (*Diaz et al., 2002*), while a WRKY transcription factor SUSIBA2 regulated endosperm starch synthesis in barley and rice (*Sun et al., 2003*; *Su et al., 2015*). Moreover, the bZIP transcription factor was also bound to a conserved cis-element to regulate storage starch and storage proteins in maize (*Zhang et al., 2016a*), wheat (*Albani et al., 1997*), and rice (*Onodera et al., 2001*). Recently, one endosperm-specific NAC-type TF, TaNAC019, was revealed to directly mediate the accumulation of storage proteins *via* TaSPA and TaGAMyb to regulate SSIIa and sucrose synthase 1 (SuSy1) consequently affecting the starch accumulation in wheat (*Gao et al., 2021*). This was distinguished with previous studies of ZmNAC128 and ZmNAC130 that regulated the transcription of brittle 2 (BT2) and 16-kDa γ-zein in maize (*Zhang et al., 2019*). Still, both were subjected to the regulation of the balance between storage starch and storage proteins. Interestingly, the balance between storage starch and storage proteins also required spatio-temporal coordinating TFs and was subjected to the control of other pivotal upstream regulators to these TFs. In maize, during seed filling, a group of spatio-temporal

coordinating transcription factors (including OPAQUE2, Prolamin Binding Factor1, NAC128, NAC130, and OPAQUE11) were reported to regulate the synthesis of starch and protein in endosperm. And ZMABI19 bind to the promoters of O2 and other transcription factors (*i.e.*, Prolamin Binding Factor1, NAC128, NAC130, and OPAQUE11) that play a key role in seed filling and plant hormone response to regulate their expression (*Yang et al., 2020*). However, the pivotal role of ZMABI19 in maize seed development still needs to be further clarified by exploring the regulation mechanism of ZMABI19 at both transcriptional and translational levels, as well as other upstream factors regulating embryo and endosperm development in coordination with ZMABI19 (*Yang et al., 2020*). To sum up, the regulation of transcription factors on starch biosynthesis shows different levels and forms in diverse environments (Fig. 3).

Functions of starch biosynthetic enzymes

The function of starch biosynthetic enzymes usually depends on posttranslational regulation, including phosphorylation, the formation of a transient complex, and so on (Fig. 2). For starch biosynthesis in cereal endosperms, the phosphorylation-dependent multienzyme complex is essential. The phosphorylation-dependent SSI/SSIIa/BEIIa/BEIIb complex was detected in barley endosperm (*Ahmed et al., 2015*; *Hirose & Terao, 2004*). From SSIIa/SSIIIa/SSIVb/BEI/BEIIb/pullulanase (PUL) in the amyloplast of rice endosperm, a 700 kD protein complex could be formed (*Crofts, Nakamura & Fujita, 2017*; *Guo et al., 2017*; *Fujita et al., 2009*). The formation of BEs and SSs complexes depends on the phosphorylated BE and phosphorylase 1 (Pho1) isoenzymes, while their segregation is activated upon the suppressed dephosphorylation (*Pang et al., 2018*; *Rahman et al., 1997*; *Secco, Baumann & Poirier, 2010*; *Kang et al., 2013*; *Mizuno et al., 2001*). Besides, the regulation of phosphorylation is also greatly associated with the seed development period. A 260 kDa SSI/BEIIa/BEIIb complex formed in the middle and late development period of the grain endosperm instead of the early stage (*Tetlow et al., 2008*). However, the SSIIa/SSI/BEIIb tripolyprotein complex of the initial amyloid matrix participated in synthesizing a starch-branched chain during late seed development (*Liu et al., 2014*, *2012a*). Interestingly, the formation and action sites of the starch complex were also different. The phosphorylation site of SSIIa and BEIIb varied with species (*Crofts, Nakamura & Fujita, 2017*; *Li & Gilbert, 2016*). For example, the amino acid sequence of Thr323 was conserved in rice, maize, and barley but not in wheat. A 670 kDa protein complex consisting of PPDK/AGPase/SSIII/SSIIa/BEIIa/BEIIa was formed to regulate carbon distribution among amino acids, lipids, and starch in the maize endosperm (*Guo et al., 2012*). The Ser residue of BEIIb was phosphorylated by kinases, of which Ser286 and Ser297 were highly conservative between species, but the phosphor-Ser649 was not conservative, which seemed to be confined to the enzyme in cereals and was not universal (*Makhmoudova et al., 2014*; *Liu et al., 2012*).

Importantly, as an important rate-limiting enzyme for starch synthesis, AGPase subunits form a complex with different roles of large and small subunits to make ADP-Glucose, and thereby, the enhanced activity of AGPase would greatly increase the starch content (*Geigenberger, 2011*). AGPase was activated by sucrose (*Tiessen et al., 2012*),

pyridoxal, DTT, and 3-PGA, while suppressed by Pi and nitrate (*Scheible et al., 1997*) to adapt to environmental changes (*Geigenberger, 2011*).

Starch biosynthetic enzymes also functioned *via* the formation and segregation of transient complexes (Fig. 2). Proteomic analysis of soluble fractions from different developmental stages of seeds or endosperms showed that the upregulated expression of many starch-biosynthetic enzymes led to efficient starch biosynthesis in different cereal crops (*Mechin et al., 2007*; *Xu et al., 2010*; *Mu et al., 2009*; *Kazuaki, Kanako & Kazufumi, 2010*; *Long et al., 2017*; *Satoh et al., 2008*). It was also well demonstrated that the size of starch granules correlated with the activity of granule-associated starch biosynthetic enzymes in wheat (*Cao et al., 2015*). Likewise, in maize endosperms, the formation of starch granules were associated with phosphorylation modification of the transient complexes that constituted GBSS, SSI, SSIII, BEI, BEIIa, BEIIb, and Pho1 (*Grimaud et al., 2008*). The developmentally altered SGAPs mainly played significant roles in polyglucan elongation and granule structure modification in developing rice endosperms (*Yu & Wang, 2016*).

Here, to promote efficient carbon partitioning during starch and protein storage, a synergetic network is composed of starch biosynthesis and protein biosynthesis, as well as protein folding and PPDK pathways (Fig. 2 and Table S1).

Granule formation in starch biosynthesis

Granule formation in storage starch shows distinct specific mechanisms from transient starch, and some related enzymes, including SSIV, FLO6 and ISA (Fig. 2). SSI, SSII, SSIII, and GBSS mainly showed activity on linear oligosaccharides, while SSIV seemed to focus on linear maltooligosaccharides (*Ryoo et al., 2007*; *Cuesta-Seijo et al., 2016*; *Lu et al., 2018*; *Dian, Jiang & Wu, 2005*; *Fujita et al., 2006*). SSI is referred to as "DP < 10, soluble starch synthase" with an assigned role of type of amylopectin structure, when the soluble starch synthases extends progressively longer glucan chains from SSI to SSIII, with SSIV plays roles in granule initiation of starch (*Kosar-Hashemi et al., 2007*; *Fujita et al., 2011*; *Cuesta-Seijo et al., 2016*).

Moreover, FLO6 serves a vital function to regulate starch biosynthesis and granule initiation of endosperm starch in rice (*Peng et al., 2014*). Unlike in *Arabidopsis* leaves, the initiation of starch granules in developing seeds largely depends on the distinct interaction with ISA1 in rice, *e.g.*, the interaction of FLO6 with ISA1 (*Dinges et al., 2003*; *Utsumi et al., 2011*; *Peng et al., 2014*). Interestingly, PROTEIN TARGETING TO STARCH 2 (PTST2), the homologous protein of FLO6 in leaves, is not interacted with ISA1, whereas the interaction between PTST2 and SSIV is explored to affect granule numbers (*Seung et al., 2017*). Nonetheless, PTST2/FLO6 performs a conserved function in granule initiation of leaf and endosperms, but further investigations are required to determine the specific mechanism.

Starch synthesis in rice

As one of the most important food crops, grains of rice (*Oryza sativa* L.) consist of embryo, endosperm and seed coat, among which endosperm is a major storage organ for grain

development (*Yu & Wang, 2016*). As the major storage material, starch accounts for 85% dry weights of the cereal endosperm, and thus, serves as one main food source for human beings (*Ferreira et al., 2017*). Since utilizations of the dwarf gene (*Miura et al., 2009*) and heterosis (*Tian et al., 2009*), the yields of rice have been significantly improved twice. However, with the improvement of people's living standard, the demand for rice quality has been getting higher and higher. Therefore, the rice qualities, especially for eating and cooking qualities (ECQs), determine its economic value and consumer recognition in the commercial market, and have attracted the focus of both consumers and rice breeders (*Lau et al., 2015*). Rice quality mainly includes appearance characteristics, ECQs and minor element contents (*Rabiei et al., 2004*; *Okpala et al., 2017*). However, rice quality shows various preferences due to differences in dietary culture (*Ferrero & Nguyen, 2004*). Although some regions prefer trace elements and appearances (*Lau et al., 2015*), more regions, including China and some European countries, pay more attention to taste qualities (*Ferrero & Nguyen, 2004*). Therefore, starch not only is the main storage form of carbohydrate in plants, but also performed important values of biological and economical (*Sulpice et al., 2009*; *Zeeman, Kossmann & Smith, 2010*). With the increasing demand for rice of good qualities, it is vital to explore starch biosynthesis and its regulatory mechanisms, which would be important for the oriented genetic improvement of rice qualities.

As shown in above, starch deposition of grains depends greatly on T6P in endosperm (*Lawlor & Paul, 2014*; *Yadav et al., 2014*). In rice, OsTPP7 is involved in increased Tre6P turnover and plays central roles to promote starch mobilization (*Kretzschmar et al., 2015*). A model has been proposed to illuminate the roles of T6P in carbon partitioning and plant yield (*Langlois, Shulman & Arbesman, 2015*). Accumulation of T6P induced by high sucrose inhibits the SnRK1 activity to repress growth, while low sugar levels would promote the conversion of TRE from T6P, and thereby, the phosphorylated SnRK1 subsequently activate C/S1 bZIP transcription factors for resource sequestration in sinks (*Langlois, Shulman & Arbesman, 2015*). This model is confirmed by several reports from cereal crops. The allogeneic expression of the *OsTPP1* gene in developing maize ears significantly improved yield stability under both normal conditions and mild drought stress (*Nuccio et al., 2015*). Also, in OsMADS6-TPP1 maize transgenics, lower T6P contents but increased sucrose levels were observed in ear spikelets and developing ears, indicating the function of MADS in the improved sink of reproductive tissues (*Nuccio et al., 2015*). Interestingly, the T6P-C/S1 bZIP-SnRK1 regulatory module has been revealed in *Arabidopsis* (*Ma et al., 2011*; *ÓHara, Paul & Wingler, 2013*; *Lunn et al., 2014*). Interestingly, Tre6P not only plays roles in the sucrose-Tre6P sensor nexus (*Martins et al., 2013*) but also involves the coordination of carbon and nitrogen balance (*Figueroa et al., 2016*). Using $^{14}CO_2$ and $^{13}CO_2$ labelling, the increased Tre6P has been revealed to decrease the sucrose content, but increase the levels of amino acids (*Figueroa et al., 2016*).

The mutation of *OsFLO6*, an ortholog of Arabidopsis PROTEIN TARGETING TO STARCH 2 (PTST2), affects the endosperm starch synthesis and alters starch properties of, which is associated with defects in granule initiation (*Peng et al., 2014*; *Seung et al., 2017*).

Table 1 Strategies for grain improvement through starch biosynthesis.

Pathway	Strategy	Effectiveness
ATP supply	Down-regulated ANK	Increased ADPG, UDPG and starch contents
Sucrose synthesis	Over-expressed SUT1	Increased starch content
Sucrose → UDPG	Enhanced SuSy activity	Increased ADPG, UDPG and starch contents
UDPG → ADPG	Mutated Brittle1	Increased lipid content, but decreased protein and amylopectin contents
	Enhanced AGP activity	Increased starch content
	Over-expressed AGPase	Increased starch content
ADPG → Starch	Over-expressed GBSSI/Wx	Increased GC and AC
	Over-expressed SBE/ISA3	Increased GC and GT
	Over-expressed SSII	Increased GC, GT and GT
	Over-expressed SSIV	Change starch structure
	Down-regulated AMY	Increased amylopectin contents
	Over-expressed PPDK	Increased starch content, but decreased protein content
	Down-regulated Pho	Increased starch content

However, mechanism underlying starch granule initiation in rice grains maybe different from *Arabidopsis* leaves (*Peng et al., 2014*). Rice FLO6 may interact with ISA1 based on protein interaction assays (*Peng et al., 2014*), while no evidence indicates *in vivo* interaction of PTST2 with ISA1 in *Arabidopsis* by using both *isa1* and *ptst2* mutants (*Seung et al., 2017*; *Delatte et al., 2005*). Unlike as an ISA1/ISA2 complex in Arabidopsis, ISA1 primarily exists as a homodimer in rice (*Streb & Zeeman, 2012*). Aside from possessing starchless amyloplasts, the ISA1-deficient mutants in rice also failed to initiate starch granule, interestingly, the both traits were presented in *flo6*, but the phenomenon of accumulate phytoglycogen as shown *isa1* was not detected in *flo6* (*Kawagoe et al., 2005*; *Peng et al., 2014*). Therefore, granule initiation in cereals endosperm requires the conserved PTST2/FLO6 complex as that in leaves (*Peng et al., 2014*; *Seung et al., 2017*), but its underlying mechanisms still requires more studies, especially for different plant tissues.

Strategies for grain improvement through starch biosynthesis

Compared with conventional breeding, genetic engineering seems to be more cost-effective and efficient to improve the screening of grain quality. Biosynthesis of storage starch requires the transport of carbon precursors and ATP from leaf organs to storage organs such as developing seeds through a long-distance transport of phloem. Further transformation of sucrose starch into amyloplasts through a series of enzymatic activity reactions and the transport of carbon precursors (*e.g.*, ADPG, G6P), which are finally stored in the endosperm of seeds. Therefore, the modified synthesis of endosperm starch can be achieved at least by the following pathways (Table 1), including (i) accelerating sucrose transport through leaf-phloem-seed; (ii) promoting the conversion of sucrose to UDPG in endosperm cells; (iii) promoting UDPG to enter amyloplasts in endosperm cells. Some starch-mediated strategies are summarized here for further applications of quality improvement in crop breeding.

Promoted conversion from sucrose to starch

Although more enhanced transportation would benefit starch biosynthesis, overexpressed SUTs, one of the major sucrose transporters, could not significantly increase the starch content (Table 1). Nonetheless, it is feasible to promote the conversion to starch from sucrose that has entered the storage organs. Promoted conversion of sucrose to starch could effectively increase the starch content through the enhanced activity of SuSy. Overexpressed SuSy would significantly increase the contents of UDPG, ADPG, and starch (*Bowsher et al., 2007*; *Li et al., 2013*; *Patron et al., 2004*), and lead to higher AGP activity and higher amylopectin/amylose ratio (*Asano et al., 2002*; *Cho et al., 2011*). Therefore, it is feasible to increase the starch content by expressing SuSy into plastids to produce more ADPG. One possible explanation is that the SuSy–AGP–ADPG transporter-mediated starch synthesis and amylopectin or SP-regulated degradation reached a balance (*Kazuaki, Kanako & Kazufumi, 2010*; *Li et al., 2013*; *Lee et al., 2016*; *Davies et al., 2003*). Besides, SuSy competed with acid invertase to substrate sucrose and reached a balance to regulate the starch content (*Baroja-Fernández et al., 2009*; *Murayama & Handa, 2007*; *Jia et al., 2008*). This is supposed to be another reasonable mechanism. Therefore, the promoted conversion to starch from sucrose in the storage organs is feasible and seems to be subjected to the concentration balance of sucrose and starch (Table 1).

Increased supply of ATP

The supply of ATP is essential for storage starch biosynthesis; thus, the storage starch could be enhanced through the increased supply of ATP. For example, downregulated expression of plastidial adenylate kinase, an enzyme that catalyzes ATP to ADP and AMP, would increase the supply of ATP in amyloid and double starch content (Table 1). This may be related to the weakened competition between adenylate kinase and AGP to increase the ATP pool (*Fernandez et al., 2017*).

Promoted ADPG transport

As shown above, the downregulation of genes encoding plastidial adenylate kinase could increase the content of ADPG, which was one of the key precursors in starch synthesis. Besides increased synthesis, the enhanced transport of cytosolic ADPG to amyloid appeared to be another reasonable pathway to increase ADPG (Table 1). The enhanced expression of BT1 protein could promote the transport of cytosolic ADPG to amyloid, thereby increasing the endosperm's starch content (*Patron et al., 2004*; *Bowsher et al., 2007*; *Kirchberger et al., 2007*; *Li et al., 2017b*). However, the *bt1* mutant had abnormal growth and infertility, which was not only related to decreased ADPG transport activity and starch deficiency in the endosperm amyloid (*Kirchberger et al., 2007*) but may also be related to some processes in the mitochondria (*Bahaji et al., 2011*). Nonetheless, due to the white heart endosperm and the decreased amylose content, the *bt1* mutant can serve as one of the floury materials in special food fields.

Enhanced activity of AGPase

As an important rate-limiting enzyme, the enhanced activity of AGPase would greatly increase the starch content (Table 1). Two ways were proposed to apply this strategy in seed improvement (*Wang et al., 2013*; *Peng et al., 2014*). One was the heterologous expression of the *E. coli glgC* gene in plants to produce AGP isomerase, which could significantly enhance AGP activity in seeds (*Nagai et al., 2009*). In contrast, another was the heterologous expression of the AGP large subunit encoding *SH2* gene (*Pérez-Ruiz et al., 2006*) and the small subunit encoding *BT2* gene (*Pérez-Ruiz et al., 2006*) in rice, which could significantly enhance AGPase activity and increase starch content. Thus, ways to enhance the activity of AGPase in seeds mainly focused on the heterologous expression of AGP isomerase. Therefore, it appears to be infeasible in breeding applications at present, given the legal limitations.

Regulated activity of starch synthase

Undoubtedly, starch biosynthetic enzymes' regulation would greatly influence the biosynthesis of storage starch in seeds and mediate the grain quality, especially for eating and cooking qualities (ECQs). In rice, overexpressed GBSSI/Wx affected amylose content (AC) and gel consistency (GC) but had fewer effects on gelatinization temperature (GT) (*Hanashiro et al., 2008*). However, the overexpression of SSII affected AC, GC, and GT (*Tian et al., 2009*; *Lin et al., 2013*). Besides, the overexpression of ISA and SBE3 was prone to affect GC and GT (*Yun, Takayuki & Yasushi, 2011*). In addition to improving grain quality, the overexpression of some starch synthases would preferentially increase the starch content, *e.g.*, SSIV (*Guo et al., 2017*; *Gámez-Arjona et al., 2011*).

Besides, modifications of starch biosynthetic genes could be a feasible pathway to improve grain quality and yields (Table 1). Recently, the editing of *ISA1 via* CRISPR/CRISPR-associated endonuclease 9 (CRISPR/Cas9) system has affected GT and starch chain length distribution during endosperm development, which have potential implications for quality improvement in rice (*Chao et al., 2019*). Moreover, repression of SSI by RNA interference (RNAi) could greatly affect starch biosynthesis and amylopectin chain distribution in rice under high temperature (*Zhao et al., 2019*). The suppression of α-amylase genes could also improve seed quality in rice under high temperature (*Hakata et al., 2012*).

Prevented degradation of starch

A network balance between starch synthesis and degradation resulted in enrichment of starch in endosperm. Therefore, it is feasible to increase starch content *via* preventing starch degradation (*Bahaji et al., 2014*; *Fujita et al., 2009*; *Li et al., 2013*). Alpha-amylase (*Hakata et al., 2012*; *Seung et al., 2013*) and the starch phosphorylation-related enzyme GWD (*Ral et al., 2012*) performed important regulatory roles in the degradation of endosperm starch. Under high temperature, the downregulated expression of alpha-amylase encoding genes would increase starch content (*Hakata et al., 2012*). Although the downregulated expression of GWD also increased starch content, it did not display the matched traits of dry weight, tiller number, and effective branch number of rice

(*Ral et al., 2012*; *Koumoto et al., 2013*). Thus, it seems to be infeasible to produce varieties of high-quality through the single regulation of starch degradation enzymes, but indeed, it also provides a way to improve the contents of starch (Table 1).

Elevated contents of starch in leaves

Although leaf starch synthesis did not directly affect grain yield or quality as endosperm starch synthesis did, the biotechnological application could also be an effective way to improve crop starch content by altering or modifying related enzyme activities.
The overexpression of OsCRCT, a CO_2-Responsive CONSTANS, CONSTANS-like and Time of Chlorophyll a/b Binding Protein1 (CCT) Protein (CRCT), would significantly increase the starch content in the phloem of the leaf blade and leaf sheath during vegetative stages, which was supposed to be an alternative or potential approach to improve yields of food and biofuel (*Morita et al., 2015*). Recently, in maize, plants' tolerance to high temperature has been realized through the modification of 6-phosphogluconate dehydrogenase (PGD) and originally plastid-localized enzymes (*Ribeiro et al., 2020*). PGD3 showed thermal stability in amyloplasts by fusing the chloroplast peptide encoding *Waxy1* into the open coding reading frame of PGD1 and PGD2, thus significantly improving plants' heat resistance and yield in maize (*Ribeiro et al., 2020*). All these suggested the potential application of leaf starch biosynthetic genes to improve grain quality and yield (Table 1).

Breeding of high-amylose cereal varieties

Resistant starch (RS) is the sum of starch that could not digest and absorb by the small intestine (*Reddy, Suriya & Haripriya, 2013*), and its consumption can modulate postprandial metabolic responses (*MacNeil et al., 2013*). So, it possesses potential values for special populations, *i.e.*, diabetics. The formation of RS largely depends on *GBSSI/ W. expression*. SSIIIa regulates the formation of RS through the high expression of *Wx* gene, while its mutation would greatly suppress the *Wx* expression to produce resistant starch and amylose–lipid complexes (*Ryoo et al., 2007*; *Hanashiro et al., 2008*; *Li et al., 2014b*; *Zhou et al., 2016*). Other functioning enzymes in the formation of RS consist of pullulanase (*Long et al., 2018*) and amylase (*Hakata et al., 2012*). Recently, maize high-amylose lines with AC of more than 55% showed decreased expression of *BEIIb* and *SSIIIa* but the enhanced expression of ISA2, which was prone to extend amylopectin chains but restrain the length of short amylose chains (*Zhong et al., 2020*). Interestingly, we recently also found that the mutation of one plastid genes, *OsGUN4*, caused the high contents of amylose in rice (*Li et al., 2021*), which may be largely associated with the upregulated expression of *GBSSI*. Therefore, the formation of RS or high-amylose appears to be more relevant to the balance of *GBSSI* and other starch biosynthetic genes, *i.e.*, *SSIIIa*, *BEIIb*, and *PUL/ISA*.

CONCLUSION

Starch biosynthesis not only plays a critical role in the formation of grain yield and quality in cereal crops but also involves the coordination of different biological processes and various organs. These processes include sucrose synthesis and transport in source organs

(such as leaves), sucrose and energy delivery from source organs throughout the vascular system (phloem) to sink organs (endosperm), conversion from sucrose to ADPG in the endosperm, and formation of amylopectin- and amylose-starch in the endosperm. The target-oriented improvement on yield and grain quality in cereal crops would optimize the current demand for starch to meet the living standard and be beneficial to overcome the problems in the availability of arable land by using the known mechanisms of starch biosynthesis.

ADDITIONAL INFORMATION AND DECLARATIONS

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Ruiqing Li conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Wenyin Zheng performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Meng Jiang performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Huali Zhang conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The factors involved in starch biosynthesis are available in the Supplementary File.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.12678#supplemental-information.

REFERENCES

Ahmed Z, Tetlow IJ, Ahmed R, Morell MK, Emes MJ. 2015. Protein-protein interactions among enzymes of starch biosynthesis in high-amylose barley genotypes reveal differential roles of heteromeric enzyme complexes in the synthesis of A and B granules. *Plant Science* **233**:95–106 DOI 10.1016/j.plantsci.2014.12.016.

Albani D, Hammond-Kosack MC, Smith C, Conlan S, Colot V, Holdsworth M, Bevan MW. 1997. The wheat transcriptional activator SPA: a seed-specific bZIP protein that recognizes the GCN4-like motif in the bifactorial endosperm box of prolamin genes. *Plant Cell* **9**:171–184 DOI 10.1105/tpc.9.2.171.

Annunziata MG, Apelt F, Carillo P, Krause U, Feil R, Mengin V, Lauxmann MA, Köhl K, Nikoloski Z, Stitt M, Lunn JE. 2017. Getting back to nature: a reality checks for experiments in controlled environments. *Journal of Experimental Botany* **68(16)**:4463–4477 DOI 10.1093/jxb/erx220.

Aoki N, Hirose T, Scofield GN, Whitfeld PR, Furbank RT. 2003. The sucrose transporter gene family in rice. *Plant and Cell Physiology* **44**:223–232 DOI 10.1093/pcp/pcg030.

Aoki N, Scofield GN, Wang XD, Patrick JW, Offler CE, Furbank RT. 2004. Expression and localisation analysis of the wheat sucrose transporter TaSUT1 in vegetative tissues. *Planta* **219**:176–184 DOI 10.1007/s00425-004-1232-7.

Asano T, Kunieda N, Omura Y, Ibe H, Kawasaki T, Takano M, Sato M, Furuhashi H, Mujin T, Takaiwa F, Wu C, Tada Y, Satozawa T, Sakamoto M, Shimada H. 2002. Rice SPK, a calmodulin-like domain protein kinase, is required for storage product accumulation during seed development: phosphorylation of sucrose synthase is a possible factor. *Plant Cell* **14(3)**:619–628 DOI 10.1105/tpc.010454.

Baerenfaller K, Massonnet C, Walsh S, Baginsky S, Bühlmann P, Hennig L, Hirsch-Hoffmann M, Howell KA, Kahlau S, Radziejwoski A, Russenberger D, Rutishauser D, Small I, Stekhoven D, Sulpice R, Svozil J, Wuyts N, Stitt M, Hilson P, Granier C, Gruissem W. 2012. Systems-based analysis of Arabidopsis leaf growth reveals adaptation to water deficit. *Molecular Systems Biology* **8**:606 DOI 10.1038/msb.2012.39.

Bahaji A, Li J, Sánchez-López ÁM, Baroja-Fernández E, Muñoz FJ, Ovecka M, Almagro G, Montero M, Ezquer I, Etxeberria E, Pozueta-Romero J. 2014. Starch biosynthesis, its regulation and biotechnological approaches to improve crop yields. *Biotechnology Advances* **32**:87–106 DOI 10.1016/j.biotechadv.2013.06.006.

Bahaji A, Muñoz FJ, Ovecka M, Baroja-Fernández E, Montero M, Li J, Hidalgo M, Almagro G, Sesma MT, Ezquer I, Pozueta-Romero J. 2011. Specific delivery of AtBT1 to mitochondria complements the aberrant growth and sterility phenotype of homozygous AtBT1 Arabidopsis mutants. *Plant Journal* **68(6)**:1115–1121 DOI 10.1111/j.1365-313X.2011.04767.x.

Baker RF, Leach KA, Boyer NR, Swyers MJ, Benitez-Alfonso Y, Skopelitis T. 2016. Sucrose transporter zmsut1 expression and localization uncover new insights into sucrose phloem loading. *Plant Physiology* **172**:1876–1898 DOI 10.1104/pp.16.00884.

Baroja-Fernández E, Montero M, Muñoz FJ, Montero M, Etxeberria E, Sesma MT, Ovecka M, Bahaji A, Ezquer I, Li J, Prat S, Pozueta-Romero J. 2009. Enhancing sucrose synthase activity in transgenic potato (*Solanum tuberosum* L.) tubers results in increased levels of starch, ADPglucose and UDPglucose and total yield. *Plant Cell Physiol* **50(9)**:1651–1662 DOI 10.1093/pcp/pcp108.

Bihmidine S, Julius BT, Dweikat I, Braun DM. 2016. *Tonoplast Sugar Transporters (SbTSTs)* putatively control sucrose accumulation in sweet sorghum stems. *Plant Signaling & Behavior* **11**:e1117721 DOI 10.1080/15592324.2015.1117721.

Blauth SL, Kim KN, Klucinec J, Shannon JC, Thompson D, Guiltinan M. 2002. Identification of mutator insertional mutants of starch-branching enzyme 1 (SBE1) in *Zea mays* L. *Plant Molecular Biology* **48**:287–297 DOI 10.1023/a:1013335217744.

Bledsoe SW, Henry C, Griffiths CA, Paul MJ, Feil R, Lunn JE, Stitt M, Lagrimini LM. 2017. The role of tre6p and snrk1 in maize early kernel development and events leading to stress-induced kernel abortion. *BMC Plant Biology* **17(1)**:74 DOI 10.1186/s12870-017-1018-2.

Borrill P, Fahy B, Smith AM, Uauy C. 2015. Wheat grain filling is limited by grain filling capacity rather than the duration of flag leaf photosynthesis: a case study using NAM RNAi plants. *PLOS ONE* **10**:e0134947 DOI 10.1371/journal.pone.0134947.

Bowsher CG, Scrase-Field E, Esposito S, Emes MJ, Tetlow IJ. 2007. Characterization of ADP-glucose transport across the cereal endosperm amyloplast envelope. *Journal of Experimental Botany* **58**:1321–1332 DOI 10.1093/jxb/erl297.

Cai H, Chen Y, Zhang M, Cai R, Cheng B, Ma Q, Zhao Y. 2017. A novel GRAS transcription factor, ZmGRAS20, regulates starch biosynthesis in rice endosperm. *Physiology and Molecular Biology of Plants* **23**:1–12 DOI 10.1007/s12298-016-0404-9.

Cao H, Yan X, Chen GX, Zhou JW, Li XH, Ma WJ, Yan Y. 2015. Comparative proteome analysis of A- and B-type starch granule associated proteins in bread wheat (*Triticum aestivum* L.) and *Aegilops crassa*. *Journal of Proteomics* **112**:95–112 DOI 10.1016/j.jprot.2014.08.002.

Chao SF, Cai YC, Feng BB, Jiao GA, Sheng ZH, Luo J, Tang SQ, Wang JL, Hu PS, Wei XJ. 2019. Editing of rice isoamylase gene isa1 provides insights into its function in starch formation. *Rice Science* **26(2)**:77–87 DOI 10.1016/j.rsci.2018.07.001.

Chen J, Yi Q, Cao Y, Wei B, Zheng L, Xiao Q, Xie Y, Gu Y, Li Y, Huang H, Wang Y, Hou X, Long T, Zhang J, Liu H, Liu Y, Yu G, Huang Y. 2016. ZmbZIP91 regulates expression of starch synthesis-related genes by binding to actcat elements in their promoters. *Journal of Experimental Botany* **67**:1327–1338 DOI 10.1093/jxb/erv527.

Chen J, Zhang J, Liu H, Hu Y, Huang Y. 2012. RETRACTED: molecular strategies in manipulation of the starch synthesis pathway for improving storage starch content in plants (review and prospect for increasing storage starch synthesis). *Plant Physiology and Biochemistry* **61(6)**:1–8 DOI 10.1016/j.plaphy.2012.08.013.

Cho YH, Hong JW, Kim EC, Yoo SD. 2012. Regulatory functions of SnRK1 in stress-responsive gene expression and in plant growth and development. *Plant Physiology* **158(4)**:1955–1964 DOI 10.1104/pp.111.189829.

Cho JI, Kim HB, Kim CY, Hahn TR, Jeon JS. 2011. Identification and characterization of the duplicate rice sucrose synthase genes *Ossus5* and *Ossus7* which are associated with the plasma membrane. *Molecules and Cells* **31**:553–561 DOI 10.1007/s10059-011-1038-y.

Crofts N, Nakamura Y, Fujita N. 2017. Critical and speculative review of the roles of multi-protein complexes in starch biosynthesis in cereals. *Plant Science* **262**:1–8 DOI 10.1016/j.plantsci.2017.05.007.

Crumpton-Taylor M, Pike M, Lu KJ, Hylton CM, Feil R, Eicke S, Lunn J, Zeeman SC, Smith AM. 2013. Starch synthase 4 is essential for coordination of starch granule formation with chloroplast division during Arabidopsis leaf expansion. *New Phytologist* **200(4)**:1064–1075 DOI 10.1111/nph.12455.

Cuesta-Seijo JA, Nielsen MM, Ruzanski C, Krucewicz K, Beeren SR, Rydhal MG, Yoshimura Y, Striebeck A, Motawia MS, Willats WGT, Palcic MM. 2016. In vitro biochemical characterization of all barley endosperm starch synthases. *Frontiers in Plant Science* **6**:1265 DOI 10.3389/fpls.2015.01265.

Davies EJ, Tetlow IJ, Bowsher CG, Emes MJ. 2003. Molecular and biochemical characterization of cytosolic phosphoglucomutase in wheat endosperm (*Triticum aestivum* L. cv. Axona). *Journal of Experimental Botany* **54**:1351–1360 DOI 10.1093/jxb/erg151.

Delatte T, Trevisan M, Parker ML, Zeeman SC. 2005. Arabidopsis mutants Atisa1 and Atisa2 have identical phenotypes and lack the same multimeric isoamylase, which influences the branch point distribution of amylopectin during starch synthesis. *Plant Journal* **41**:815–830 DOI 10.1111/j.1365-313X.2005.02348.x.

Delvallé D, Dumez S, Wattebled F, Roldán I, Planchot V, Berbezy P, Colonna P, Vyas D, Chatterjee M, Ball S, Mérida A, D'Hulst C. 2005. Soluble starch synthase I: a major determinant for the synthesis of amylopectin in Arabidopsis thaliana leaves. *Plant Journal* **43**:398–412 DOI 10.1111/j.1365-313X.2005.02462.x.

Dian W, Jiang H, Wu P. 2005. Evolution and expression analysis of starch synthase III and IV in rice. *Journal of Experimental Botany* **56**:623–632 DOI 10.1093/jxb/eri065.

Diaz I, Vicente-Carbajosa J, Abraham Z, Martínez M, Isabel-La Moneda I, Carbonero P. 2002. The GAMYB protein from barley interacts with the DOF transcription factor BPBF and activates endosperm-specific genes during seed development. *Plant Journal* **29**:453–464 DOI 10.1046/j.0960-7412.2001.01230.x.

Dinges JR, Colleoni C, James MG, Myers AM. 2003. Mutational analysis of the pullulanase-type debranching enzyme of maize indicates multiple functions in starch metabolism. *Plant Cell* **15**:666–680 DOI 10.1105/tpc.007575.

Enami K, Ozawa T, Motohashi N, Nakamura M, Tanaka K, Hanaoka M. 2011. Plastid-to-nucleus retrograde signals are essential for the expression of nuclear starch biosynthesis genes during amyloplast differentiation in tobacco BY-2 cultured cells. *Plant Physiology* **157**:518–530 DOI 10.1104/pp.111.178897.

Fahy B, Siddiqui H, David LC, Powers SJ, Borrill P, Uauy C, Smith AM. 2018. Final grain weight in wheat is not strongly influenced by sugar levels or activities of key starch synthesising enzymes during grain filling. *Journal of Experimental Botany* **70**:5461–5475 DOI 10.1093/jxb/ery314.

Feike D, Seung D, Graf A, Bischof S, Ellick T, Coiro M, Soyk S, Eicke S, Mettler-Altmann T, Lu KJ, Trick M, Zeeman SC, Smith AM. 2016. The starch granule-associated protein early starvation1 is required for the control of starch degradation in *Arabidopsis thaliana* leaves. *Plant Cell* **28**:1472–1489 DOI 10.1105/tpc.16.00011.

Fernandez O, Ishihara H, George GM, Mengin V, Flis A, Sumner D. 2017. Foliar starch turnover occurs in long days and in falling light at the end of the day. *Plant Physiology* **174**:2199–2212 DOI 10.1104/pp.17.00601.

Ferreira SJ, Senning M, Fischerstettler M, Streb S, Ast M, Neuhaus HE, Zeeman SC, Sonnewald S, Sonnewald U. 2017. Simultaneous silencing of isoamylases ISA1, ISA2 and ISA3 by multi-target RNAi in potato tubers leads to decreased starch content and an early sprouting phenotype. *PLOS ONE* **12(7)**:e0181444 DOI 10.1371/journal.pone.0181444.

Ferrero A, Nguyen N. 2004. Constraints and opportunities for the sustainable development of rice-based production systems in Europe. In: *FAO Rice Conference*, Vol. 43. 12–13.

Figueroa CM, Feil R, Ishihara H, Watanabe M, Kölling K, Krause U. 2016. Trehalose 6-phosphate coordinates organic and amino acid metabolism with carbon availability. *Plant Journal* **85(3)**:410–423 DOI 10.1111/tpj.13114.

Fu FF, Xue HW. 2010. Co-expression analysis identifies Rice Starch Regulator1, a rice AP2/EREBP family transcription factor, as a novel rice starch biosynthesis regulator. *Plant Physiology* **154**:927–938 DOI 10.1104/pp.110.159517.

Fujita N, Satoh R, Hayashi A, Kodama M, Itoh R, Aihara S, Nakamura Y. 2011. Starch biosynthesis in rice endosperm requires the presence of either starch synthase I or IIIa. *Journal of Experimental Botany* **62(14)**:4819–4831 DOI 10.1093/jxb/err125.

Fujita N, Toyosawa Y, Utsumi Y, Higuchi T, Hanashiro I, Ikegami A, Akuzawa S, Yoshida M, Mori A, Inomata K, Itoh R, Miyao Akio, Hirochika H, Satoh H, Nakamura Y. 2009. Characterization of pullulanase (PUL)-deficient mutants of rice (*Oryza sativa* L.) and the function of PUL on starch biosynthesis in the developing rice endosperm. *Journal of Experimental Botany* **60**:1009–1023 DOI 10.1093/jxb/ern349.

Fujita N, Yoshida M, Asakura N, Ohdan T, Miyao A, Hirochika H, Nakamura Y. 2006. Function and characterization of starch synthase I using mutants in rice. *Plant Physiology* **140(3)**:1070–1084 DOI 10.1104/pp.105.071845.

Fujita N, Yoshida M, Kondo T, Saito K, Utsumi Y, Tokunaga T, Nishi A, Satoh H, Park JH, Jane JL, Miyao A, Hirochika H, Nakamura Y. 2007. Characterization of SSIIIa-deficient mutants of rice: the function of SSIIIa and pleiotropic effects by SSIIIa deficiency in the rice endosperm. *Plant Physiology* **144(4)**:2009–2023 DOI 10.1104/pp.107.102533.

Fulton DC, Stettler M, Mettler T, Vaughan CK, Li J, Francisco P, Gil M, Reinhold H, Eicke S, Messerli G. 2008. a noncatalytic protein required for starch breakdown, acts upstream of three active β-amylases in Arabidopsis chloroplasts. *Plant Cell* **20(4)**:1040–1058 DOI 10.1105/tpc.107.056507.

Gao Y, An K, Guo W, Chen Y, Zhang R, Zhang X, Chang S, Rossi V, Jin F, Cao X, Xin M, Peng H, Hu Z, Guo W, Du J, Ni Z, Sun Q, Yao Y. 2021. The endosperm-specific transcription factor TaNAC019 regulates glutenin and starch accumulation and its elite allele improves wheat gain quality. *Plant Cell* **33(3)**:603–622 DOI 10.1093/plcell/koaa040.

Geigenberger P. 2011. Regulation of starch biosynthesis in response to a fluctuating environment. *Plant Physiology* **155(4)**:1566–1577 DOI 10.1104/pp.110.170399.

Geiger D. 2011. Plant sucrose transporters from a biophysical point of view. *Molecular Plant* **4(3)**:395–406 DOI 10.1093/mp/ssr029.

Gould N, Thorpe MR, Pritchard J, Christeller JT, Williams LE, Roeb G, Schurr U, Minchin PEH. 2012. AtSUC2 has a role for sucrose retrieval along the phloem pathway: evidence from carbon-11 tracer studies. *Plant Science* **188**:97–101 DOI 10.1016/j.plantsci.2011.12.018.

Graf A, Smith AM. 2011. Starch and the clock: the dark side of plant productivity. *Trends in Plant Science* **16(3)**:169–175 DOI 10.1016/j.tplants.2010.12.003.

Grimaud F, Rogniaux H, James MG, Myers AM, Planchot V. 2008. Proteome and phosphoproteome analysis of starch granule-associated proteins from normal maize and mutants affected in starch biosynthesis. *Journal of Experimental Botany* **59**:3395–3406 DOI 10.1093/jxb/ern198.

Guo H, Liu Y, Li X, Yan Z, Xie Y, Xiong H, Zhao L, Gu J, Zhao S, Liu L. 2017. Novel mutant alleles of the starch synthesis gene *TaSSIVb-D* result in the reduction of starch granule number per chloroplast in wheat. *BMC Genomics* **18(1)**:358 DOI 10.1186/s12864-017-3724-4.

Guo X, Ronhovde K, Yuan L, Yao B, Soundararajan MP, Elthon T, Zhang C, Holding DR. 2012. Pyrophosphate-dependent fructose-6-phosphate 1-phosphotransferase induction and attenuation of hsp gene expression during endosperm modification in quality protein maize. *Plant Physiology* **158(2)**:917–929 DOI 10.1104/pp.111.191163.

Gámez-Arjona FM, Li J, Raynaud S, Baroja-Fernández E, Muñoz FJ, Ovecka M, Ragel P, Bahaji A, Pozueta-Romero J, Mérida Á. 2011. Enhancing the expression of starch synthase class IV results in increased levels of both transitory and long-term storage starch. *Plant Biotechnology Journal* **9(9)**:1049–1060 DOI 10.1111/j.1467-7652.2011.00626.x.

Hakata M, Kuroda M, Miyashita T, Yamaguchi T, Kojima M, Sakakibara H, Mitsui T, Yamakawa H. 2012. Suppression of α-amylase genes improves quality of rice grain ripened under high temperature. *Plant Biotechnology Journal* **10(9)**:1110–1117 DOI 10.1111/j.1467-7652.2012.00741.x.

Hanashiro I, Itoh K, Kuratomi Y, Yamazaki M, Igarashi T, Matsugasako J, Takeda Y. 2008. Granule-bound starch synthase I is responsible for biosynthesis of extra-long unit chains of amylopectin in rice. *Plant and Cell Physiology* **49**:925–933 DOI 10.1093/pcp/pcn066.

Haupt S, Duncan GH, Holzberg S, Oparka KJ. 2001. Evidence for symplastic phloem unloading in sink leaves of barley. *Plant Physiology* **125**:209–218 DOI 10.1104/pp.125.1.209.

Hirose T, Terao T. 2004. A comprehensive expression analysis of the starch synthase gene family in rice (*Oryza sativa* L.). *Planta* **220**:9–16 DOI 10.1007/s00425-004-1314-6.

Horrer D, Flütsch S, Pazmino D, Matthews JSA, Thalmann M, Nigro A, Leonhardt N, Lawson T, Santelia D. 2016. Blue light induces a distinct starch degradation pathway in guard cells for stomatal opening. *Current Biology* **26**:362–370 DOI 10.1016/j.cub.2015.12.036.

Huang H, Xie S, Xiao Q, Wei B, Zheng L, Wang Y, Cao Y, Zhang X, Long T, Li Y, Hu G, Liu H, Liu Y, Huang Z, Zhang J, Huang Y. 2016. Sucrose and ABA regulate starch biosynthesis in maize through a novel transcription factor, *ZmEREB156*. *Scientific Reports* **6**:27590 DOI 10.1038/srep27590.

Ishimaru K, Hirose T, Aoki N, Takahashi S, Ono K, Yamamoto S, Wu J, Saji S, Baba T, Ugaki M, Matsumoto T, Ohsugi R. 2001. Antisense expression of a rice sucrose transporter OsSUT1 in rice (*Oryza sativa* L.). *Plant and Cell Physiology* **42**:1181–1185 DOI 10.1093/pcp/pce148.

Jia L, Zhang B, Mao C, Li J, Wu Y, Wu P, Wu Z. 2008. Oscyt-inv1 for alkaline/neutral invertase is involved in root cell development and reproductivity in rice (*Oryza sativa* L.). *Planta* **228(1)**:51–59 DOI 10.1007/s00425-008-0718-0.

Kang G, Li S, Zhang M, Peng H, Wang C, Zhu Y, Guo T. 2013. Molecular cloning and expression analysis of the starch-branching enzyme III gene from common wheat (*Triticum aestivum*). *Biochemical Genetics* **51**:377–386 DOI 10.1007/s10528-013-9570-4.

Kawagoe Y, Kubo A, Satoh H, Takaiwa F, Nakamura Y. 2005. Roles of isoamylase and ADP-glucose pyrophosphorylase in starch granule synthesis in rice endosperm. *Plant Journal* **42**:164–174 DOI 10.1111/j.1365-313X.2005.02367.x.

Kawakatsu T, Yamamoto MP, Touno SM, Yasuda H, Takaiwa F. 2009. Compensation and interaction between RISBZ1 and RPBF during grain filling in rice. *Plant Journal* **59**:908–920 DOI 10.1111/j.1365-313X.2009.03925.x.

Kazuaki O, Kanako S, Kazufumi Y. 2010. Two solanesyl diphosphate synthases with different subcellular localizations and their respective physiological roles in Oryza sativa. *Journal of Experimental Botany* **61(10)**:2683–2692 DOI 10.1093/jxb/erq103.

Kirchberger S, Leroch M, Huynen MA, Wahl M, Neuhaus HE, Tjaden J. 2007. Molecular and biochemical analysis of the plastidic ADP-glucose transporter (ZmBT1) from *Zea mays*. *Journal of Biological Chemistry* **282**:22481–22491 DOI 10.1074/jbc.M702484200.

Kosar-Hashemi B, Li Z, Larroque O, Regina A, Yamamori M, Morell MK, Rahman S. 2007. Multiple effects of the starch synthase II mutation in developing wheat endosperm. *Functional Plant Biology* **34(5)**:431–438 DOI 10.1071/FP06288.

Koumoto T, Shimada H, Kusano H, She KC, Iwamoto M, Takano M. 2013. Rice monoculm mutation *moc2*, which inhibits outgrowth of the second tillers, is ascribed to lack of a fructose-1,6-bisphosphatase. *Plant Biotechnology* **30(1)**:47–56 DOI 10.5511/plantbiotechnology.12.1210a.

Kretzschmar T, Pelayo MA, Trijatmiko KR, Gabunada LF, Alam R, Jimenez R. 2015. A trehalose-6-phosphate phosphatase enhances anaerobic germination tolerance in rice. *Nature Plants* **1**:15124–15128 DOI 10.1038/NPLANTS.2015.124.

Kühn C, Grof CP. 2010. Sucrose transporters of higher plants. *Current Opinion in Plant Biology* **13**:288–298 DOI 10.1016/j.pbi.2010.02.001.

Langlois C, Shulman S, Arbesman CE. 2015. From leaf to kernel: trehalose-6-phosphate signaling moves carbon in the field. *Plant Physiology* **169**:912–913 DOI 10.1104/pp.15.01177.

Lau WCP, Rafii MY, Ismail MR, Puteh A, Latif MA, Ramli A. 2015. Review of functional markers for improving cooking, eating, and the nutritional qualities of rice. *Frontiers in Plant Science* **6(832)**:1–11 DOI 10.3389/fpls.2015.00832.

Lawlor DW, Paul MJ. 2014. Source/sink interactions underpin crop yield: the case for trehalose 6-phosphate/snrk1 in improvement of wheat. *Frontiers in Plant Science* **5**:418 DOI 10.3389/fpls.2014.00418.

Lee SK, Eom JS, Hwang SK, Shin D, An G, Okita TW, Jeon JS. 2016. Plastidic phosphoglucomutase and ADP-glucose pyrophosphorylase mutants impair starch synthesis in rice pollen grains and cause male sterility. *Journal of Experimental Botany* **67**:5557–5569 DOI 10.1093/jxb/erw324.

Lee SK, Hwang SK, Han M, Eom JS, Kang HG, Han Y, Choi SB, Cho MH, Bhoo SH, An G, Hahn TR, Okita TW, Jeon JS. 2007. Identification of the ADPglucose pyrophosphorylase isoforms essential for starch synthesis in the leaf and seed endosperm of rice (*Oryza sativa* L.). *Plant Molecular Biology* **65**:531–546 DOI 10.1007/s11103-007-9153-z.

Li K, Bao J, Corke H, Sun M. 2017b. Association analysis of markers derived from starch biosynthesis related genes with starch physicochemical properties in the USDA rice mini-core collection. *Frontiers in Plant Science* **8**:1–17 DOI 10.3389/fpls.2017.00424.

Li J, Baroja-Fernández E, Bahaji A, Muñoz FJ, Ovecka M, Montero M, Sesma MT, Alonso-Casajús N, Almagro G, Sánchez-López AM, Hidalgo M, Zamarbide M, Pozueta-Romero J. 2013. Enhancing sucrose synthase activity results in increased levels of starch and ADP-glucose in maize (*Zea mays* L.) seed endosperms. *Plant and Cell Physiology* **54(2)**:282–294 DOI 10.1093/pcp/pcs180.

Li Y, Fan C, Xing Y, Yun P, Luo L, Yan B, Peng B, Xie W, Wang G, Li X, Xiao J, Xu C, He Y. 2014b. *Chalk5* encodes a vacuolar H+-translocating pyrophosphatase influencing grain chalkiness in rice. *Nature Genetics* **46**:398–404 DOI 10.1038/ng.2923.

Li C, Gilbert RG. 2016. Progress in controlling starch structure by modifying starch-branching enzymes. *Planta* **243**:13–22 DOI 10.1007/s00425-015-2421-2.

Li R, Jiang M, Zheng W, Zhang H. 2021. GUN4-mediated tetrapyrrole metabolites regulates starch biosynthesis during early seed development in rice. *Journal of Cereal Science* **101**:103317 DOI 10.1016/j.jcs.2021.103317.

Li L, Nelson CJ, Trösch J, Castleden I, Huang S, Millar AH. 2017a. Protein degradation rate in Arabidopsis thaliana leaf growth and development. *Plant Cell* **29**:207–228 DOI 10.1105/tpc.16.00768.

Li G, Wang D, Yang R, Logan K, Chen H, Zhang S, Skaggs MI, Lloyd A, Burnett WJ, Laurie JD, Hunter BG, Dannenhoffer JM, Larkins BA, Drews GN, Wang X, Yadegaria R. 2014a. Temporal patterns of gene expression in developing maize endosperm identified through transcriptome sequencing. *Proceedings of the National Academy of Sciences of the United States of America* **111**:7582–7587 DOI 10.1073/pnas.1406383111.

Lin Q, Facon M, Putaux JL, Dinges JR, Myers AM. 2013. Function of isoamylase-type starch debranching enzymes isa1 and isa2 in the *Zea mays* leaf. *New Phytologist* **200**:1009–1021 DOI 10.1111/nph.12446.

Liu F, Makhmoudova A, Lee EA, Wait R, Emes MJ, Tetlow IJ. 2014. The amylose extender mutant of maize conditions novel protein-protein interactions between starch biosynthetic enzymes in amyloplasts. *Journal of Experimental Botany* **83**:4423–4440 DOI 10.1093/jxb/erp297.

Liu F, Romanova N, Lee EA, Ahmed R, Evans M, Gilbert EP, Morell MK, Emes MJ, Tetlow IJ. 2012a. Glucan affinity of starch synthase IIa determines binding of starch synthase I and starch-branching enzyme IIb to starch granules. *Biochemical Journal* **448**:373–387 DOI 10.1042/BJ20120573.

Liu F, Zaheer A, Lee EA, Elizabeth D, Liu Q, Regina A. 2012. Allelic variants of the amylose extender mutation of maize demonstrate phenotypic variation in starch structure resulting from modified protein-protein interactions. *Journal of Experimental Botany* **63**:1167–1183 DOI 10.1093/jxb/err341.

Long W, Dong B, Wang Y, Pan P, Wang Y, Liu L, Chen X, Liu X, Tian Y, Chen L, Wan J. 2017. Floury endosperm8, encoding the UDP-glucose pyrophosphorylase 1, affects the synthesis and structure of starch in rice endosperm. *Journal of Plant Biology* **60**:513–522 DOI 10.1007/s12374-017-0066-3.

Long J, Zhang B, Li X, Zhan X, Xu X, Xie Z. 2018. Effective production of resistant starch using pullulanase immobilized onto magnetic chitosan/Fe_3O_4 nanoparticles. *Food Chemistry* **239**:276–286 DOI 10.1016/j.foodchem.2017.06.117.

Lu KJ, Pfister B, Jenny C, Eicke S, Zeeman SC. 2018. Distinct functions of starch synthase 4 domains in starch granule formation. *Plant Physiology* **176**:566–581 DOI 10.1104/pp.17.01008.

Lunn JE, Delorge I, Figueroa CM, Van Dijck P, Stitt M. 2014. Trehalose metabolism in plants. *Plant Journal* **79(4)**:544–567 DOI 10.1111/tpj.12509.

López-González C, Juárez-Colunga S, Morales-Elías NC, Tiessen A. 2019. Exploring regulatory networks in plants: transcription factors of starch metabolism. *PeerJ* **7**:e6841 DOI 10.7717/peerj.6841.

Ma J, Hanssen M, Lundgren K, Hernández L, Delatte T, Ehlert A, Liu CM, Schluepmann H, Dröge-Laser W, Moritz T. 2011. The sucroseregulated Arabidopsis transcription factor bZIP11 reprograms metabolism and regulates trehalose metabolism. *New Phytologist* **191(3)**:733–745 DOI 10.1111/j.1469-8137.2011.03735.x.

MacNeil S, Rebry RM, Tetlow IJ, Emes MJ, McKeown B, Graham TE. 2013. Resistant starch intake at breakfast affects postprandial responses in type 2 diabetics and enhances the glucose-dependent insulinotropic polypeptide–insulin relationship following a second meal.

Applied Physiology, Nutrition, and Metabolism **38(12)**:1187–1195
DOI 10.1139/apnm-2013-0023.

Macneill GJ, Sahar M, Minow M, Patterson JA, Tetlow IJ, Emes MJ. 2017. Starch as a source, starch as a sink: the bifunctional role of starch in carbon allocation. *Journal of Experimental Botany* **16(16)**:4433–4453 DOI 10.1093/jxb/erx291.

Makhmoudova A, Williams D, Brewer D, Massey S, Patterson J, Silva A, Vassall KA, Liu F, Subedi S, Harauz G, Siu KWM, Tetlow IJ, Emes MJ. 2014. Identification of multiple phosphorylation sites on maize endosperm starch branching enzyme IIb, a key enzyme in amylopectin biosynthesis. *Journal of Biological Chemistry* **289(13)**:9233–9246 DOI 10.1074/jbc.M114.551093.

Malinova I, Alseekh S, Feil R, Fernie AR, Baumann O, Schöttler MA, Lunn JE, Fettke J. 2017. Starch synthase 4 and plastidal phosphorylase differentially affect starch granule number and morphology. *Plant Physiology* **174**:73–85 DOI 10.1104/pp.16.01859.

Mangelsen E, Wanke D, Kilian J, Sundberg E, Harter K, Jansson C. 2010. Significance of light, sugar, and amino acid supply for diurnal gene regulation in developing barley caryopses. *Plant Physiology* **153**:14–33 DOI 10.1104/pp.110.154856.

Martins MC, Hejazi M, Fettke J, Steup M, Feil R, Krause U, Arrivault S, Vosloh D, Figueroa CM, Ivakov A, Yadav UP, Piques M, Metzner D, Stitt M, Lunn JE. 2013. Feedback inhibition of starch degradation in Arabidopsis leaves mediated by trehalose 6-phosphate. *Plant Physiology* **163**:1142–1163 DOI 10.1104/pp.113.226787.

Martínez-Barajas E, Delatte T, Schluepmann H, de Jong GJ, Somsen GW, Nunes C. 2011. Wheat grain development is characterized by remarkable trehalose 6-phosphate accumulation pregrain filling: tissue distribution and relationship to SNF1-related protein kinase1 activity. *Plant Physiology* **156**:373–381 DOI 10.1104/pp.111.174524.

Matsushima R, Maekawa M, Kusano M, Kondo H, Fujita N, Kawagoe Y, Sakamoto W. 2014. Amyloplast-localized substandard starch grain4 protein influences the size of starch grains in rice endosperm. *Plant Physiology* **164**:623–636 DOI 10.1104/pp.113.229591.

Matsushima R, Maekawa M, Kusano M, Tomita K, Kondo H, Nishimura H, Crofts N, Fujita N, Sakamto W. 2016. Amyloplast membrane protein substandard starch grain6 controls starch grain size in rice endosperm. *Plant Physiology* **170**:1445–1459 DOI 10.1104/pp.15.01811.

Mechin V, Thevenot C, Guilloux ML, Prioul JL, Damerval C. 2007. Developmental analysis of maize endosperm proteome suggests a pivotal role for pyruvate orthophosphate dikinase. *Plant Physiology* **143**:1203–1219 DOI 10.1104/pp.106.092148.

Miura K, Agetsuma M, Kitano H, Yoshimura A, Matsuoka M, Jacobsen SE, Ashikari M. 2009. A metastable DWARF1 epigenetic mutant affecting plant stature in rice. *Proceedings of the National Academy of Sciences of the United States of America* **106(27)**:11218–11223 DOI 10.1073/pnas.0901942106.

Mizuno K, Kobayashi E, Tachibana M, Kawasaki T, Fujimura T, Funane K, Kobayashi M, Baba T. 2001. Characterization of an isoform of rice starch branching enzyme, SBE4, in developing seeds. *Plant and Cell Physiology* **42**:349–357 DOI 10.1093/pcp/pce042.

Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group. 2009. Preferred reporting items for systematic reviews and meta-analyses: the prisma statement. *PLOS Medicine* **6(7)**:e1000097 DOI 10.1371/journal.pmed1000097.

Morita R, Sugino M, Hatanaka T, Misoo S, Fukayama H. 2015. CO_2-responsive constans, constans-like, and time of chlorophyll a/b binding protein expression1 protein is a positive regulator of starch synthesis in vegetative organs of rice. *Plant Physiology* **167(4)**:1321–1331 DOI 10.1104/pp.15.00021.

Mu H, Ke JH, Liu W, Zhuang CX, Yip WK. 2009. UDP-glucose pyrophosphorylase2 (*Osugp2*), a pollen-preferential gene in rice, plays a critical role in starch accumulation during pollen maturation. *Chinese Science Bulletin* **54**:234–243 DOI 10.1007/s11434-008-0568-y.

Murayama S, Handa H. 2007. Genes for alkaline/neutral invertase in rice: alkaline/neutral invertases are located in plant mitochondria and also in plastids. *Planta* **225(5)**:1193–1203 DOI 10.1007/s00425-006-0430-x.

Myers AM, Morell MK, James MG, Ball SG. 2000. Recent progress toward understanding biosynthesis of the amylopectin crystal. *Plant Physiology* **122**:989–997 DOI 10.1104/pp.122.4.989.

Nagai YS, Sakulsingharoj C, Edwardsg E, Satoh H, Greene TW, Blakeslee B, Okita TW. 2009. Control of starch synthesis in cereals: metabolite analysis of transgenic rice expressing an up-regulated cytoplasmic ADP-glucose pyrophosphorylase in developing seeds. *Plant and Cell Physiology* **50(3)**:635–643 DOI 10.1093/pcp/pcp021.

Nelson CJ, Alexova R, Jacoby RP, Millar AH. 2014. Proteins with high turnover rate in barley leaves estimated by proteome analysis combined with in planta isotope labeling. *Plant Physiology* **166**:91–108 DOI 10.1104/pp.114.243014.

Nishi A, Nakamura Y, Tanaka N, Satoh H. 2001. Biochemical and genetic analysis of the effects of *amylose-extender* mutation in rice endosperm. *Plant Physiology* **127**:459–472 DOI 10.1104/PP.010127.

Nougué O, Corbi J, Ball SG, Manicacci D, Tenaillon MI. 2014. Molecular evolution accompanying functional divergence of duplicated genes along the plant starch biosynthesis pathway. *BMC Evolutionary Biology* **14**:103 DOI 10.1186/1471-2148-14-103.

Nuccio ML, Wu J, Mowers R, Zhou HP, Meghji M, Primavesi LF. 2015. Expression of trehalose-6-phosphate phosphatase in maize ears improves yield in well-watered and drought conditions. *Nature Biotechnol* **33**:862–869 DOI 10.1038/nbt.3277.

Nunes C, O'Hara LE, Primavesi LF, Delatte TL, Schluepmann H, Somsen GW. 2013. The Trehalose 6-Phosphate/SnRK1signaling pathway primes growth recovery following relief of sink limitation. *Plant Physiology* **162**:1720–1732 DOI 10.1104/pp.113.220657.

Nuttall JG, O'Leary GJ, Panozzo JF, Walker CK, Barlow KM, Fitzgerald GJ. 2017. Models of grain quality in wheat—A review. *Field Crops Research* **202**:136–145 DOI 10.1016/j.fcr.2015.12.011.

O'Hara LE, Paul MJ, Wingler A. 2013. How do sugars regulate plant growth and development? New insight into the role of trehalose-6-phosphate. *Molecular Plant* **6**:261–274 DOI 10.1093/mp/sss120.

Okpala NE, Duan L, Shen G, Zhang G, Qi X. 2017. Comparisons of cooking and eating qualities of two indica rice cultivars. *Journal of Rice Research* **5(2)**:1–5 DOI 10.4172/2375-4338.1000180.

Onodera Y, Suzuki A, Wu CY, Washida H, Takaiwa F. 2001. A rice functional transcriptional activator, RISBZ1, responsible for endosperm-specific expression of storage protein genes through GCN4 motif. *Journal of Biological Chemistry* **276**:14139–14152 DOI 10.1074/jbc.M007405200.

Ortiz-Marchena MI, Albi T, Lucas-Reina E, Said FE, Romero-Campero FJ. 2014. Photoperiodic control of carbon distribution during the floral transition in Arabidopsis. *Plant Cell* **26**:565–584 DOI 10.1105/tpc.114.122721.

Pan D, Strelow LI, Nelson OE. 1990. Many maize inbreds lack an endosperm cytosolic phosphoglucomutase. *Plant Physiology* **93**:1650–1653 DOI 10.1104/pp.93.4.1650.

Pang Y, Zhou X, Chen Y, Bao JS. 2018. Comparative phosphoproteomic analysis of the developing seeds in two indica rice (*Oryza sativa* L.) cultivars with different starch quality. *Journal of Agricultural and Food Chemistry* **66**:3030–3037 DOI 10.1021/acs.jafc.8b00074.

Patron NJ, Greber B, Fahy BF, Laurie DA, Parker ML, Denyer K. 2004. The lys5 mutations of barley reveal the nature and importance of plastidial ADP-glc transporters for starch synthesis in cereal endosperm. *Plant Physiology* **135**:2088–2097 DOI 10.1104/pp.104.045203.

Paul MJ, Jhurreea D, Zhang Y, Primavesi LF, Delatte T, Schluepmann H, Wingler A. 2010. Upregulation of biosynthetic processes associated with growth by trehalose 6-phosphate. *Plant Signaling & Behavior* **5**:386–392 DOI 10.4161/psb.5.4.10792.

Paul MJ, Primavesi LF, Jhurreea DJ, Zhang Y. 2008. Trehalose metabolism and signaling. *Annual Review of Plant Biology* **59**:417–441 DOI 10.1146/annurev.arplant.59.032607.092945.

Peng C, Wang Y, Liu F, Ren Y, Zhou K, Lv J, Zheng M, Zhao S, Zhang L, Wang C, Jiang L, Zhang X, Guo X, Bao Y, Wan J. 2014. *FLOURY ENDOSPERM6* encodes a CBM48 domain-containing protein involved in compound granule formation and starch synthesis in rice endosperm. *Plant Journal* **77**:917–930 DOI 10.1111/tpj.12444.

Pfister B, Lu KJ, Eicke S, Feil R, Lunn JE, Streb S, Zeeman SC. 2014. Genetic evidence that chain length and branch point distributions are linked determinants of starch granule formation in Arabidopsis. *Plant Physiology* **165(4)**:1457–1474 DOI 10.1104/pp.114.241455.

Pfister B, Sánchez-Ferrer A, Diaz A, Lu K, Otto C, Holler M, Shaik FR, Meier F, Mezzenga R, Zeeman SC. 2016. Recreating the synthesis of starch granules in yeast. *eLife* **5**:e15552 DOI 10.7554/eLife.15552.

Pfister B, Zeeman SC. 2016. Formation of starch in plant cells. *Cellular and Molecular Life Sciences* **73(14)**:2781–2807 DOI 10.1007/s00018-016-2250-x.

Pérez-Ruiz JM, Spínola MC, Kirchsteiger K, Moreno J, Sahrawy M, Cejudo FJ. 2006. Rice NTRC is a high-efficiency redox system for chloroplast protection against oxidative damage. *Plant Cell* **18(9)**:2356–2368 DOI 10.1105/tpc.106.041541.

Rabiei B, Valizadeh M, Ghareyazie B, Moghaddam M, Ali AJ. 2004. Identification of QTLs for rice grain size and shape of Iranian cultivars using SSR markers. *Euphytica* **137(3)**:325–332 DOI 10.1023/B:EUPH.0000040452.76276.76.

Rahim MS, Mishra A, Katyal M, Thakur S, Roy J. 2020. Marker-trait association identified candidate starch biosynthesis pathway genes for starch and amylose-lipid complex gelatinization in wheat (*Triticum aestivum* L.). *Euphytica* **216(9)**:1–22 DOI 10.1007/s10681-020-02688-6.

Rahman S, Abrahams S, Abbott D, Mukai Y, Samuel M, Morell M, Appels R. 1997. A complex arrangement of genes at a starch branching enzyme I locus in the d-genome donor of wheat. *Genome* **40**:465–474 DOI 10.1139/g97-062.

Ral JP, Bowerman AF, Li Z, Sirault X, Furbank R, Pritchard JR, Bloemsma M, Cavanagh CR, Howitt CA, Morell MK. 2012. Down-regulation of glucan, water-dikinase activity in wheat endosperm increases vegetative biomass and yield. *Plant Biotechnology Journal* **10(7)**:871–882 DOI 10.1111/j.1467-7652.2012.00711.x.

Reddy CK, Suriya M, Haripriya S. 2013. Physico-chemical and functional properties of resistant starch prepared from red kidney beans (*Phaseolus vulgaris* L.) starch by enzymatic method. *Carbohydrate Polymers* **95(1)**:220–226 DOI 10.1016/j.carbpol.2013.02.060.

Regina A, Kosarhashemi B, Li Z, Pedler A, Mukai Y, Yamamoto M, Gale K, Sharp PJ, Morell MK, Rahman S. 2005. Starch branching enzyme IIb in wheat is expressed at low levels in the endosperm compared to other cereals and encoded at a non-syntenic locus. *Planta* **222**:899–909 DOI 10.1007/s00425-005-0032-z.

Reinders A, Sivitz AB, Ward JM. 2012. Evolution of plant sucrose uptake transporters. *Frontiers in Plant Science* **3**:22 DOI 10.3389/fpls.2012.00022.

Ribeiro C, Hennen-Bierwagen TA, Myers AM, Cline K, Settles MA. 2020. Engineering 6-phosphogluconate dehydrogenase improves grain yield in heat-stressed maize. *Proceedings of the National Academy of Sciences of the United States of America* **117(52)**:33177–33185 DOI 10.1073/pnas.2010179117.

Roldán I, Wattebled F, Mercedes LM, Delvallé D, Planchot V, Jiménez S, Pérez R, Ball S, D'Hulst C, Mérida A. 2010. The phenotype of soluble starch synthase IV defective mutants of Arabidopsis thaliana suggests a novel function of elongation enzymes in the control of starch granule formation. *Plant Journal* **49**:492–504 DOI 10.1111/j.1365-313X.2006.02968.x.

Ryoo N, Yu C, Park CS, Baik MY, Park IM, Cho MH, Bhoo SH, An G, Hahn TR, Jeon JS. 2007. Knockout of a starch synthase gene OsSSIIIa/Flo5 causes white-core floury endosperm in rice (*Oryza sativa* L.). *Plant Cell Reports* **26**:1083–1095 DOI 10.1007/s00299-007-0309-8.

Sabelli PA, Larkins BA. 2009. The development of endosperm in grasses. *Plant Physiology* **149(1)**:14–26 DOI 10.1104/pp.108.129437.

Satoh H, Nishi A, Yamashita K, Takemoto Y, Tanaka Y, Hosaka Y, Sakurai A, Fujita N, Nakamura Y. 2003. Starch-branching enzyme I-deficient mutation specifically affects the structure and properties of starch in rice endosperm. *Plant Physiology* **133(3)**:1111–1121 DOI 10.1104/pp.103.021527.

Satoh H, Shibahara K, Tokunaga T, Nishi A, Tasaki M, Hwang SK, Okita TW, Kaneko N, Fujita N, Yoshida M, Hosaka Y, Sato A, Utsumi Y, Ohdan T, Nakamura Y. 2008. Mutation of the plastidial α-glucan phosphorylase gene in rice affects the synthesis and structure of starch in the endosperm. *Plant Cell* **20(7)**:1833–1849 DOI 10.1105/tpc.107.054007.

Sauer N. 2007. Molecular physiology of higher plant sucrose transporters. *FEBS Letters* **581(12)**:2309–2317 DOI 10.1016/j.febslet.2007.03.048.

Scheible WR, Gonzalezfontes A, Lauerer M, Mullerrober B, Caboche M, Stitt M. 1997. Nitrate acts as a signal to induce organic acid metabolism and repress starch metabolism in tobacco. *Plant Cell* **9(5)**:783–798 DOI 10.2307/3870432.

Schulz A, Beyhl D, Marten I, Wormit A, Neuhaus E, Poschet G, Buttner M, Schneider S, Sauer N, Hedrich R. 2011. Protondriven sucrose symport and antiport are provided by the vacuolar transporters SUC4 and TMT1/2. *Plant Journal* **68**:129–136 DOI 10.1111/j.1365-313X.2011.04672.x.

Scialdone A, Mugford ST, Feike D, Skeffington A, Borrill P, Graf A, Smith AM, Howard M. 2013. Arabidopsis plants perform arithmetic division to prevent starvation at night. *eLife* **2**:e00669 DOI 10.7554/eLife.00669.

Scofield GN, Hirose T, Aoki N, Furbank RT. 2007. Involvement of the sucrose transporter, OsSUT1, in the long-distance pathway for assimilate transport in rice. *Journal of Experimental Botany* **58**:3155–3169 DOI 10.1093/jxb/erm153.

Scofield G, Hirose T, Gaudron J, Upadhyaya N, Ohsugi R, Furbank RT. 2002. Antisense suppression of the rice sucrose transporter gene, *OsSUT1*, leads to impaired grain filling and germination but does not affect photosynthesis. *Functional Plant Biology* **29**:815–826 DOI 10.1071/PP01204.

Secco D, Baumann A, Poirier Y. 2010. Characterization of the rice pho1 gene family reveals a key role for ospho1;2 in phosphate homeostasis and the evolution of a distinct clade in dicotyledons. *Plant Physiology* **152**:1693–1704 DOI 10.1104/pp.109.149872.

Seung D, Boudet J, Monroe JD, Schreier TB, David LC, Abt M, Lu KJ, Zanella M, Zeeman SC. 2017. Homologs of protein targeting to starch control starch granule initiation in Arabidopsis leaves. *Plant Cell* **29**:1657–1677 DOI 10.1105/tpc.17.00222.

Seung D, Thalmann M, Sparla F, Hachem MA, Sang KL, Issakidis-Bourguet E, Svensson E, Zeeman SC, Santelia D. 2013. *Arabidopsis thaliana* AMY3 is a unique redox-regulated chloroplastic α-amylase. *Journal of Biological Chemistry* **288**:33620–33633 DOI 10.1074/jbc.M113.514794.

She KC, Kusano H, Koizumi K, Yamakawa H, Hakata M, Imamura T, Fukuda M, Naito N, Tsurumaki Y, Yaeshima M, Tsuge T, Matsumoto K, Kudoh M, Itoh E, Kikuchi S, Kishimoto N, Yazaki J, Ando T, Yano M, Aoyama T, Sasaki T, Satoh H, Shimada H. 2010. A novel factor floury endosperm2 is involved in regulation of rice grain size and starch quality. *Plant Cell* **22**:3280–3294 DOI 10.1105/tpc.109.070821.

Skeffington AW, Graf A, Duxbury Z, Gruissem W, Smith AM. 2014. Glucan, water dikinase exerts little control over starch degradation in Arabidopsis leaves at night. *Plant Physiology* **165**:866–879 DOI 10.1104/pp.114.237016.

Stitt M, Zeeman SC. 2012. Starch turnover: pathways, regulation and role in growth. *Current Opinion in Plant Biology* **15**:282–292 DOI 10.1016/j.pbi.2012.03.016.

Streb S, Zeeman SC. 2012. Starch metabolism in Arabidopsis. *The Arabidopsis Book* **10**:e0160 DOI 10.1199/tab.0160.

Su J, Hu C, Yan X, Jin Y, Chen Z, Guan Q. 2015. Expression of barley SUSIBA2 transcription factor yields high-starch low-methane rice. *Nature* **523(7562)**:602–606 DOI 10.1038/nature14673.

Sulpice R, Pyl E-T, Ishihara H, Trenkamp S, Steinfath M, Witucka-Wall H, Gibon Y, Usadel B, Poree F, Piques MC. 2009. Starch as a major integrator in the regulation of plant growth. *Proceedings of the National Academy of Sciences of the United States of America* **106(25)**:10348–10353 DOI 10.1073/pnas.0903478106.

Sun C, Palmqvist S, Olsson H, Borén M, Ahlandsberg S, Jansson C. 2003. A novel WRKY transcription factor, SUSIBA2, participates in sugar signaling in barley by binding to the sugar-responsive elements of the iso1 promoter. *Plant Cell* **15(9)**:2076–2092 DOI 10.1105/tpc.014597.

Sun Y, Reinders A, LaFleur KR, Mori T, Ward JM. 2010. Transport activity of rice sucrose transporters OsSUT1 and OsSUT5. *Plant and Cell Physiology* **51(1)**:114–122 DOI 10.1093/pcp/pcp172.

Suzuki R, Imamura T, Nonaga Y, Kusano H, Teramura H, Sekine KT, Yamashita T, Shimada H. 2020. A novel FLOURY ENDOSPERM2 (FLO2)-interacting protein, is involved in maintaining fertility and seed quality in rice. *Plant Biotechnology* **37(1)**:47–55 DOI 10.5511/plantbiotechnology.19.1212b.

Tetlow IJ, Beisel KG, Cameron S, Makhmoudova A, Liu F, Bresolin NS. 2008. Analysis of protein complexes in wheat amyloplasts reveals functional interactions among starch biosynthetic enzymes. *Plant Physiology* **146(4)**:1878–1891 DOI 10.1104/pp.108.116244.

Thalmann M, Pazmino D, Seung D, Horrer D, Nigro A, Meier T, Kölling K, Pfeifhofer HW, Zeeman SC, Santelia D. 2016. Regulation of leaf starch degradation by abscisic acid is important for osmotic stress tolerance in plants. *Plant Cell* **28(8)**:1860–1878 DOI 10.1105/tpc.16.00143.

Thitisaksakul M, Jiménez RC, Arias MC, Beckles DM. 2012. Effects of environmental factors on starch biosynthesis and composition. *Journal of Cereal Science* **56(1)**:67–80 DOI 10.1016/j.jcs.2012.04.002.

Tian Z, Qian Q, Liu Q, Yan M, Liu X, Yan C, Liu G, Gao Z, Tang S, Zeng D, Wang Y, Yu J, Gu M, Li J. 2009. Allelic diversities in rice starch biosynthesis lead to a diverse array of rice eating and cooking qualities. *Proceedings of the National Academy of Sciences of the United States of America* **106(53)**:21760–21765 DOI 10.1073/pnas.0912396106.

Tiessen A, Nerlich A, Faix B, Hümmer C, Fox S, Trafford K. 2012. Subcellular analysis of starch metabolism in developing barley seeds using a non-aqueous fractionation method. *Journal of Experimental Botany* **63**:2071–2087 DOI 10.1093/jxb/err408.

Utsumi Y, Utsumi C, Sawada T, Fujita N, Nakamura Y. 2011. Functional diversity of isoamylase oligomers: the isa1 homo-oligomer is essential for amylopectin biosynthesis in rice endosperm. *Plant Physiology* **156**:61–77 DOI 10.1104/pp.111.173435.

Wang JC, Xu H, Zhu Y, Liu QQ, Cai XL. 2013. *OsbZIP58*, a basic leucine zipper transcription factor, regulates starch biosynthesis in rice endosperm. *Journal of Experimental Botany* **64**:3453–3466 DOI 10.1093/jxb/ert187.

Wei X, Jiao G, Lin H, Sheng Z, Shao G, Xie L, Hu P. 2017. GRAIN INCOMPLETE FILLING 2 regulates grain filling and starch synthesis during rice caryopsis development. *Journal of Integrative Plant Biology* **59**:134–153 DOI 10.1111/jipb.12510.

Weise SE, Weber AP, Sharkey TD. 2004. Maltose is the major form of carbon exported from the chloroplast at night. *Planta* **218**:474–482 DOI 10.1007/s00425-003-1128-y.

Wu C, Colleoni C, Myers AM, James MG. 2002. Enzymatic properties and regulation of zpu1, the maize pullulanase-type starch debranching enzyme. *Archives of Biochemistry and Biophysics* **406(1)**:21–32 DOI 10.1016/S0003-9861(02)00412-5.

Wuriyanghan H, Zhang B, Cao WH, Ma B, Lei G, Liu YF. 2009. The ethylene receptor etr2 delays floral transition and affects starch accumulation in rice. *Plant Cell* **21(5)**:1473–1494 DOI 10.1105/tpc.108.065391.

Xiao Q, Wang Y, Du J, Li H, Wei B, Wang Y, Li Y, Yu G, Liu H, Zhang J, Liu Y, Hu Y, Huang Y. 2017. ZmMYB14 is an important transcription factor involved in the regulation of the activity of the ZmBT1 promoter in starch biosynthesis in maize. *FEBS Journal* **284(18)**:3079–3099 DOI 10.1111/febs.14179.

Xu SB, Yu HT, Yan LF, Wang T. 2010. Integrated proteomic and cytological study of rice endosperms at the storage phase. *Journal of Proteome Research* **9(10)**:4906–4918 DOI 10.1021/pr900954p.

Yadav UP, Ivakov A, Feil R, Duan GY, Walther D, Giavalisco P, Piques M, Carillo P, Hubberten H-M, Stitt M, Lunn JE. 2014. The sucrose-trehalose 6-phosphate (tre6p) nexus: specificity and mechanisms of sucrose signalling by tre6p. *Journal of Experimental Botany* **65(4)**:1051–1068 DOI 10.1093/jxb/ert457.

Yamamoto MP, Onodera Y, Touno SM, Takaiwa F. 2006. Synergism between RPBF Dof and RISBZ1 bZIP activators in the regulation of rice seed expression genes. *Plant Physiology* **141(4)**:1694–1707 DOI 10.1104/pp.106.082826.

Yang T, Guo L, Ji C, Wang H, Wang J, Zheng X, Xiao Q, Wu Y. 2020. The B3 domain-containing transcription factor ZmABI19 coordinates expression of key factors required for maize seed development and grain filling. *The Plant Cell* **33(1)**:104–128 DOI 10.1093/plcell/koaa008.

Yu H, Wang T. 2016. Proteomic dissection of endosperm starch granule associated proteins reveals a network coordinating starch biosynthesis and amino acid metabolism and glycolysis in rice endosperms. *Frontiers in Plant Science* **7**:707 DOI 10.3389/fpls.2016.00707.

Yun MS, Takayuki U, Yasushi K. 2011. Rice debranching enzyme isoamylase3 facilitates starch metabolism and affects plastid morphogenesis. *Plant and Cell Physiology* **52(6)**:1068–1082 DOI 10.1093/pcp/pcr058.

Zeeman SC, Kossmann J, Smith AM. 2010. Starch: its metabolism, evolution, and biotechnological modification in plants. *Annual Review of Plant Biology* **61(1)**:209–234 DOI 10.1146/annurev-arplant-042809-112301.

Zeeman SC, Tiessen A, Pilling E, Kato KL, Donald AM, Smith AM. 2002. Starch synthesis in Arabidopsis. Granule synthesis, composition, and structure. *Plant Physiology* **129**:516–529 DOI 10.1104/pp.003756.

Zhang JJ, Chen J, Yi Q, Hu YF, Liu HM, Liu YH, Huang Y. 2014. Novel role of zmanac36 in co-expression of starch synthetic genes in maize endosperm. *Plant Molecular Biology* **84**:359–369 DOI 10.1007/s11103-013-0153-x.

Zhang Z, Dong J, Ji C, Wu Y, Messing J. 2019. NAC-type transcription factors regulate accumulation of starch and protein in maize seeds. *Proceedings of the National Academy of Sciences of the United States of America* **116(23)**:11223–11228 DOI 10.1073/pnas.1904995116.

Zhang Y, Primavesi LF, Jhurreea D, Andralojc PJ, Mitchell RAC, Powers SJ. 2009. Inhibition of SNF1 related protein kinase1 activity and regulation of metabolic pathways by trehalose-6-phosphate. *Plant Physiology* **149**:1860–1871 DOI 10.1104/pp.108.133934.

Zhang L, Ren Y, Lu B, Yang C, Feng Z, Liu Z. 2016b. *Floury endosperm*7 encodes a regulator of starch synthesis and amyloplast development essential for peripheral endosperm development in rice. *Journal of Experimental Botany* **67**:633–647 DOI 10.1093/jxb/erv469.

Zhang DP, Wu JG, Zhang YJ, Shi CH. 2012. Phenotypic and candidate gene analysis of a new floury endosperm mutant (*osagpl2-3*) in rice. *Plant Molecular Biology Reporter* **30**:1303–1312 DOI 10.1007/s11105-012-0435-5.

Zhang Z, Zheng X, Yang J, Messing J, Wu Y. 2016a. Maize endosperm-specific transcription factors O2 and PBF network the regulation of protein and starch synthesis. *Proceedings of the National Academy of Sciences of the United States of America* **113(39)**:10842–10847 DOI 10.1073/pnas.1613721113.

Zhao Q, Du X, Han Z, Ye Y, Pan G, Asad M, Zhou Q, Cheng F. 2019. Suppression of starch synthase I (SSI) by RNA interference alters starch biosynthesis and amylopectin chain distribution in rice plants subjected to high temperature. *The Crop Journal* **7(5)**:3–16 DOI 10.1016/j.cj.2019.03.009.

Zhong Y, Liu L, Qu J, Li S, Guo D. 2020. The relationship between the expression pattern of starch biosynthesis enzymes and molecular structure of high amylose maize starch. *Carbohydrate Polymers* **247(12)**:116681 DOI 10.1016/j.carbpol.2020.116681.

Zhou H, Wang L, Liu G, Meng X, Jing Y, Shu X, Kong X, Sun J, Yu H, Smith SM, Wu D, Li J. 2016. From the cover: critical roles of soluble starch synthase SSIIIa and granule-bound starch synthase Waxy in synthesizing resistant starch in rice. *Proceedings of the National Academy of Sciences of the United States of America* **113(45)**:12844–12849 DOI 10.1073/pnas.1615104113.