REVIEW

Carbohydrate reserves and seed development: an overview

Manuel Aguirre[1,2] · Edward Kiegle[1] · Giulia Leo[1] · Ignacio Ezquer[1]

Received: 22 December 2017 / Accepted: 23 April 2018

Abstract

Seeds are one of the most important food sources, providing humans and animals with essential nutrients. These nutrients include carbohydrates, lipids, proteins, vitamins and minerals. Carbohydrates are one of the main energy sources for both plant and animal cells and play a fundamental role in seed development, human nutrition and the food industry. Many studies have focused on the molecular pathways that control carbohydrate flow during seed development in monocot and dicot species. For this reason, an overview of seed biodiversity focused on the multiple metabolic and physiological mechanisms that govern seed carbohydrate storage function in the plant kingdom is required. A large number of mutants affecting carbohydrate metabolism, which display defective seed development, are currently available for many plant species. The physiological, biochemical and biomolecular study of such mutants has led researchers to understand better how metabolism of carbohydrates works in plants and the critical role that these carbohydrates, and specially starch, play during seed development. In this review, we summarize and analyze the newest findings related to carbohydrate metabolism's effects on seed development, pointing out key regulatory genes and enzymes that influence seed sugar import and metabolism. Our review also aims to provide guidelines for future research in the field and in this way to assist seed quality optimization by targeted genetic engineering and classical breeding programs.

Abbreviations

AGP	ADPG pyrophosphorylase
ADPG	ADP-glucose
CW	Cell wall
DAP	Days after pollination
DBE	Starch-debranching enzyme
FRK	Fructokinase
G1P	Glucose-1-phosphate
GBSSI	Granule-bound starch synthase I
GWD	Glucan, water dikinases
PK	Piruvate kinase
SBE	Starch-branching enzymes
SS	Starch synthase
SuSy	Sucrose synthase
SUT	SUC transporters
UDPG	UDP-glucose

Introduction

Developing seeds are a well-studied system to analyze the transport and compartmentalization of photoassimilates and sink metabolism, where the role of carbon flow is central. Seed formation can be divided into three stages: embryogenesis, maturation and desiccation. Each stage is characterized by specific sequences of molecular events (Baud et al. 2002) and metabolic profiles (Angeles-Núñez and Tiessen 2010). Developing seeds are complex structures formed by a testa of maternal origin that contains the fertilization products: embryo and endosperm. Development occurs in a series of specific spatiotemporal steps, with a phase of cell division followed by cell elongation, and a phase in which reserve storage compounds are sequestered. In many species, this sequence of events spreads in a wavelike manner, creating a developmental gradient that displays strict molecular, metabolical and structural–mechanical coordination (Ruan and Chourey 2006). The accumulation of storage compounds in

Manuel Aguirre and Edward Kiegle have contributed equally to this work.

A contribution to the special issue 'Seed Biology'.

Communicated by L. Lepiniec, H. North, G. Ingram.

✉ Ignacio Ezquer
juan.ezquer@unimi.it

[1] Dipartimento di BioScienze, Università degli Studi di Milano, 20133 Milan, Italy

[2] FNWI, University of Amsterdam, 1098 XH Amsterdam, The Netherlands

seeds relies on their capacity to import sucrose from maternal tissues (Weber et al. 2005). Sucrose synthesised in green (photosynthetically active) tissues is transported through the phloem to support growth and maturation of heterotrophic tissues such as seeds (Zhang et al. 2007). Thus, seed filling depends above all on the rate of photoassimilate supply and on metabolic regulation of transport (Weber et al. 2005). Sucrose is the main product of photosynthesis, so the overall capacity of heterotrophic tissues to import photoassimilates depends on the ability of their individual cells to import, metabolize and store sucrose. The discharge paths depend upon the particular seed sink strength and specific nutritional requirements at each developmental stage. This process provides most of our food and feed due to the accumulation of the major storage products strongly enhanced in crop plants by breeding efforts: starch, protein and oil. Such storage products are synthesised and stored in either the cotyledons (as in legume seeds) or the endosperm (as in cereal grains) or in both tissues (as in tobacco seeds). Table 1 shows in detail the nutrient partitioning displayed by some important seed crops.

The carbohydrate composition of seeds consists of oligosaccharides such as fructans (Cimini et al. 2015) and polysaccharides. Starch is the main polysaccharide stored in seeds. It represents the major source of carbohydrates in the human diet, and it is also the main plant carbohydrate used by the food industry and is therefore of great economic relevance. Cereal grains and legume seeds are by far the most important starch sources, and they are used to produce pasta, bread, rice, flours and couscous, for example. Such products form the basis of human alimentation. Other polysaccharides present in plant seeds include cell wall polysaccharides (cellulose, hemicelluloses and pectin). In some cases, cell wall polysaccharides have been proposed to act as seed storage polysaccharides, including mixed-linkage glucan in the monocot Brachypodium distachyon (Guillon et al. 2012) and mannan in the seeds of several species such as guar (*Cyamopsis tetragonoloba*) (reviewed in Nishinari et al. 2007). Cell wall polysaccharides have many applications in food and non-food industry (Ying et al. 2013; Mudgil et al. 2014; Chateigner-Boutin et al. 2016). Cell wall polysaccharides are also important because some of them contribute to dietary fibers. Dietary fibers are defined as edible plant components that are not digested in the small intestine but fermented in the colon. They include cell wall polysaccharides, resistant starch, resistant oligosaccharides and lignin. Dietary fibers can regulate intestinal activity by increasing fecal mass and accelerating intestinal transit. Several studies have reported that a fiber-rich diet helps to reduce cholesterol levels and lowers the risk of suffering impaired glucose tolerance and insulin resistance (Weickert and Pfeiffer 2018).

The availability of mutant legumes, grasses and crucifers with altered development and carbohydrate metabolism has facilitated the understanding of the genetic basis of seed carbohydrate accumulation. Decades of research on the genetic programmes underlying plant embryogenesis and seed maturation have led researchers to propose different models to explain key regulatory networks and enzymes involved in the control of carbohydrate flow in developing seeds. In many crops, these products are of fundamental economic importance for the post-harvest industry (Lee et al. 2017; Nakamura et al. 2017; Xu et al. 2017; Guo et al. 2018). The disruption of carbohydrate metabolic pathways at different levels can lead to dramatic developmental defects (discussed in the last section of this manuscript).

This review summarizes recent progress in understanding the role of key genes controlling seed-specific carbohydrate flow, with special emphasis on the control of seed development. The purpose of this manuscript is to provide the reader with a comprehensive view of the relationships between carbohydrate metabolite homeostasis and carbon partitioning, the distribution of storage compounds such as starch, and the influence of these factors on seed development. We also provide some speculative views to encourage further experimentation. Since the coordination of seed development is considered to be different between clades, species and genera, we highlight regulatory targets in monocots and dicots that could be used by breeding programs to improve seed quality.

Seed development and differentiation is tightly linked to metabolic reprogramming

One of the factors considered to have contributed to the rise of angiosperms to ecological dominance is double fertilization event and the development of a seed formed by a diploid embryo and a triploid endosperm, both of them enclosed by a testa, derived from maternal integuments (De Bodt et al. 2005). Embryogenesis takes place protected by the diploid maternally derived integuments, which eventually form the seed coat (Lafon-Placette and Köhler 2014). Endosperm works as a nourishing tissue, controlling the growth of a small embryo that quickly enlarges after fertilization (Fiume and Fletcher 2012). After fertilization, the embryo goes through a phase of active cell division, followed by a phase of morphogenesis, and finally a maturation process, during which several types of species-specific storage products are accumulated (Bentsink and Koornneef 2008). Over time, seeds have evolved remarkable developmental strategies that enabled plants to colonize diverse ecological niches across the globe. Seeds represent a major adaptive advantage that enabled seed plants to dominate today's flora (Wang 2018). During human history, starch-rich crops have formed the basis of our nutrition; thus,

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Table 1 Seed storage composition of monocots, eudicots and gymnosperm species

Clade	Clade	Family	Name ([ab])	Carbohydrate	Oil	Protein	References
GYMNOSPERMS		PINACEAE	*Pinus pinea* (pine nut)[a]	13 (total)	68.3	13.6	Kim et al. (2017)
		GNETACEAE	*Gnetum africanum* (African jointfir)[b]	0.8 (CW) 87.6 (carbohydrates) 88.4 (total)	3.1	17.5	Ekop (2007)
ANGIOSPERMS	NYMPHAEALES	NYMPHAEACEAE	*Nymphaea lotus* (Egyptian lotus)[b]	5.6–6.6 (CW) 81–82.4 (carbohydrates) 86–88 (total)	6.1–7.1	3	Muhammad et al. (2011)
			Hordeum vulgare (barley)[b]	13.4–42.1 (CW) 0.1 (glucose) 67.7–73.8 (starch)	2.7–3.2	10.8–14.1	Beloshapka et al. (2016)
			Zea mays (maize "yellow corn")[b]	13.5 (CW) 0.2 (glucose) 65 (starch)	5.1	7.09	Beloshapka et al. (2016)
			Avena sativa (oat)[b]	9.9–11.1 (CW) 0.1 (glucose) 65.3–73.4 (starch)	7.4–8.5	10.8–12.7	Beloshapka et al. (2016)
			Oryza sativa (rice)[b]	7 (CW) 0.1 (glucose) 77 (starch)	4.4–4.6	9.8–12.8	Beloshapka et al. (2016)
			Triticum aestivum (wheat)[b]	67 (starch) 70–75 (total)	1.5–3.5	13–17	Högy and Fangmeier (2008) and Tausz et al. (2017)
	MONOCOTS	POACEAE	*Sorghum bicolor* (sorghum)[b]	12.5 (CW) 0.2 (glucose) 70.5 (starch)	4.3	10.19	Beloshapka et al. (2016)
			Phalaris canariensis (canary grass seed)[b]	20.8 (CW) 0.1 (glucose) 49.7 (starch)	7.3	17.4	Beloshapka et al. (2016)
			Eleusine coracana (millet)[b]	15.3 (CW) 0.1 (glucose) 64.9 (starch)	5	11.5	Beloshapka et al. (2016)
			Secale cereale (rye)[b]	20.4–25.2 (CW) 1.7–2.5 (glucose) 54.9–60.3 (starch) 79–90.9 (total)	2.5–2.8	11.4–15.8	Nyström et al. (2008)
			x *Triticosecale* " *Triticum* x *Secale"* (triticale)[b]	73.1 (total)	1.8	13.1	Zhu (2018)
			Elaeis guineensis (oil palm)[b]	18.1 (total)	54.8	7.8	Kok et al. (2011)
		ARECACEAE	*Phoenix dactylifera* (date palm)[a]	67.2–74.3 (CW) 2–4.7 (other carbohydrates) 69.2–79 (total)	5.6–8.7	4.8–6.9	Habib and Ibrahim (2009) and Nehdi et al. (2018)
	EUDICOTS	BRASSICACEAE	*Brassica napus* (rapeseed)[b]	22–24 (total)	41–50	24.1–26.5	Barthet and Daun (2011), Hua et al. (2012) and Khan et al. (2018)
			Arabidopsis thaliana[b]	2 (total)	30–40	30–40	Baud et al. (2008)
		AMARANTHACE AE	*Chenopodium quinoa* (quinoa)[b]	19.9 (CW) 1.3 (glucose) 55.7 (starch)	6.2	9.3	Beloshapka et al. (2016)

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Table 1 (continued)

Clade	Clade	Family	Name ([ab])	Carbohydrate	Oil	Protein	References
		LINACEAE	*Linum usitatissimum* (flaxseed hull)[b]	50–51 (total)	19.5–20.8	16.5–17.8	Herchi et al. (2014)
		ROSACEAE	*Prunus dulcis* (almond)[a]	21.5 (total)	49.9	21.1	Kim et al. (2017)
		JUGLANDACEAE	*Juglans regia* (walnut)[a]	13.7 (total)	65.2	15.2	Kim et al. (2017)
			Carya illinoinensis (pecan)[a]	13.8 (total)	71.9	9.1	Kim et al. (2017)
		BETULACEAE	*Corylus avellana* (hazelnut)[a]	16.7 (total)	60.7	14.9	Kim et al. (2017)
		PROTEACEAE	*Macadamia integrifolia* (macadamia nut)[a]	13.8 (total)	75.7	7.9	Kim et al. (2017)
		ANACARDIACEAE	*Pistacia vera* (pistachio)[a]	27.1 (total)	45.3	20.1	Kim et al. (2017)
			Anacardium occidentale (cashew)[a]	30.1 (total)	43.8	18.22	Kim et al. (2017)
		LECYTHITACEAE	*Bertholletia excelsa* (Brazil nut)[a]	11.7 (total)	67.1	14.3	Kim et al. (2017)
		FAGACEAE	*Castanea sativa* (chest nut)[a]	45.5 (total)	2.2	2.42	Kim et al. (2017)
		EUPHORBIACEAE	*Ricinus communis* (castor bean)[b]	2.4–3 CW	40–56	22.1–24.3	Akande et al. (2012) and Perdomo et al. (2013)
		PHABACEAE	*Medicago truncatula* (barrel medic tree)[b]	2 (starch) 3 (total)	9	35	Djemel et al. (2005) and Song et al. (2017a, b)
			Medicago orbicularis (button medic)[b]	9 (starch)	2.5	1	Song et al. (2017)
			Glycine max (soybean)[b]	2 (total)	20	40	Song et al. (2017a)
			Pongamia pinnata (pongam oil tree)[b]	7 (total)	35	20	Bala et al. (2011), Scott et al. (2008) and Song et al. (2017a)
			Arachis hypogea (peanut)[a]	16 (total)	49	26	Kim et al. (2017)
			Cicer arietinum (chick pea)[b]	44 (total)	6	23	Huang et al. (2007), Rachwa-Rosiak et al. (2015) and Song et al. (2017)
			Lupinus luteus "*angustifolius* and *albus*" (yellow lupin)[b]	2 (total)	8	38	Song et al. (2017a)
			Pisum sativum (garden pea)[b]	40 (total)	3	27	Song et al. (2017a)
			Vicia faba (broad bean)[b]	45 (total)	3	30	Song et al. (2017a)

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Table 1 (continued)

Clade	Clade	Family	Name ([ab])	Carbohydrate	Oil	Protein	References
			Phaseolus vulgaris (common bean)[b]	19 (total)	20	23	Song et al. (2017a)
			Lotus japonicus (birdsfoot trefoil)[b]	1 (total)	7	43	Dam et al. (2009) and Song et al. (2017a)

The table contains datasets of seed storage composition from different plant species (based on bibliography included in the table). Superscripts following the common names indicate whether sugar, oil and protein contents are expressed as percentage fresh weight ([a]) or dry weight ([b]). In the seed carbohydrate composition column, and according to the cited studies, we have indicated in parentheses the percentages of starch, glucose, cell wall components (indicated as CW) and total carbohydrates where these data were known. CW components are the data reported as "fibers" in the sources reviewed and comprise plant cell wall-derived polysaccharides (mostly cellulose, and to a lesser extent, hemicellulose and lignin)

unraveling carbohydrate biosynthesis and its relationships to structure and functionality is of enormous interest and represents a prerequisite for the targeted improvement of starch crops (Onda and Mochida 2016). Centuries of artificial selection, together with several decades of agricultural research during the twentieth and twenty-first century, have elucidated the qualitative and quantitative traits associated with seed components. Moreover, molecular approaches that can increase the quantity and improve the quality of seed products have been developed (Collard and Mackill 2008). Today, breeders have a tremendous interest in deciphering the genetic control of seed development and metabolism. Seed development progresses temporally and spatially in a coordinated way within the different seed organs and is influenced by mitotic activity, transcriptional regulation, metabolic flow and finally storage processes (Locascio et al. 2014). In recent years, the genetic programs underlying plant embryogenesis and seed maturation have been well characterized (Pfister and Zeeman 2016; Stein et al. 2017; Meng et al. 2017; Pirone et al. 2017; Doughty et al. 2014; Locascio et al. 2014; Li and Li 2015; Orozco-Arroyo et al. 2015). Proper endosperm development is necessary for correct embryogenesis (Hehenberger et al. 2012). In *Arabidopsis*, mutations affecting endosperm proliferation, cellularization or breakdown have been well documented. Such mutations cause morphological disruption, altering development and causing embryo abortion in *Arabidopsis* (Kondou et al. 2008; Yang et al. 2008; Costa et al. 2014) and maize (Fouquet et al. 2011). Seed coat failure can also affect dramatically embryo viability (Berger 2003; Auger et al. 2010; Chen et al. 2013; Ehlers et al. 2016). Embryonic development depends entirely on an adequate supply of nutrients from maternal tissues. Significant progress has been made in understanding the translocation of photoassimilates from source tissues to sink tissues (Bihmidine et al. 2013). However, the mechanisms by which sucrose is transported from the maternal seed coat of *Arabidopsis* to the embryo and the endosperm (as well as downstream pathways) have remained elusive. Specific transporters have been identified that play a key role in sucrose flow from the seed coat to filial tissues (Chen et al. 2015). Chen et al. (2015) showed that blocking the carbon flow at maternal seed coat tissues can induce significant delay in embryo development. In analogous way to the seed coat in dicots, in monocots, the pericarp, a maternal structure that encloses the filial storage organs (embryo and endosperm), exerts a major role controlling the metabolic flow toward filial tissues (Radchuk and Borisjuk 2014; Rolletschek et al. 2015). This close interdependence of both fertilization products requires a dynamic metabolic flow to ensure coordinated growth and development.

Seed carbohydrate composition in different systems

Storage compounds of seeds are primarily composed of sugars, proteins and lipids, and the distribution of these metabolites varies depending on the developmental program of each species. The composition and relative amount of these storage compounds have been quantified in different seed tissues of many species (Table 1).

Endosperm structure in mature seeds varies considerably among different species. In monocots (such as *Poaceae*), a large starchy endosperm persists as a storage tissue until germination. In a developmental context, plants with this type of seeds are referred to as "albuminous" or "endospermous" (Yan et al. 2014). In *Solanaceae* species like tomato (*Solanum lycopersicum*), mature seeds display a hard and thick endosperm cell layer, which undergoes extensive weakening during seed germination (Nonogaki et al. 2000). In contrast, the endosperm of "exalbuminous" or "cotyledonous" seeds such as soybean (*Glycine max*) and pea (*Pisum sativum*) is absorbed during embryo development and the storage tissues are the enlarged cotyledons (Lee et al. 2012). In mature seeds of *Brassicaceae* (e.g., *Arabidopsis thaliana*), the residual endosperm is confined to a peripheral aleurone-like

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cell layer (Lee et al. 2012). In *Brassicaceae* species, the endosperm acts as a mechanical barrier to inhibit embryonic growth and as a nutrient reserve for seed germination and early seedling establishment (Müller et al. 2006).

The "endospermous" versus "cotyledonous" dichotomy establishes two very different developmental programs between species, and consequently major differences in transcriptional reprogramming events, storage and maturation phases, and metabolism of storage compounds. In the endosperm of "albuminous" *Poaceae*, a common feature is that carbohydrates, especially starch, are by far the most abundant component (about 80% of the seed composition), while proteins, and particularly oils, represent a minor fraction (12 and 3%, respectively) (Table 1). Such nutrient partitioning can be considered an "energetic" strategy. In endospermous seeds, such as those of cereals, mobilization of the major reserves within seed storage tissues occurs only during germination, to provide the growing seedling with nutrients until it becomes autotrophic (Bewley et al. 2013). In species of the *Poaceae* family, like wheat, a progressive accumulation of both proteins and starch increases during late seed development (Shewry et al. 2009), whereas sucrose, accumulated early in development, is consumed gradually as growth progresses (Weichert et al. 2010).

In castor bean (*Ricinus communis*), another endosperm accumulator, storage nutrient accumulation works slightly differently. In this species, the most abundant storage compounds are fatty acids (from 40 to 56% of seed composition), the remainder being proteins, and an almost insignificant accumulation of carbohydrates (Akande et al. 2012; Perdomo et al. 2013). On the other hand, in oil palm (*Elaeis guineensis*), fatty acids comprise 55% of the storage compounds, carbohydrates 18% and protein just 8% of stored nutrients (Kok et al. 2011).

"Exalbuminous" or "cotyledonous" species, like those in the Fabaceae family, have a completely different storage composition. Some of them, like broad bean (*Vicia faba*), button medic (*Medicago orbicularis*) and chick pea (*Cicer arietinum*), primarily sequester carbohydrates, followed by proteins, and a small amount of oils. In contrast, in soybeans (*Glycine max*), barrel clover (*Medicago truncatula*), yellow lupin (*Lupinus luteus*) and common bean (*Phaseolus vulgaris*), proteins are the main reserve component of seeds (20–40%). In peanut (*Arachis hypogaea*), fatty acids (approximately 50%) are far more abundant than proteins and starch (Kim et al. 2017). Oil contents also represent a major storage component in soybean (*Glycine max*), pongam oil tree (*Pongamia pinnata*), birdsfoot trifoil (*Lotus japonicus*) and common bean (*Phaseolus vulgaris*). Studies done in *Vicia faba* have demonstrated that at early stages of development, and its endosperm contains a large amount of hexose sugars, derived from high invertase activity on sucrose (Weber et al. 1996; Draper 1997; Borisjuk et al. 1998; Weschke et al. 2003; Melkus et al. 2011). As development progresses, the activity of invertases ceases and causes decreased hexose levels and increased sucrose levels in the endosperm. A similar trend in sugar accumulation has been reported for *Pisum sativum* and *Zea mays* during seed development (Jaynes and Nelson 1971; Borisjuk et al. 2002).

In the *Brassica* family, the model species *Arabidopsis thaliana* is considered a typical "oleaginous" plant, since seeds accumulate mainly fatty acids (approximately 40%). Protein content in *Arabidopsis* also represents an important pool (roughly 40%) compared to carbohydrates (about 2%). In *Arabidopsis* seeds, starch content reaches its maximum between 6 and 9 days after pollination (DAP) and then decreases abruptly. The highest levels of hexoses (glucose and fructose) are detected at 3 DAP and then decrease drastically to undetectable levels in mature seeds (Baud et al. 2002). There have been important studies in rapeseed (*Brassica napus*), which is closely related to *Arabidopsis*, in which metabolism of sugars has been analyzed in dissected embryo and endosperm (Hills 2004). Rapeseed contains an important pool of carbohydrates (22–24%). In the endosperm, at initial phases of development, imported sucrose is cleaved by invertases. This results in high levels of hexoses and low amounts of sucrose. As seed development proceeds, glucose and fructose levels decrease with an increase in sucrose content. Sucrose represents 97% of sugar composition in embryo during the seed development process (Hills 2004).

In other eudicot families, the carbohydrate fraction represents an important component of total seed composition. Carbohydrates represent the major component in *Amaranthaceae*, *Linaceae* and *Fagaceae*, identical to the storage strategy of basal angiosperms like *Nymphaeaceae*. Furthermore, carbohydrates represent an important pool in seeds of *Rosaceae* (21.5%), *Juglandaceae* (13.7%), *Betulaceae* (167%), *Proteaceae* (13.8%), *Anacaridacea*e (27.1%), *Lecythitaceae* (11.7%) families. In gymnosperms, reported carbohydrate levels in seeds range from approximately 13% in pine nut *(Pinus pinea)* to the approximately 88% found in African jointfir (*Gnetum africanum*).

The sucrolytic pathway triggers a metabolic switch during seed development

The presence of sucrose hydrolyzing enzymes, which produce hexoses from sucrose cleavage, is critical for the establishment of the pre-storage phase during seed development via regulation of source/sink relations (Herbers and Sonnewald 1998; Baroja-Fernández et al. 2003; Wang et al. 2010a, b; Adhikari et al. 2016). Sucrolytic routes leading to major storage compounds in most angiosperms have been well described (schematically summarized in Fig. 1).

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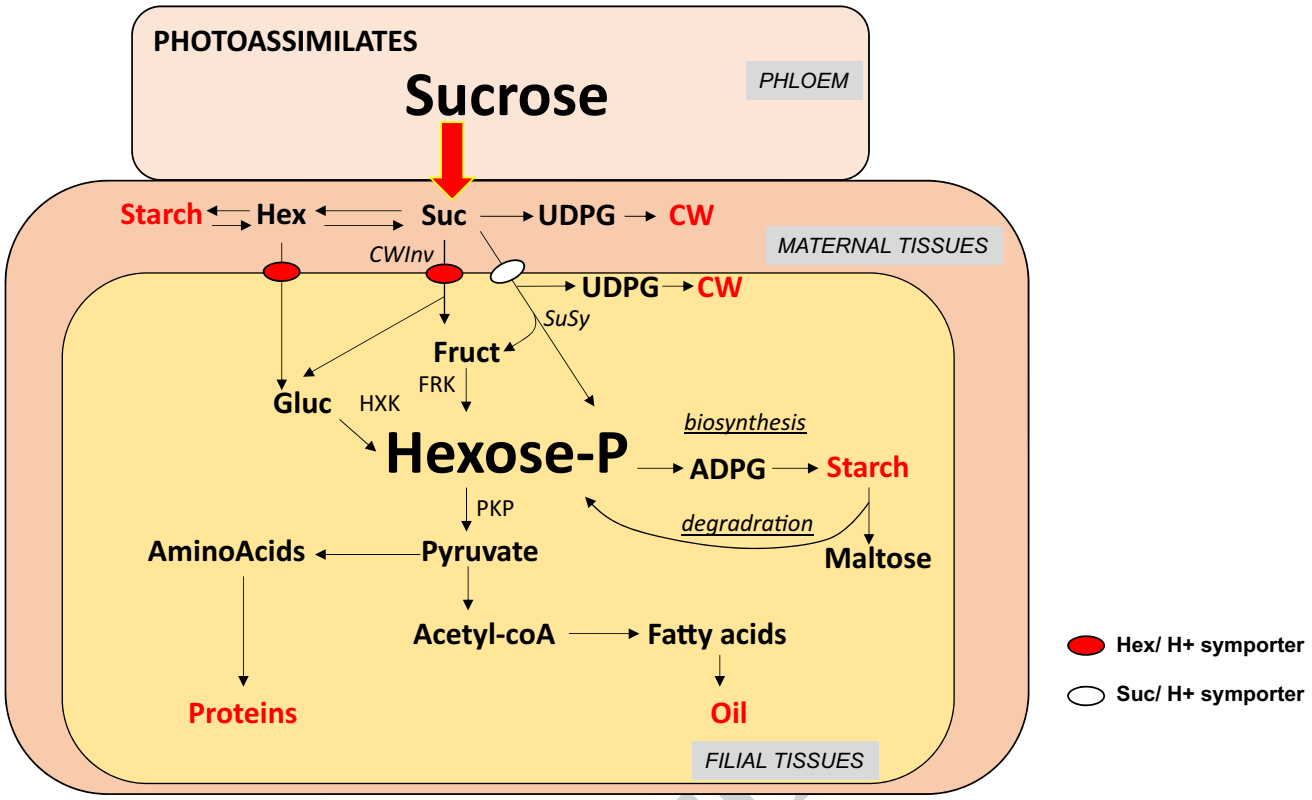

Fig. 1 General view of the metabolic pathways connecting carbon partitioning to the main storage compounds in seeds and key enzymatic steps involved in seed development. Photoassimilates from source tissues enter maternal tissues via the phloem. Sucrose plays a central role and is partitioned into different storage-specific pathways by multiple enzymes, leading to the accumulation of starch, oil and proteins. Seed maternal tissues (like seed coat in dicots or pericarp in monocots) control the rate of delivery of sucrose uptake into the seed by means of sucrose transporters and hexose transporters (described in Fig. 2). Once in the filial tissues, sucrose is metabolized by the action of cell wall invertases and SuSy, releasing hexose phosphates into the cytosol. CWinv cleave sucrose in the apoplastic space between maternal and filial tissues. UDPG is used as a precursor for cell wall biogenesis. Starch is synthesized in the plastid via a biosynthetic pathway that uses PGI, PGM, AGP and SS enzymes. Starch degradation involves α- and β-amylases (forming maltose) units and the action of different starch phosphorylating enzymes (necessary for starch degradation); GWD and glucan phosphate phosphatases. Hexose can be metabolized through the oxidative pentose phosphate pathway and the glycolytic pathways, providing precursors for fatty acid production in the form of acetyl-CoA. Pyruvate kinase catalyzes the essential irreversible transphosphorylation from phosphoenol pyruvate to pyruvate. Phosphoenol pyruvate is a key metabolic intermediate directing carbon partitioning toward protein and oil accumulation. *Abbreviations ADPG* ADP-glucose; *AGP* ADPG pyrophosphorylase; *Hex* Hexose; *CWinv* cell wall invertase; *SuSy* sucrose synthase; *CW* cell wall; *UDPG* UDP-glucose

Sucrose cleavage in sink tissues can be catalyzed either by invertases (EC 3.2.1.26) or by sucrose synthases (SuSy, EC 2.4.1.13) (Fig. 1). Starting from sucrose, invertase generates glucose and fructose, while SuSy renders UDP-glucose (UDPG) and fructose. Hexoses enter the hexose-P pool in the cytosol. These monosaccharides, translocated by hexose transporters, are essential for proper seed development. In Arabidopsis, the glucose transporter mutants *erdl6* and *gpt1* formed seeds with altered seed storage nutrient composition that affected seed development (Poschet et al. 2011; Hedhly et al. 2016). Once in the cytosol, carbon can be preferentially partitioned into either oil, protein or starch accumulation (discussed in detail later) (Baud et al. 2008) (Fig. 1). Little is known about the developmental consequences of altering carbohydrate-related genes, but there are many mutants reported in the literature with phenotypic defects. We cannot describe all of them in detail here, but it is important to summarize at least those most representative in key model species. Due to limited space, we have included list of mutants corresponding to one dicotyledonous species (Arabidopsis; Table 2) and two monocotyledonous species (maize and rice; Tables 3 and 4, respectively).

Mutations of invertase and other sucrolytic enzymes that alter the hexose/sucrose ratio have been shown to produce phenotypic effects during seed development in many species (Angeles-Núñez and Tiessen 2011, 2012; Adhikari et al. 2016; Hedhly et al. 2016; Stein et al. 2017; Meng et al. 2017; Pirone et al. 2017; Solís-Guzmán et al. 2017; Durand et al. 2017). In *Arabidopsis* seeds, the transition from a pre-storage to a maturation (storage) phase is characterized by a

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Table 2 List of carbohydrate metabolism-related genes characterized in *Arabidopsis*

Type of protein encoded	Mutant	Gene	Locus	Function	Phenotype	References
Enzymes	*Sucrose-phosphate synthase 3f (sps3), sucrose-phosphate synthase 4f (sps4)*	*SPS3, SPS4*	AT1G04920, AT4G10120	Reduction in sucrose-phosphate synthase activity and glycosyl group transferase activity	Abnormal seed development	Bahaji et al. (2015) and Solís-Guzmán et al. (2017)
	Fructokinase 6 (frk6), fructokinase 7 (frk7)	*FRK6, FRK7*	AT1G06030, AT5G51830	Fructose phosphorylation activity. Fructokinase activity	In the *frk6/frk7* double mutant: reduced seed size and weight. "Wrinkled" seed phenotype and abnormal surface shape. Smaller oil bodies in the embryo and altered levels of fatty acids	Stein et al. (2017)
	Atp citrate lyase a-1 (acla1)	*ACLA1*	AT1G10670	Cytosolic acetyl-CoA metabolic activity	Reduced number of reproductive structures per plant, reduced seed yield and germination	Fatland (2005)
	Phosphoglucan, water dikinase 1 (gwd1), phosphoglucan, water dikinase (gwd2), phosphoglucan, water dikinase (pwd)	*GWD1, GWD2, PWD*	AT1G10760, AT4G24450, AT5G26570	Alpha-glucan, water dikinase activity, Phosphoglucan, water dikinase activity, Chloroplast phosphoglucan, water dikinase activity	Reduced seed number and size. Increased seed density and reduced lipid concentration. Highly increased starch concentrations in seeds. Altered mucilage composition. Shrunk seeds with altered seed coat morphology and increased permeability. Reduced seed germination	Andriotis et al. (2010) and Pirone et al. (2017)
	Alpha-amylase-like 3 (amy3)	*AMY3*	AT1G69830	Plastidic alpha-amylase activity	No starch accumulation in seed at maturity	Yu et al. (2005)
	Phosphoglucomutase 2 (pgm2), phosphoglucomutase 3 (pgm3)	*PGM2 PGM3*	AT1G70730, AT1G23190	Cytosolic phosphoglucomutase activity	In the *pgm2/pgm3* double mutant: lethal, reduced seed number. Seed abortion	Malinova et al. (2014)

Table 2 (continued)

Type of protein encoded	Mutant	Gene	Locus	Function	Phenotype	References
	Trehalose-6-phosphate synthase 1 (tps1)	*TPS1*	AT1G78580	Trehalose biosynthesis. Glycolytic activity. Sucrose synthase activity. Deregulation of glucose sensing and signaling genes	Arrested at torpedo stage during embryo development. Reduced embryo growth. Altered content of reserve nutrients. Increased starch concentration	Baud and Graham (2006) and Gómez et al. (2005, 2006)
	Disproportionating enzyme 2 (dpe2)	*DPE2*	AT2G40840	Maltose glucan phosphorylase activity. Cytosolic transglucosydase and amylomaltase activity	No starch accumulation at seed maturity	Chia et al. (2005)
	Haiku 2 (iku2)	*IKU2*	AT3G19700	Leucine rich repeat (LRR) kinase activity	Reduced seed size and abnormal seed shape. Reduced embryo and endosperm size. Altered seed storage nutrient composition. Reduced concentrations of lipids, proteins and starch	Fatihi et al. (2013), Meng et al. (2017) and Wang et al. (2010a, b)
	Branching enzyme 1 (be1)	*BE1*	AT3G20440	Uncoupled carbohydrate metabolism. Cell division and cell differentiation are affected. Failure of synthesis and accumulation of storage compounds	Embryo arrest in heart stage. Reduced cell number and cell layers in embryo. SAM and vascular strands absence in embryo. Lack of reserve nutrients. Partial rescue by sugar supplementation. Lethality in homozygotes	Pfister and Zeeman (2016) and Wang et al. (2010a, b)
	Plastidial pyruvate kinase 1 (pkp1), plastidial pyruvate kinase 2 (pkp2), plastidial pyruvate kinase 3 (pkp3)	*PKP1, PKP2, PKP3*	AT3G22960, AT5G52920, AT1G32440	Uncoupled carbohydrate–lipid metabolism Reduced glycolytic activity	Starch over-accumulation in seeds and decreased levels of lipids. Delayed embryo elongation. *pkp2-1* and *pkp2-2* lines produced wrinkled seeds (more severe in the double *pkp2-1/pkp2-2*	Baud et al. (2009), Lonien and Schwender (2009), Mentzen et al. (2008), Baud et al. (2008) and Andre et al. (2007)

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Table 2 (continued)

Type of protein encoded	Mutant	Gene	Locus	Function	Phenotype	References
	Beta-amylase 1 (bam1), beta-amylase 2 (bam2), beta-amylase 3 (bam3), beta-amylase 4 (bam4)	*BAM1, BAM2, BAM3, BAM4*	AT3G23920, AT3G49670, AT4G17090, AT5G55700	(*bam1*) Chloroplast beta-amylase activity (*bam2*) Beta-amylase activity (*bam3*) Plastidial beta-amylase activity (*bam4*) Beta-amylase activity	(*bam1* and *bam3*)No starch accumulation in seed at maturity (*bam2* and *bam4*) Starch excess and reduced lipid content in mature seeds	Andriotis et al. (2010) and Fulton et al. (2008)
	Starch-excess 4 (sex4)	*SEX4*	AT3G52180	Glucan phosphate phosphatase activity	Starch excess in mature seeds	Andriotis et al. (2010)
	Phosphoglucose isomerase 1 (pgi1)	*PGI1*	AT4G24620	Plastidic phosphoglucose isomerase activity	Reduced seed weight. Reduced starch accumulation in seed	Bahaji et al. (2011), Bahaji et al. (2018) and Hedhly et al. (2016)
	Propyzamide-hypersensitive 1 (phs1-1)	*PHS1-1*	AT5G23720	Glucan phosphorylase activity	No starch accumulation in seed at maturity	Zeeman et al. (2004)
	Cytosolic phosphoglucose isomerase (cpgi)	*CPGI*	AT5G42740	Cytosolic phosphoglucose isomerase activity	Reduced seed number. High rates of seed abortion	(Kunz et al. (2014)
	ADP-glucose pyrophosphorylase 1 (adg1)	*ADG1*	AT5G48300	ADP-glucose pyrophosphorylase catalytic activity	Starch deficiency. Marked reduction in maltose accumulation.	Andriotis et al. (2010)
	Sucrose synthase 2 (sus2), sucrose synthase 3 (sus3)	*SUSY2, SUSY3*	AT5G49190, AT4G02280	Sucrose synthase activity during early seed maturation phase Sucrose synthase activity during late seed maturation phase	Altered timing of carbon partitioning in seeds. Reduced concentrations of starch in embryo and seed coat. Altered timing of seed development Increased lipid concentration during seed development	Angeles-Núñez and Tiessen (2010, 2012)
	Phosphoglucomutase (pgm1)	*PGM1*	AT5G51820	Plastidic phosphoglucomutase activity	Reduced number and size of seed. Increased seed density and reduced lipid concentration. Increased starch concentration in seed	Andriotis et al. (2012) and Periappuram et al. (2000)
Transporters	*Sucrose-proton symporter 5 (suc5)*	*SUC5*	AT1G71890	Sucrose transporter activity	Reduced dry weight, slight delay in embryo development. Reduced fatty acid accumulation in seed	Baud et al. (2005)

Table 2 (continued)

Type of protein encoded	Mutant	Gene	Locus	Function	Phenotype	References
	Erd6-like 6 (erdl6)	*ERDL6*	AT1G75220	Vacuolar glucose transporter activity	Altered seed storage nutrient composition. Increased seed concentrations of glucose, lipids and protein. Increase in the total seed yield per plant	Poschet et al. (2011)
	Growing plus-end tracking 1 propyzamide	*GPT1*	AT2G37070	Glucose-6-phosphate transporter activity in reproductive tissues	Embryo lethal. No starch accumulation in seed	Hedhly et al. (2016)
	Sweet 11 (sweet11), sweet 12 (sweet12), sweet 15 (sweet15)	*SWEET 11, SWEET 12, SWEET 15*	AT3G48740, AT5G23660, AT5G13170	Sucrose efflux transporter activity	In the *sweet11/sweet12/sweet15* triple mutant: retarded embryo development, reduced seed weight, reduced starch and lipid content, "wrinkled" seed phenotype, increased starch accumulation in the seed coat and reduced starch accumulation in the embryo	Chen et al. (2015), Griffiths et al. (2016) and Durand et al. (2017)
	Maltose excess 1 (mex1-1)	*MEX1-1*	AT5G17520	Maltose transporter activity	No starch accumulation in seeds	Griffiths et al. (2016), Niittylä et al. (2004) and Reidel et al. (2008)
Transcription factors	*Leafy cotyledon 2 (lec2)*	*LEC2*	AT1G28300	Transcription factor with a B3 domain, that plays a critical role both in early and late embryo developmental stages	Bigger seed coat and smaller embryos	Angeles-Núñez and Tiessen (2011, 2012) and Baud et al. (2007)
	Miniseed 3 (mini3)	*MINI3*	AT1G55600	Transcription factor with WRKY domain	Reduced seed size. Altered seed storage nutrient composition. Reduced concentrations of lipids, proteins and starch. Reduced concentration of glucose	Fatihi et al. (2013), Luo et al. (2005), Meng et al. (2017) and Wang et al. (2010a, b)

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Table 2 (continued)

Type of protein encoded	Mutant	Gene	Locus	Function	Phenotype	References
	Pheres 1 (phe1)	*PHE1*	AT1G65330	Type I MADS-box transcription factor	Reduced seed size. Altered seed storage nutrients composition. Reduced concentrations of lipids, proteins and starch. Increased concentrations of sucrose in late seed development	Fatihi et al. (2013)
	Wrinkled 1 (wri1)	*WRI1*	AT3G54320	Transcription factor of the AP2/ERWEBP class	Starch over-accumulation in seeds and decreased levels of lipids. Delayed embryo elongation. "Wrinkled" seed phenotype	Adhikari et al. (2016), An et al. (2017) and Ma et al. (2016); Ruuska and Girke (2002) and Baud et al. (2007)
	Apetala 2 (ap2)	*AP2*	AT4G36920	Floral member of the AP2/EREBP class of transcription factors, involved in the floral organ identity, establishment of floral meristem identity, suppression of floral meristem indeterminacy and ovule and seed coat development	Bigger seeds. Increased levels of carbohydrate accumulation	Jofuku et al. (2005)
	Transparent testa glabra 1 (ttg1)	*TTG1*	AT5G24520	Transcription factor with gene regulatory activity in accumulation of anthocyanidin and derivatives, seed coat pigmentation and seed coat differentiation, including mucilage production	Increased dry weight of seed. Higher starch accumulation in the embryo at 6 DAP. Higher accumulation of protein and fatty acid	Chen et al. (2015)

Genes are grouped according to the type of protein that they encode (enzymes, transporters and transcription factors), and among these groups, genes are ordered alphanumerically by their locus code

Table 3 List of carbohydrate metabolism-related genes characterized in maize

Type of protein encoded	Name	Gene	Locus	Function	Phenotype	References
Enzymes	*Brittle endosperm 2 (bt2)*	*BT2*	GRMZM2G068506	ADP-glucose pyrophosphorylase	Brittle endosperm. Reduced starch content in endosperm	Hannah et al. (2001) and Xie et al. (2017) and Huang et al. (2014)
	Isoamylase 2 (isa2)	*ISA2*	GRMZM2G090905	Isoamylase activity. Starch-debranching enzyme invlolved in amylopectin biosynthesis in endosperm	*dull1/isa2* homozygous double mutants are starch deficient and accumulate phytoglycogen ("sugary" mutant phenotype)	Lin et al. (2012)
	Miniature seed 1 (mnl)	*MN1*	GRMZM2G119689	Cell wall invertase	Miniature seed phenotype, marked by a loss of > 70% of seed weight at maturity	Cheng et al. (1996) and Liu et al. (2017)
	Sugary 1(su1)	*SU1*	GRMZM2G138060	Isoamylase activity. Starch-debranching enzyme	"Sugary" mutant phenotype. Wrinkled and translucent endosperm when dry. Phytoglycogen accumulation. No starch accumulation. Increased sucrose concentration; decreased concentration of amylopectin	Dinges et al. (2001) and Lin et al. (2012)
	Starch synthase dull 1 (dull1)	*DULL1*	GRMZM2G141399	Glycogen synthase activity. Starch binding	*dull1/isa2* homozygous double mutants are starch deficient and accumulate phytoglycogen ("sugary" mutant phenotype)	Lin et al. (2012)
	Sucrose synthase 1 (susy1), sucrose synthase 2 (Sh1)	*SUSY1, SH1*	GRMZM2G152908 GRMZM2G089713	Involved in sucrose metabolism Sucrose-cleaving enzyme	Endosperm-specific shrunken seed phenotype. Reduced fatty acid accumulation	Li et al. (2013) and Chourey et al. (1998)
	Shrunken 2 (sh2)	*SH2*	GRMZM2G429899	ADP-glucose pyrophosphorylase	Shrunken endosperm. Increased accumulation of hexose and sucrose in seeds. Reduced starch content in the endosperm	Boehlein et al. (2015), Huang et al. (2014) and Xie et al. (2017)
Transporter	*Brittle endosperm 1 (bt1)*	*BT1*	GRMZM2G144081	ADP-glucose transporter	Reduced starch content in seed	Kirchberger et al. (2007) and Xiao et al. (2017)

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Table 3 (continued)

Type of protein encoded	Name	Gene	Locus	Function	Phenotype	References
Transcription factors	*Leafy cotyledon 1 (lec1)*	*LEC1*	GRMZM2G011789	Transcription factor that plays a critical role both in early and late embryo developmental stages	Expression of *ZmLEC1* complements *atlec1* mutant in *Arabidopsis*. Constitutive expression of *ZmLEC1* during early seed development increased oil accumulation both in embryo and endosperm. Reduced seed germination	Shen et al. (2010)
	Wrinkled 1 a (wri1a), wrinkled 1 b (wri1b)	*WRI1A*, *WRI1B*	GRMZM2G124524 GRMZM2G174834	Transcription factors involved in glycolysis, fatty acid and TAG-related biosynthetic pathways	Expression of both *ZmWri1a and Zmwri1b* complement the *awri* mutant in *Arabidopsis*. Overexpression of *WRI1A* enhances accumulation of fatty acids, organic acids and amino acids in maize seed	Pouvreau et al. (2011) and Shen et al. (2010)

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clear metabolic switch from high hexose/sucrose ratios at 5 and 11 DAP to very low ratios at 14 DAP (Baud et al. 2002). Sugar metabolism and transport are highly compartmentalized in seeds; therefore, small differences in hexose/sucrose ratio can have dramatic effects on seed development and storage metabolism (Morley-Smith et al. 2008). An altered hexose/sucrose ratio in *SuSy* mutants was shown to modify carbon partitioning and maturation of *Arabidopsis* seeds (Angeles-Núñez and Tiessen 2010). The *LEC2* transcription factor mutant displayed a low hexose/sucrose ratio due to an alteration in *SuSy* expression that induced alterations in storage compound accumulation in developing seeds (including altered oil, proteins and starch contents). The *SuSy* and *LEC2* putative regulatory elements have been well described (Angeles-Núñez and Tiessen 2012). Mutation of *LEC2* also dramatically affected the delivery of photosynthates from the seed coat to the embryo (sink strength). This led to the formation of smaller seeds with altered seed weight ratios (more seed coat and less embryo weight).

It is widely accepted that SuSy catalyzes the synthesis of the main carbon source that enters cellular metabolism in seeds, controlling the channeling of incoming sucrose into starch and cell wall polysaccharides (Fallahi et al. 2008; Chourey et al. 2012; Li et al. 2013; Doughty et al. 2014) (Fig. 1). There are several lines of evidence that point out the importance of SuSy in sink organs of crop plants, where reduction in SuSy activity has been shown to reduce the availability of carbon for synthesis of storage products and growth. This is the case for the *rugosus4* (*rug4*) mutation of pea (Craig et al. 1999) and the *shrunken1* (*sh1*) and *sucrose synthase1* (*sus1*) mutations of maize (Chourey et al. 2012), where the disruption of highly expressed seed-specific *SuSy* isoforms resulted in marked seed phenotypes, along with reduced seed *SuSy* activity and reduced starch accumulation. In a similar way, mutation of genes encoding proteins with different kinds of sucrose-phosphate synthase activity, like *sp3, sp4* and *tps1* in *Arabidopsis*, or *sps1* and *sps11* in rice, result in abnormal, or often arrested seed development (Hashida et al. 2016; Solís-Guzmán et al. 2017). Free hexoses, fructose and glucose, can be phosphorylated by hexokinases (EC 2.7.1.1) and fructokinase (FRK; EC 2.7.1.4), channeling carbon flow to fatty acid synthesis and therefore oil accumulation (Stein et al. 2017) (Fig. 1). Mutations of Arabidopsis FRKs, like *frk6* or *frk7*, or of a transcriptional regulator of that pathway *WRINKLED1* (*wri1*) result in small seeds with altered lipid concentrations (Baud et al. 2009; Stein et al. 2017). Pyruvate kinase (PK, EC 2.7.1.40), which controls the final step of glycolysis and catalyzes the transfer of a phosphate group from phosphoenolpyruvate (PEP) to adenosine diphosphate (ADP), yielding pyruvate and ATP (Fig. 1). Furthermore, mutations affecting plastidic pyruvate kinase (PKP) displayed reduced oil accumulation and produced a wrinkled seed phenotype (Baud et al. 2009).

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Table 4 List of carbohydrate metabolism-related genes characterized in rice

Type of protein encoded	Mutant	Gene	Locus	Function	Phenotype	References
Enzymes	*Plastidial phosphorylase 1 (pho1)*	*PHO1*	Os01g0110100	Plastid alpha-glucan phosphorylase activity	Shrunken seeds. Reduced starch content in seed. Small starch granule accumulation and modified amylopectin structure. Altered seed composition	Satoh et al. (2008)
	Substandard starch grain 4 (ssg4)	*SSG4*	Os01g0179400	Involved in plastid starch metabolism	Enlarged starch granules in the endosperm. Reduced number of starch granules. Seeds with chalky interior. Reduced seed size. Increased concentration of sucrose and D-glucose. Reduced concentration of D-fructose	Matsushima et al. (2014)
	Sucrose-phosphate synthase 1 (sps1), sucrose-phosphate synthase 11 (sps11)	*SPS1, SPS11*	Os01g0919400, Os11g0236100	Involved in sucrose synthesis from UDP-glucose and fructose-6-phosphate	Sterility in *ossps1* single mutant and in *ossps1/ossps11* double mutant	Hashida et al. (2016)
	Floury endosperm 6	*FLO6*	Os03g0686900	Involved in compound starch granule formation and starch synthesis in endosperm	Slow grain filling rate. Decreased starch content in endosperm. Defective starch granule formation in endosperm cells. Loosely packed starch granules. Small and floury white endosperm	Peng et al. (2014)
	Branching enzyme like (bel1)	*BEL1*	Os06g0108900	Starch-branching enzyme activity. Involved in starch synthesis	Reduced seed size. Altered profile of starch chain length distribution	Satoh (2003)
	Granule-bound starch synthase 1 (waxy)	*WAXY*	Os06g0133000	Amylase synthesis activity	Seeds with snow-white endosperm. Little or no amylose accumulation in seed	Matsushima et al. (2014) and Shahid et al. (2016)
	Soluble starch synthase 1 (ss1) Soluble starch synthase 3-1 (ss3a-1)	*SS1, SS3A-1*	Os06g0160700, Os04g0624600	Glycogen synthase activity, starch binding, starch synthase activity. Involved in the pathway of starch biosynthesis	Seeds with chalky interior. Seed weight and starch content slightly reduced. Round and loosely packed amyloplasts. Reduced size of starch granules in endosperm. Reduced levels of amylopectin and increased levels of amylose	Fujita et al. (2007, 2011)

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Table 4 (continued)

Type of protein encoded	Mutant	Gene	Locus	Function	Phenotype	References
	ADP-glucose phosphorylase small subunit (agps2), ADP-glucose phosphorylase large subunit 2 (agpl2)	*AGPS2, AGPL2*	Os08g0345800, Os01g0633100	Involved in starch synthesis	Shrunken endosperm, poorly developed. Decreased starch level, starch granules smaller. Increased sucrose, glucose and fructose accumulation. Reduced seed size and shape, slightly elongated	Lee et al. (2007), Tang et al. (2016) and Wei et al. (2017)
	Isoamylase 1	*ISA1*	Os08g0520900	Alpha-amylase activity Little amylopectin, increased alpha-glucan	Sugary endosperm, abnormal seed size and shape. Little amylopectin and increased alpha-glucan content in seed	Streb and Zeeman (2014) and Satoh (2003)
	Brittle 1-3 (bt1)	*BT1-3*	Os06g0602700	ADPG transporter activity	Defective endosperm appearance. Reduced grain weight. Reduced starch and amylose content in seed. Altered physicochemical properties of starch in seed	Li et al. (2017a, b)
Transporter	*Nuclear factor y (nf-yb1)*	*NF-YB1*	Os02g0725900	Heteromeric transcription factor that plays an important role in embryogenesis, flowering time control and endosperm development among others	Reduced seed size (width and thickness) and weight. Decreased grain filling rate between 6 and 12 DAF. Increased chalkiness of seed and endosperm. Reduced amylose in endosperm. Altered physicochemical characteristics of starch contained by the seed	Xu et al. (2016)
	Silent information regulator 1 (srt1)	*SRT1*	Os04g0271000	NAD^+-dependent histone deacetylase	Low seed set, low starch content in seed and high chalky endosperm. Starch accumulation stopped at 3 DAPS in endosperm and pericarp cells. Arrested seed development. Reduced seed weight	Zhang et al. (2016)

Table 4 (continued)

Type of protein encoded	Mutant	Gene	Locus	Function	Phenotype	References
Transcription factors	*Rice starch regulator 1 (rsr1)*	*RSR1*	Os05g0121600	AP2/EREBP-type transcription factor that negatively regulates starch biosynthesis	Increased accumulation of starch. Increased seed size and weight. Seeds with white-colored chalky appearance. Altered physicochemical characteristics of starch contained by the seed	Fu and Xue (2010)

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Blocking endosperm cellularization also affects the amount of nutrients stored in the seed, which are fundamental for the subsequent growth of the embryo. Endosperm nuclear division precedes embryo cell proliferation. Consecutive endosperm and embryo cell division are controlled by regulatory mechanisms that involve sugar signaling (Wang and Ruan 2012, 2013; Bergareche et al. 2018). For instance, studies done in cotton seeds demonstrated that the asymmetric spatial expression of the cell wall invertase gene *GhCWIN1* in the embryo sac regulated the sequential development of endosperm and embryo by invertase-mediated sugar signaling. This may be achieved by establishment of a spatial gradient of glucose concentration (higher in the endosperm with respect to the embryo), thus favoring endosperm nuclear division over embryo cell proliferation during seed set (Wang and Ruan 2012). In addition, the metabolic switch from seed expansion to the storage phase is strongly affected by sugar signals. The transition from cell division and expansion to storage activities in seed is associated with a decrease in invertase activity and an increase in SuSy activity, resulting in an increased sucrose/glucose ratio. A correlation was observed between decreased glucose concentrations and reduced mitotic activity in legume embryos (Borisjuk et al. 1998), largely due to a decrease in *cw-Inv* gene expression (Weber 1995). Also, the highest expression levels of SuSy coincide with rapid starch filling in rice grains (Wang et al. 1999). Experiments done with labeled sucrose in oilseed rape seeds showed that the transport of sucrose from the integuments to the embryo occurs via the micropylar endosperm and that sucrose uptake via chalazal endosperm is involved in filling the central endosperm vacuole, the main storage pool for hexoses during seed development (Morley-Smith et al. 2008). In *Arabidopsis*, failure of endosperm cellularization in *fertilization independent seed 2* (*fis2*) mutant seeds correlated with impaired embryo development and increased hexose levels, suggesting that arrest of embryo development is a consequence of failed nutrient translocation to the developing embryo (Hehenberger et al. 2012). At early developmental stages, embryo formation strongly relies on nutrient provisioning via the endosperm. If the latter is not fully functional, the embryo will most probably starve and abort, as inferred by several studies in which impaired cellularization caused seed abortion (Scott et al. 1998; Hehenberger et al. 2012; Chen et al. 2015).

The floral patterning regulator *APETALA2 (AP2),* together with *AtSUC5*, is involved in the hydrolytic control of sucrose from seeds as described in *Arabidopsis* (Baud et al. 2005). The *ap2* mutant shows larger seeds compared to wild type (Jofuku et al. 2005). *Ap2* mutants displayed higher hexose levels than wild-type seeds between 5 and 13 DAP (Ohto et al. 2005). Apparently, AP2 can regulate cell wall invertase activity and hence the hexose/sucrose ratio, thus influencing sugar transfer from maternal tissues

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to the embryo and the endosperm. Sucrose hydrolysis is a fundamental component of plant performance (Cheng and Chourey 1999; Weichert et al. 2010; Faix et al. 2012). In this context, the "invertase control hypothesis" was proposed many years ago. The hypothesis, initially demonstrated in dicotyledons (Wobus and Weber 1999), was later also demonstrated in monocotyledonous plants. The mutation of maize cell wall invertase *INCW2* resulted in miniature kernels (*mn1* mutation) and development of a severely reduced endosperm (Cheng et al. 1996; Taliercio et al. 1999; Vilhar 2002; Fatihi et al. 2013). The observation that a soluble invertase expressed during early development of seed (*IVR2*) can affect yield under limited photosynthetic activity conditions suggests that soluble invertases also play a critical role in the supply of hexoses to support cell division during the pre-storage phase (Andersen 2002; Bihmidine et al. 2013; Wan et al. 2017).

Maternal tissues regulate photoassimilate import and sink strength of seeds

Seed filling depends primarily on photoassimilate supply and sink strength, but also depends on carbon partitioning and remobilization. The overall capacity of heterotrophic tissues to uptake photoassimilates depends on the ability of individual cells to import, metabolize and store sucrose. Although some seeds can undergo greening, embryo development relies on the supply of photoassimilates from maternal tissues. The discharge paths depend on the particular resistance of the seed sink and its developmental stage. In organs that can release sugar via the apoplast, there are two possible routes for subsequent absorption by storage cells: hydrolysis of sucrose by an apoplastic invertase and the subsequent release of glucose and fructose units, or direct import of sucrose by active transport at the plasma membrane. As detailed in Fig. 2, different apoplastic barriers exist between genetically distinct tissues such as maternal integuments and endosperm/embryo. Photoassimilates produced in mother tissues are delivered to the developing seed via the vascular system. This facilitates the coordination of physiological and developmental processes between the mother and its progeny (van Bel et al. 2013). The maternal symplasm represents the major route by which nutrients reach the seed (Radchuk and Borisjuk 2014). The vasculature does not extend beyond the seed coat (McDonald et al. 1995; Etchells et al. 2012); thus, both embryo and endosperm are apoplastically isolated from the maternal tissues. Numerous pathways for nutrient flow are available and depend on the structure of the seed in each species (reviewed in Radchuk and Borisjuk 2014). The import of sucrose occurs via the apoplast of tissues that surround the embryo (Weber et al. 2005). In legume cotyledons and barley endosperm, sucrose accumulation increases during maturation, and this marks the switch from maternal control to filial control of seed growth (Weber et al. 2005). In legume seeds, feeding with sucrose alters the meristematic state, induces cell expansion and endopolyploidization (Weber et al. 1996; Rolletschek 2005) and promotes cotyledon storage activity at the transcript level (Ambrose et al. 1987; Dante et al. 2014). In maize kernels, the vascular bundle finishes directly at the placenta–chalazal region. In *Arabidopsis*, the sucrose pool which arrives in the seed coat via the funicular phloem enters the outer integument of the seed coat through plasmodesmatal connections. Nutrients must be transported from the outer to the inner integuments successively, since the outer integument and the inner integument constitute independent symplasms and consequently transferred to the endosperm and embryo (each one constituting an independent symplasm) (Stadler 2005; Ingram 2010). In common bean, fava bean and pea, seed coat parenchyma is the major site for the uptake of sucrose released from the maternal tissues to the seed apoplasm (Wang et al. 1995). In grain crops, like wheat and barley, sucrose is unloaded via the nucellar projection and it is redistributed toward the endosperm, enabling control of seed growth by maternal tissues (Wang and Fisher 1994; Thiel et al. 2008; Melkus et al. 2011; Bihmidine et al. 2016; Brandt et al. 2018). In cereal grains, the pericarp, a maternal tissue that surrounds the embryo and endosperm, plays a critical role controlling the flow of nutrients during seed development (including sucrose unloading, starch biosynthesis and carbon remobilization) (for a complete review, see Rolletschek et al. (2015). A defective nucellar projection compromises nutrient flow into the endosperm, with a concomitant reduction in final grain size (Radchuk 2006; Melkus et al. 2011; Yin and Xue 2012; Andriotis et al. 2012; Pirone et al. 2017).

It has been shown that several sucrose transporters can participate in the provision of nutrients to the embryo (Fig. 2). The way in which sucrose is released from maternal tissues (the seed coat) for supporting development of filial tissues (the embryo) is not well understood, except for the contribution of a subset of transporters. Evidence from studies in pea (*Pisum sativum*) and bean (*Phaseolus vulgaris*) seeds implicated SUF transporters (SUcrose/H^+ cotransporter family) in sucrose efflux from the seed coat (Ritchie et al. 2003; Zhou et al. 2007). Three sucrose transporter genes expressed in the developing grain of wheat have been identified (Aoki et al. 2002). The role of specific sucrose transporters in *Arabidopsis* seeds was demonstrated during later developmental stages, revealing the orchestrated action of three specific sucrose transporters (*SWEET11, 12* and *15*) for efflux of sucrose from the integument into the apoplasm, as well as from the endosperm to support growth and development of the embryo (Chen et al. 2015). *SUC5* may be responsible for uptake of sucrose into the endosperm

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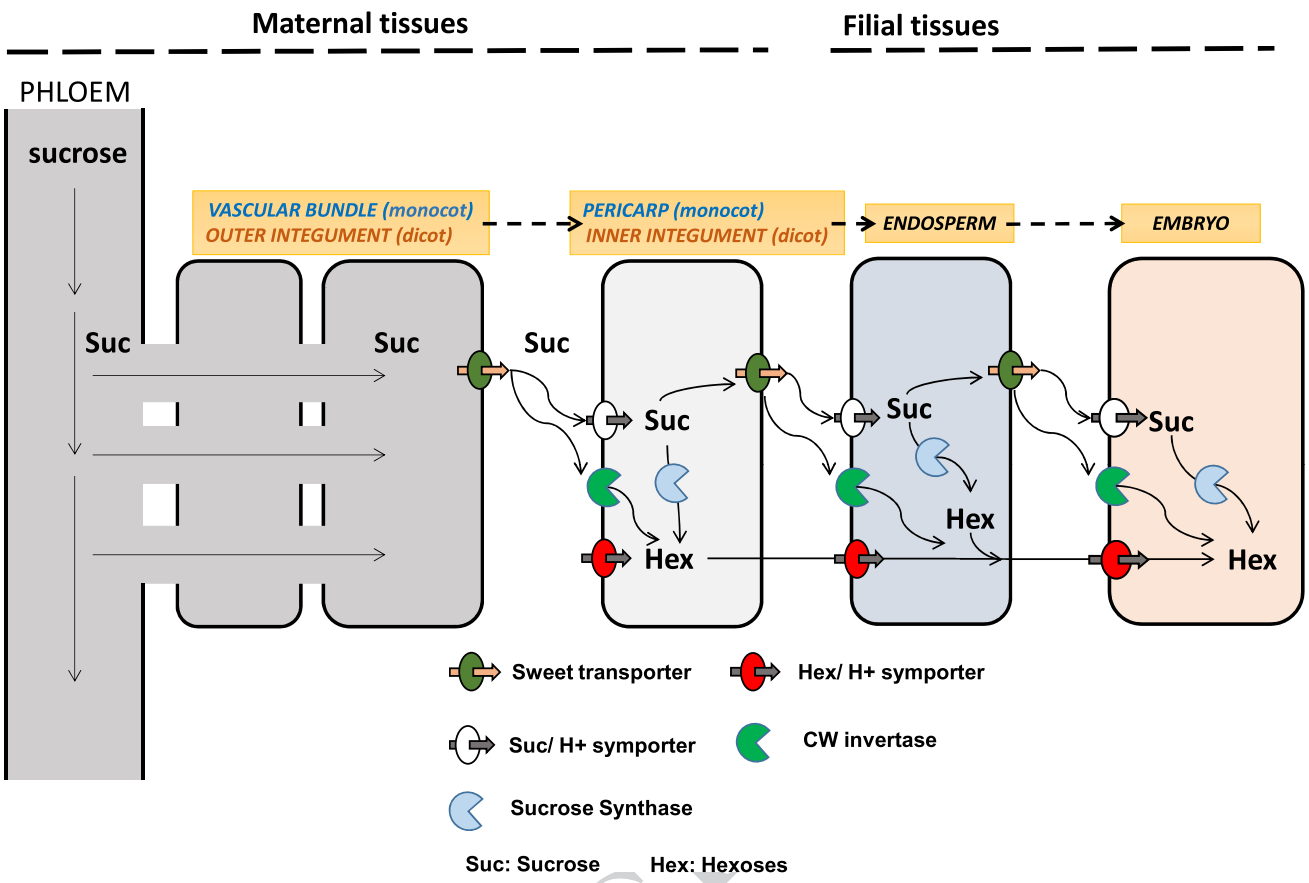

Fig. 2 Sucrose unloading and multistep sequential apoplastic transport during early stages of seed development. Sucrose arrives to the seed through the phloem and enters the vascular bundles/outer integuments via plasmodesmatal connections. In *Arabidopsis*, the outer integument functions as a symplastic extension of the funicular phloem and plays a similar role to the vascular compartments in grains and cereal legumes: distribution and import of photoassimilates into filial tissues (Stadler 2005; Kunieda et al. 2013). Several studies suggest the absence of symplastic connections between seed coat, endosperm and embryo. These tissues are separated by three apoplastic borders: (1) between the vascular bundles/outer integuments and inner integuments/pericarp, (2) between the inner integuments/pericarp and the endosperm and (3) between the endosperm and the embryo (Stadler 2005; Kunieda et al. 2013; Creff et al. 2015; Turbant et al. 2016). The bypass of these borders inevitably requires the existence of a sucrose carrier-mediated transport (SWEET transporter) acting at each interface (Chen et al. 2015b; Griffiths et al. 2016; Durand et al. 2017). The SUC transporters (SUTs) may be responsible for sucrose loading from the apoplasm and are essential for sucrose translocation into each symplastic area (Lalonde et al. 2004; Baud et al. 2005; Zhou et al. 2007; Pommerrenig et al. 2013; Ruan et al. 2008). At the inner integument, sucrose can be either transported toward the filial tissues via the apoplast (through SUTs) or metabolized by cell wall invertases (CWinv) or sucrose synthase (SuSy), with the resulting monosaccharides translocated by hexose transporters. Sucrose can be cleaved by *SuSy* in the cellularizing endosperm, and the resulting UDPG can be used to meet cell wall biosynthesis demands (Ruan et al. 2008). Sucrose and hexose transporters play a major role in delivering sugars to the embryo, and some sucrose can be transported to the globular embryo and processed by CWinv to provide the hexose needed for cell division (Wang and Ruan 2012). Nevertheless, hexose import may dominate over sucrose import during the early stages of seed development

from the apoplasm between the seed coat and the endosperm in *Arabidopsis* (Baud et al. 2005). The impact in *Arabidopsis* seed development was similar in the *suc5* single mutant and the *sweet11, 12, 15* triple mutant; both mutants manifested severe seed defects, including delayed embryo development, reduced seed weight, and reduced starch and lipid content, with a clear "wrinkled" seed phenotype (Chen et al. 2015; Griffiths et al. 2015).

Starch biosynthesis and breakdown pathways in seeds

A detailed examination of starch biosynthetic pathways is beyond the scope of this review. However, as starch is a major seed component, the most relevant events of this pathway are discussed in this section. The starch synthesis pathways in photosynthetic organs like leaves and in heterotrophic sink organs like seed endosperm have been described

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elsewhere (Nakamura 2002; Lee et al. 2007; Bahaji et al. 2015; Boyer et al. 2016; Pfister and Zeeman 2016; Nakamura et al. 2017; Wang et al. 2017a, b). Studies of mutants identified in many plant species have revealed that the key control steps of the starch synthesis pathway are mediated by ADP-glucose pyrophosphorylase (AGP, EC 2.7.7.27). AGP catalyzes the formation of ADP-glucose (ADPG) and inorganic pyrophosphate (PPi) from glucose-1-phosphate (Glc-1-P) and ATP. The resulting ADPG molecule serves as the glucosyl donor for starch synthesis by action of starch synthases (ADPG:(1,4)-α-D-glucan 4-α-D-glucosyltransferase, SS, EC 2.4.1.21 and 2.4.1.242) followed by combined action of starch-branching enzyme (SBE, EC 2.4.1.18) and starch-debranching enzyme (DBE; EC 3.2.1.68 for isoamylase type and EC 3.2.1.41 for pullulanase type).

Mutants impaired for AGP activity in rice and maize display a severe inhibition of starch synthesis and a significant increase in sucrose, glucose and fructose accumulation, concomitant with the development of a shrunken endosperm and an overall reduced seed size (Hannah et al. 2001; Lee et al. 2007; Huang et al. 2014; Tang et al. 2016; Wei et al. 2017). As the substrate for starch synthesis, ADPG must be transported into amyloplasts from the cytosol by an ADPG transporter located in the envelope membrane of amyloplasts. Sullivan (1991) first proposed BT1 proteins as ADPG transporters in cereal endosperms. Cereal endosperms express the plastidial ADPG carrier brittle-1 (BT1) which can transport ADPG from the cytosol into plastids (Shannon et al. 1998; Kirchberger et al. 2007). Transport studies have shown that maize ZmBT1, barley HvNST1 and wheat TaBT1 are able to transport ADPG in counter-exchange with ADP (Patron 2004; Bowsher et al. 2007; Kirchberger et al. 2007). Mutation of the rice ADPG transporter ortholog *OsBT1* induced dramatic defects in endosperm appearance and reduced grain weight (Li et al. 2017a, b). Starch synthases (SS) then transfer glucose units from ADP-glucose to the non-reducing end of an α-glucan backbone, thus elongating amylose and amylopectin molecules. SS mutants in cereals, like dull1 in maize, as well as waxy, ss1 and ss3a-1 in rice result in reduced seed weight and altered seed composition (Fujita et al. 2011; Lin et al. 2012; Shahid et al. 2016). SBEs generate α-1,6-branch linkages in α-glucans through cleavage of α-1,4 bonds. The total amylose content in cereal endosperm has been increased by the enhancement of granule-bound starch synthase I (GBSSI) expression or by eliminating SBEs, SSIIa or other enzymes involved in amylopectin synthesis (Itoh et al. 2003; Umemoto et al. 2004; Crofts et al. 2012; Zhou et al. 2016; Wang et al. 2017a). The "wrinkled" seed mutant (*rr*) of pea (*Pisum sativum* L.), the object of Mendel's studies, appeared by mutation of the gene encoding SBE1 by insertion of a transposon-like element into the coding sequence (Mendel 1865; Bhattacharyya et al. 1993). Finally, there is evidence that the disproportionating enzyme (4-α-glucanotransferase, DPE) and α-glucan phosphorylase are involved in the pathway of starch biosynthesis by affecting α-glucan phosphorylase activity (Colleoni et al. 1999; Dauvillée et al. 2006). Mutations affecting phosphorylase activity, like *dpe2* and *phs1-1* in *Arabidopsis* and *pho1* in rice, cause disruptions in the starch content of seed, which in the case of rice results in smaller seeds (Zeeman 2004; Chia et al. 2005; Satoh et al. 2008).

In recent years, there have been major advances in our understanding of starch breakdown in heterotrophic seed tissues (Wu et al. 2014; Tetlow and Emes 2017). The initial event, required for subsequent starch degradation, is the phosphorylation of amylopectin by glucan water dikinase enzymes (α-glucan, water dikinase, GWD, EC 2.7.9.4). Arabidopsis knockout mutants lacking GWD exhibited a starch-excess phenotype in seeds and delayed embryo development (Andriotis et al. 2010; Pirone et al. 2017). In rice, mutation of the plastidial α-glucan phosphorylase gene affected the synthesis and structure of starch in the endosperm, accompanied by a shrunken phenotype that appears when grown in cold conditions (Satoh et al. 2008).

Once phosphorylated, α-amylases catalyze formation of soluble starch (Wu et al. 2014). Plant α-amylases (EC 3.2.1.1), the most abundant amylolytic enzyme in the endosperm, hydrolyze α-(1,4)-glucosidic linkages in glucan polymers to release both linear and branched glucans. This facilitates the attack of the granule by other enzymes and releases soluble glucan fragments to serve as substrates for other enzymes. Mutation of the α-amylase in maize induced glassy, shrunken and translucent kernel phenotypes (James et al. 2015). Similar effects were also seen in rice mutants affecting α-amylase (Satoh 2003). The complete degradation of soluble starches proceeds with the concerted action of DBE enzymes, which catalyze the hydrolysis of α-(1,6)-glucosidic linkages of polyglucans.

The grains of the debranching enzyme mutant Bell-a in rice displayed an altered fine structure of amylopectin that is associated with size and weight reduction when compared to wild-type grains (Satoh 2003). Linearized glucans are exposed to (1) β-amylases, which catalyze the hydrolysis of α-(1,6) glucosidic linkages of polyglucans liberating the disaccharide maltose, or to (3) α-glucosidases (EC 3.2.1.20), which catalyze the release of α-D-glucose from the non-reduced ends of α-linked glucans. The resulting maltose and glucose units are then exported to the cytosol via maltose transporter (MEX1) and glucose transporters. The glucose produced in the endosperm can be taken up and converted to sucrose in the scutellum and redistributed to growing tissues such as young shoot and root tissues (Griffiths et al. 2016; Niittylä et al. 2004; Reidel et al. 2008).

Viable seed formation requires the tightly coordinated activity of many proteins involved in carbohydrate metabolism. This statement is supported by the characterization of

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a wide variety of mutants affecting carbohydrate metabolism that display defective seed phenotypes, most of which (both mutants and phenotypes) have been discussed in this review and are included in Tables 2, 3 and 4. Several transcription factors presented in the tables have not yet been directly linked to metabolic regulation, like *MINI3*, *PHE1* and *TTG1* in *Arabidopsis*, *LEC1*, *WRI1A* and *WRI1B* in maize and *NF-YB1* and *RSR1* in rice, but can affect seed development at different levels: seed size, weight, color, morphology and seed composition (Shen et al. 2010; Fu and Xue 2010; Pouvreau et al. 2011; Fatihi et al. 2013; Orozco-Arroyo et al. 2015; Chen et al. 2015a; Xu et al. 2016; Meng et al. 2016). Further research should assess to what extent these phenotypes are linked to alterations in carbohydrate metabolism.

Future perspectives

The identification of quantitative trait loci that determine seed carbohydrate contents, along with genetic engineering to overexpress or repress genes involved in carbon flow toward seed starch, oils or proteins have led to significant increases in storage compounds in several species (Weselake et al. 2009; Kurai et al. 2011; Li et al. 2013; Paul et al. 2017). A better understanding of sucrose delivery and starch biosynthesis pathways in seeds requires additional research in each specific crop at the biochemical, developmental and molecular levels, which allows plant breeders and biotechnologists to increase seed carbohydrates in a predictable way. Overall, the data discussed here suggest that breeders should give more attention to the role that metabolites play at critical points of the developmental program. A central unanswered question is the identification of nutrient sensing mechanisms and signal transduction pathways that connect carbohydrate status with seed inter-compartmental crosstalk. Carbohydrate and nitrogen metabolisms are highly interconnected, and the identification of branch points will help to clarify what determines assimilate partitioning between starch, proteins and oils. Manipulation of carbon and nitrogen partitioning constitutes a potential tool for agricultural improvements, but pleiotropic seed developmental defects can limit the applicability of this strategy.

Studies of transporter function are of particular interest from the perspective of applied science. Overexpression of the barley sucrose transporter *HvSUT1* in endosperm increased storage protein content (20%) and nitrogen assimilation (up to 14%) (Weichert et al. 2010). Similarly, expression of the amino acid transporter gene (*VfAAP1)* in pea seeds leads to increased seed biomass (therefore more carbon) (Weigelt et al. 2008). In addition, overexpression of sucrose transporters in *Arabidopsis* companion cells impacted phosphate requirements (Dasgupta et al. 2014). These studies point to the complex cross talk between carbon, nitrogen and phosphate metabolism in specific seed compartments. Synergistic effects and possible developmental defects in seed formation should not be overlooked in breeding programs attempting to modify the storage status of crop plants.

Maternal tissues such as the seed coat (dicots) and pericarp (monocots) serve a number of functions, most of which evolved to protect the seed and to promote the development of embryo and endosperm. The architecture, chemical composition and metabolism of these tissues work together to respond to developmental programs. Sucrose passing from the mother plant to the developing endosperm and embryo are distributed by the seed coat and pericarp, which represent a critical bottleneck ensuring proper nutritional distribution among all progeny during seed development and seed filling. Future studies should take into account the role of the these tissues when attempting to modulate seed development.

Current strategies to improve seed quality range from conventional breeding, marker-assisted breeding, quantitative trait loci (QTLs), mutagenesis, creation of hybrids, genetic modification (GM), new genome-editing technologies and chemical approaches. Metabolomics approaches allow the parallel assessment of the levels of a broad range of metabolites for both phenotypic and physiological characterization. These approaches allow breeders to modulate a quantitative trait and to reprogram the metabolome to produce valuable nutrients. For instance, recent work demonstrated the feasibility of creating high-amylose rice through CRISPR/Cas9-mediated targeted mutagenesis of a starch-branching enzyme (Sun et al. 2017).

Recently, methods allowing rapid, high-throughput genotyping of entire crop populations have emerged and opened the door to wider use of molecular tools in plant breeding. For instance, the importance of rice as a food crop has made it the focus of genome-scale efforts to identify factors controlling seed yield and composition. Massive sequencing efforts, including the 3000 Genomes Project, have enabled the creation of datasets and bioinformatic tools to analyze SNPs and to search for the presence or absence of genes across multiple representatives of *Oryza* species (Li et al. 2014). Using this resource, genome wide association (GWAS) and SNP marker approaches have sought to elucidate candidate genes that correspond to QTLs for important agronomic traits, including grain size and composition. Huang et al. (2012) undertook a GWAS incorporating 950 varieties and identified candidate genes for amylose content (thaumatin-like protein cluster on chromosome 12) and protein content (peptidase gene cluster on chromosome 70). Most effort has been aimed at increasing rice yield and seed size. Those results, combined with GWAS/SNP-based targets to improve quality (lower amylose and higher eating quality), may prove to be the future direction

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of marker-assisted breeding programs (Huang et al. 2012). The availability of seed to immediately apply these data to breeding programs is hoped to accelerate improvement of rice to meet the demands of a growing population and a changing climate. Hopefully, these tools will soon be available for the study of all major crop plants to accelerate seed improvement.

Acknowledgements We would like to thank the reviewer for their detailed comments and suggestions for the manuscript. We thank Prof. L. Colombo and Prof. J. Pozueta for scientific support. We also thank M. A. Garin for technical support.

Funding This work was partially supported by the Università degli Studi di Milano (UNIMI-RTD-A and Piano di sviluppo di ateneo - Biosciences dept. Linea 2-2017-2018 - CUP G43C17000590001 and Linea 2-2016-2017 - CUP G42F16001710005) and the H2020-MSCA-RISE Project (ExpoSeed GA-691109).

References

Adhikari ND, Bates PD, Browse J (2016) WRINKLED1 rescues feedback inhibition of fatty acid synthesis in hydroxylase-expressing seeds. Plant Physiol 171:179–191. https://doi.org/10.1104/pp.15.01906

Akande TO, Odunsi AA, Olabode OS, Ojediran TK (2012) Physical and nutrient characterisation of raw and processed castor (*Ricinus communis* L.) seeds in Nigeria department of animal nutrition and biotechnology, Department of Crop Production System. World J Agric Sci 8:89–95

Ambrose MJ, Wang TL, Cook SK, Hedley CL (1987) An analysis of seed development in *Pisum sativum*: IV. Cotyledon cell populations in vivo and in vitro. J Exp Bot 38:1909–1920. https://doi.org/10.1093/jxb/38.11.1909

An D, Kim H, Ju S et al (2017) Expression of camelina WRINKLED1 isoforms rescue the seed phenotype of the Arabidopsis wri1 mutant and increase the triacylglycerol content in tobacco leaves. Front Plant Sci 8:34. https://doi.org/10.3389/fpls.2017.00034

Andersen MN (2002) Soluble invertase expression is an early target of drought stress during the critical, abortion-sensitive phase of young ovary development in maize. Plant Physiol 130:591–604. https://doi.org/10.1104/pp.005637

Andre C, Froehlich JE, Moll MR, Benning C (2007) A heteromeric plastidic pyruvate kinase complex involved in seed oil biosynthesis in Arabidopsis. Plant Cell 19:2006–2022. https://doi.org/10.1105/tpc.106.048629

Andriotis VME, Pike MJ, Kular B et al (2010) Starch turnover in developing oilseed embryos. New Phytol 187:791–804. https://doi.org/10.1111/j.1469-8137.2010.03311.x

Andriotis VME, Pike MJ, Schwarz SL et al (2012) Altered starch turnover in the maternal plant has major effects on arabidopsis fruit growth and seed composition. Plant Physiol 160:1175–1186. https://doi.org/10.1104/pp.112.205062

Angeles-Núñez JG, Tiessen A (2010) Arabidopsis sucrose synthase 2 and 3 modulate metabolic homeostasis and direct carbon towards starch synthesis in developing seeds. Planta 232:701–718. https://doi.org/10.1007/s00425-010-1207-9

Angeles-Núñez JG, Tiessen A (2011) Mutation of the transcription factor LEAFY COTYLEDON 2 alters the chemical composition of Arabidopsis seeds, decreasing oil and protein content, while maintaining high levels of starch and sucrose in mature seeds. J Plant Physiol 168:1891–1900. https://doi.org/10.1016/j.jplph.2011.05.003

Angeles-Núñez JG, Tiessen A (2012) Regulation of AtSUS2 and AtSUS3 by glucose and the transcription factor LEC2 in different tissues and at different stages of Arabidopsis seed development. Plant Mol Biol 78:377–392. https://doi.org/10.1007/s11103-011-9871-0

Aoki N, Whitfeld P, Hoeren F et al (2002) Three sucrose transporter genes are expressed in the developing grain of hexaploid wheat. Plant Mol Biol 50:453–462. https://doi.org/10.1023/A:1019846832163

Auger B, Marnet N, Gautier V et al (2010) A detailed survey of seed coat flavonoids in developing seeds of *Brassica napus* L. J Agric Food Chem 58:6246–6256. https://doi.org/10.1021/jf903619v

Bahaji A, Baroja-Fernández E, Ricarte-Bermejo A et al (2015) Characterization of multiple SPS knockout mutants reveals redundant functions of the four *Arabidopsis sucrose* phosphate synthase isoforms in plant viability, and strongly indicates that enhanced respiration and accelerated starch turnover can alleviate the blockage of sucrose biosynthesis. Plant Sci 238:135–147. https://doi.org/10.1016/j.plantsci.2015.06.009

Bahaji A, Li J, Ovecka M et al (2011) *Arabidopsis thaliana* mutants lacking ADP-glucose pyrophosphorylase accumulate starch and wild-type ADP-glucose content: further evidence for the occurrence of important sources, other than ADP-glucose pyrophosphorylase, of ADP-glucose linked to leaf starch biosynthesis. Plant Cell Physiol 52:1162–1176. https://doi.org/10.1093/pcp/pcr067

Bala M, Nag TN, Kumar S et al (2011) Proximate composition and fatty acid profile of *Pongamia pinnata*, a potential biodiesel crop. J Am Oil Chem Soc 88:559–562. https://doi.org/10.1007/s11746-010-1699-2

Baroja-Fernández E, Muñoz FJ, Saikusa T et al (2003) Sucrose synthase catalyzes the de novo production of ADP-glucose linked to starch biosynthesis in heterotrophic tissues of plants. Plant Cell Physiol 44:500–509. https://doi.org/10.1093/pcp/pcg062

Barthet VJ, Daun JK (2011) Seed morphology, composition, and quality. In: Canola: chemistry, production, processing, and utilization. Elsevier, Amsterdam, pp 119–162

Baud S, Boutin JP, Miquel M et al (2002) An integrated overview of seed development in *Arabidopsis thaliana* ecotype WS. Plant Physiol Biochem 40:151–160. https://doi.org/10.1016/S0981-9428(01)01350-X

Baud S, Dubreucq B, Miquel M et al (2008) Storage reserve accumulation in arabidopsis: metabolic and developmental control of seed filling. Arab B 6:e0113. https://doi.org/10.1199/tab.0113

Baud S, Graham IA (2006) A spatiotemporal analysis of enzymatic activities associated with carbon metabolism in wild-type and mutant embryos of Arabidopsis using in situ histochemistry. Plant J 46:155–169. https://doi.org/10.1111/j.1365-313X.2006.02682.x

Baud S, Mendoza MS, To A et al (2007) WRINKLED1 specifies the regulatory action of LEAFY COTYLEDON2 towards fatty acid metabolism during seed maturation in Arabidopsis. Plant J 50:825–838. https://doi.org/10.1111/j.1365-313X.2007.03092.x

Baud S, Wuillème S, Lemoine R et al (2005) The AtSUC5 sucrose transporter specifically expressed in the endosperm is involved in early seed development in Arabidopsis. Plant J 43:824–836. https://doi.org/10.1111/j.1365-313X.2005.02496.x

Baud S, Wuillème S, To A et al (2009) Role of WRINKLED1 in the transcriptional regulation of glycolytic and fatty acid biosynthetic genes in Arabidopsis. Plant J 60:933–947. https://doi.org/10.1111/j.1365-313X.2009.04011.x

Beloshapka A, Buff P, Fahey G, Swanson K (2016) Compositional analysis of whole grains, processed grains, grain co-products,

and other carbohydrate sources with applicability to pet animal nutrition. Foods 5:23. https://doi.org/10.3390/foods5020023

Bentsink L, Koornneef M (2008) Seed dormancy and germination. Arab B 6:e0119. https://doi.org/10.1199/tab.0119

Bergareche D, Royo J, Muñiz LM, Hueros G (2018) Cell wall invertase activity regulates the expression of the transfer cell-specific transcription factor ZmMRP-1. Planta 247:429–442. https://doi.org/10.1007/s00425-017-2800-y

Berger F (2003) Endosperm: the crossroad of seed development. Curr Opin Plant Biol 6:42–50. https://doi.org/10.1016/S1369526602000043

Bewley JD, Bradford KJ, Hilhorst HWM, Nonogaki H (2013) Seeds: physiology of development, germination and dormancy, 3rd edn. Springer, New York

Bhattacharyya M, Martin C, Smith A (1993) The importance of starch biosynthesis in the wrinkled seed shape character of peas studied by Mendel. Plant Mol Biol 22:525–531. https://doi.org/10.1007/BF00015981

Bihmidine S, Hunter CT, Johns CE et al (2013) Regulation of assimilate import into sink organs: update on molecular drivers of sink strength. Front Plant Sci. https://doi.org/10.3389/fpls.2013.00177

Bihmidine S, Julius BT, Dweikat I, Braun DM (2016) Tonoplast sugar transporters (SbTSTs) putatively control sucrose accumulation in sweet sorghum stems. Plant Signal Behav 11:e1117721. https://doi.org/10.1080/15592324.2015.1117721

De Bodt S, Maere S, Van de Peer Y (2005) Genome duplication and the origin of angiosperms. Trends Ecol Evol 20(11):591–597. https://doi.org/10.1016/j.tree.2005.07.008

Boehlein SK, Shaw JR, Stewart JD et al (2015) Enhancing the heat stability and kinetic parameters of the maize endosperm ADP-glucose pyrophosphorylase using iterative saturation mutagenesis. Arch Biochem Biophys 568:28–37. https://doi.org/10.1016/J.ABB.2015.01.008

Borisjuk L, Walenta S, Weber H et al (1998) High-resolution histographical mapping of glucose concentrations in developing cotyledons of *Vicia faba* in relation to mitotic activity and storage processes: glucose as a possible developmental trigger. Plant J 15:583–591. https://doi.org/10.1046/j.1365-313X.1998.00214.x

Borisjuk L, Wang TL, Rolletschek H et al (2002) A pea seed mutant affected in the differentiation of the embryonic epidermis is impaired in embryo growth and seed maturation. Development 129:1595–1607

Bowsher CG, Scrase-Field EFAL, Esposito S et al (2007) Characterization of ADP-glucose transport across the cereal endosperm amyloplast envelope. J Exp Bot 58:1321–1332. https://doi.org/10.1093/jxb/erl297

Boyer L, Roussel X, Courseaux A et al (2016) Expression of *Escherichia coli* glycogen branching enzyme in an Arabidopsis mutant devoid of endogenous starch branching enzymes induces the synthesis of starch-like polyglucans. Plant, Cell Environ 39:1432–1447. https://doi.org/10.1111/pce.12702

Brandt R, Mascher M, Thiel J (2018) Laser capture microdissection-based RNA-Seq of barley grain tissues. Methods Protoc 1723:397–409. https://doi.org/10.1007/978-1-4939-7558-7_23

Chateigner-Boutin A-L, Ordaz-Ortiz JJ, Alvarado C et al (2016) Developing pericarp of maize: a model to study arabinoxylan synthesis and feruloylation. Front Plant Sci 7:1476. https://doi.org/10.3389/fpls.2016.01476

Chen G, Deng W, Peng F et al (2013) Brassica napus TT16 homologs with different genomic origins and expression levels encode proteins that regulate a broad range of endothelium-associated genes at the transcriptional level. Plant J 74:663–677. https://doi.org/10.1111/tpj.12151

Chen H-Y, Huh J-H, Yu Y-C et al (2015a) The Arabidopsis vacuolar sugar transporter SWEET2 limits carbon sequestration from roots and restricts Pythium infection. Plant J 83:1046–1058. https://doi.org/10.1111/tpj.12948

Chen L-Q, Lin IW, Qu X-Q et al (2015b) A cascade of sequentially expressed sucrose transporters in the seed coat and endosperm provides nutrition for the arabidopsis embryo. Plant Cell 27:607–619. https://doi.org/10.1105/tpc.114.134585

Cheng W, Taliercio E, Chourey P (1996) The miniature1 seed locus of maize encodes a cell wall invertase required for normal development of endosperm and maternal cells in the pedicel. Plant Cell 8:971–983. https://doi.org/10.1105/tpc.8.6.971

Cheng WH, Chourey PS (1999) Genetic evidence that invertase-mediated release of hexoses is critical for appropriate carbon partitioning and normal seed development in maize. Theor Appl Genet 98:485–495. https://doi.org/10.1007/s001220051096

Chia TYP, Pike MJ, Rawsthorne S (2005) Storage oil breakdown during embryo development of *Brassica napus* (L.). J Exp Bot 56:1285–1296. https://doi.org/10.1093/jxb/eri129

Chourey PS, Li QB, Cevallos-Cevallos J (2012) Pleiotropy and its dissection through a metabolic gene Miniature1 (Mn1) that encodes a cell wall invertase in developing seeds of maize. Plant Sci 184:45–53. https://doi.org/10.1016/j.plantsci.2011.12.011

Chourey PS, Taliercio EW, Carlson SJ, Ruan YL (1998) Genetic evidence that the two isozymes of sucrose synthase present in developing maize endosperm are critical, one for cell wall integrity and the other for starch biosynthesis. Mol Gen Genet 259:88–96. https://doi.org/10.1007/s004380050792

Cimini S, Locato V, Vergauwen R et al (2015) Fructan biosynthesis and degradation as part of plant metabolism controlling sugar fluxes during durum wheat kernel maturation. Front Plant Sci 6:89. https://doi.org/10.3389/fpls.2015.00089

Collard BC, Mackill DJ (2008) Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. Philos Trans R Soc B Biol Sci 363:557–572. https://doi.org/10.1098/rstb.2007.2170

Colleoni C, Dauvill D, Mouille G et al (1999) Biochemical characterization of the chlamydomonas reinhardtii alpha-1,4 glucanotransferase supports a direct function in amylopectin biosynthesis. Plant Physiol 120:1005–1014

Costa LM, Marshall E, Tesfaye M et al (2014) Central cell-derived peptides regulate early embryo patterning in flowering plants. Science 344(6180):168–172. https://doi.org/10.1126/science.1243005

Craig J, Barratt P, Tatge H et al (1999) Mutations at the rug4 locus alter the carbon and nitrogen metabolism of pea plants through an effect on sucrose synthase. Plant J 17:353–362. https://doi.org/10.1046/j.1365-313X.1999.00382.x

Creff A, Brocard L, Ingram G (2015) A mechanically sensitive cell layer regulates the physical properties of the Arabidopsis seed coat. Nat Commun 6:1–8. https://doi.org/10.1038/ncomms7382

Crofts N, Abe K, Aihara S et al (2012) Lack of starch synthase IIIa and high expression of granule-bound starch synthase I synergistically increase the apparent amylose content in rice endosperm. Plant Sci 193–194:62–69. https://doi.org/10.1016/j.plantsci.2012.05.006

Dam S, Laursen BS, Ornfelt JH et al (2009) The proteome of seed development in the model legume *Lotus japonicus*. Plant Physiol 149:1325–1340. https://doi.org/10.1104/pp.108.133405

Dante RA, Larkins BA, Sabelli PA (2014) Cell cycle control and seed development. Front Plant Sci 5:493. https://doi.org/10.3389/fpls.2014.00493

Dasgupta K, Khadilkar AS, Sulpice R et al (2014) Expression of sucrose transporter cDNAs specifically in companion cells enhances phloem loading and long-distance transport of sucrose but leads to an inhibition of growth and the perception of a phosphate limitation. Plant Physiol 165:715–731. https://doi.org/10.1104/pp.114.238410

Dauvillée D, Chochois V, Steup M et al (2006) Plastidial phosphorylase is required for normal starch synthesis in *Chlamydomonas reinhardtii*. Plant J 48:274–285. https://doi.org/10.1111/j.1365-313X.2006.02870.x

Dinges JR, Colleoni C, Myers AM, James MG (2001) Molecular structure of three mutations at the maize sugary1 locus and their allele-specific phenotypic effects. Plant Physiol 125:1406–1418

Djemel N, Guedon D, Lechevalier A et al (2005) Development and composition of the seeds of nine genotypes of the *Medicago truncatula* species complex. Plant Physiol Biochem 43:557–566. https://doi.org/10.1016/j.plaphy.2005.04.005

Doughty J, Aljabri M, Scott RJ (2014) Flavonoids and the regulation of seed size in Arabidopsis. Biochem Soc Trans 42:364–369. https://doi.org/10.1042/BST20140040

Draper J (1997) Salicylate, superoxide synthesis and cell suicide in plant defence. Trends Plant Sci 2:162–165. https://doi.org/10.1016/S1360-1385(97)85222-3

Durand M, Mainson D, Porcheron B et al (2017) Carbon source–sink relationship in *Arabidopsis thaliana*: the role of sucrose transporters. Planta 247:1–25. https://doi.org/10.1007/s00425-017-2807-4

Ehlers K, Bhide AS, Tekleyohans DG et al (2016) The MADS box genes ABS, SHP1, and SHP2 are essential for the coordination of cell divisions in ovule and seed coat development and for endosperm formation in *Arabidopsis thaliana*. PLoS ONE 11:e0165075. https://doi.org/10.1371/journal.pone.0165075

Ekop AS (2007) Determination of chemical composition of *Gnetum africanum* (AFANG) seeds. Pakistan J Nutr 6:40–43. https://doi.org/10.3923/pjn.2007.40.43

Etchells JP, Moore L, Jiang WZ et al (2012) A role for BELL-RINGER in cell wall development is supported by loss-of-function phenotypes. BMC Plant Biol 12:1. https://doi.org/10.1186/1471-2229-12-212

Faix B, Radchuk V, Nerlich A et al (2012) Barley grains, deficient in cytosolic small subunit of ADP-glucose pyrophosphorylase, reveal coordinate adjustment of C:N metabolism mediated by an overlapping metabolic-hormonal control. Plant J 69:1077–1093. https://doi.org/10.1111/j.1365-313X.2011.04857.x

Fallahi H, Scofield GN, Badger MR et al (2008) Localization of sucrose synthase in developing seed and siliques of *Arabidopsis thaliana* reveals diverse roles for SUS during development. J Exp Bot 59:3283–3295. https://doi.org/10.1093/jxb/ern180

Fatihi A, Zbierzak AM, Dormann P (2013) Alterations in seed development gene expression affect size and oil content of Arabidopsis seeds. Plant Physiol 163:973–985. https://doi.org/10.1104/pp.113.226761

Fatland BL (2005) Reverse genetic characterization of cytosolic acetyl-CoA generation by ATP-citrate lyase in Arabidopsis. Plant Cell Online 17:182–203. https://doi.org/10.1105/tpc.104.026211

Fiume E, Fletcher JC (2012) Regulation of Arabidopsis embryo and endosperm development by the polypeptide signaling molecule CLE8. Plant Cell 24:1000–1012. https://doi.org/10.1105/tpc.111.094839

Fouquet R, Martin F, Fajardo DS et al (2011) Maize rough endosperm3 encodes an RNA splicing factor required for endosperm cell differentiation and has a nonautonomous effect on embryo development. Plant Cell 23:4280–4297. https://doi.org/10.1105/tpc.111.092163

Fu F-F, Xue H-W (2010) Coexpression analysis identifies rice starch Regulator1, a Rice AP2/EREBP family transcription factor, as a novel rice starch biosynthesis regulator. Plant Physiol 154:927–938. https://doi.org/10.1104/pp.110.159517

Fujita N, Satoh R, Hayashi A et al (2011) Starch biosynthesis in rice endosperm requires the presence of either starch synthase I or IIIa. J Exp Bot 62:4819–4831. https://doi.org/10.1093/jxb/err125

Fujita N, Yoshida M, Kondo T et al (2007) Characterization of SSIIIa-deficient mutants of rice: the function of SSIIIa and pleiotropic effects by SSIIIa deficiency in the rice endosperm. Plant Physiol 144:2009–2023. https://doi.org/10.1104/pp.107.102533

Fulton DC, Stettler M, Mettler T et al (2008) AMYLASE4, a non-catalytic protein required for starch breakdown, acts upstream of three active β-amylases in Arabidopsis chloroplasts. Plant Cell Online 20:1040–1058. https://doi.org/10.1105/tpc.107.056507

Gómez LD, Baud S, Gilday A et al (2006) Delayed embryo development in the ARABIDOPSIS TREHALOSE-6-PHOSPHATE SYNTHASE 1 mutant is associated with altered cell wall structure, decreased cell division and starch accumulation. Plant J 46:69–84. https://doi.org/10.1111/j.1365-313X.2006.02662.x

Gómez LD, Baud S, Graham IA (2005) The role of trehalose-6-phosphate synthase in Arabidopsis embryo development. Biochem Soc Trans 33:280–282. https://doi.org/10.1042/BST0330280

Griffiths CA, Paul MJ, Foyer CH (2016) Metabolite transport and associated sugar signalling systems underpinning source/sink interactions. Biochim Biophys Acta Bioenerg 1857:1715–1725. https://doi.org/10.1016/j.bbabio.2016.07.007

Griffiths JS, Šola K, Kushwaha R et al (2015) Unidirectional movement of cellulose synthase complexes in Arabidopsis seed coat epidermal cells deposit cellulose involved in mucilage extrusion, adherence, and ray formation. Plant Physiol 168:502–520

Guillon F, Larré C, Petipas F et al (2012) A comprehensive overview of grain development in *Brachypodium distachyon* variety Bd21. J Exp Bot 63:739–755. https://doi.org/10.1093/jxb/err298

Guo X, Duan X, Wu Y et al (2018) Genetic engineering of maize (*Zea mays* L.) with improved grain nutrients. J Agric Food Chem. https://doi.org/10.1021/acs.jafc.7b05390

Habib HM, Ibrahim WH (2009) Nutritional quality evaluation of eighteen date pit varieties. Int J Food Sci Nutr 60:99–111. https://doi.org/10.1080/09637480802314639

Hannah LC, Shaw JR, Giroux MJ et al (2001) Maize genes encoding the small subunit of ADP-glucose pyrophosphorylase. Plant Physiol 127:173–183. https://doi.org/10.1104/pp.127.1.173

Hashida Y, Hirose T, Okamura M et al (2016) A reduction of sucrose phosphate synthase (SPS) activity affects sucrose/starch ratio in leaves but does not inhibit normal plant growth in rice. Plant Sci 253:40–49. https://doi.org/10.1016/J.PLANTSCI.2016.08.017

Hedhly A, Vogler H, Schmid MW et al (2016) Starch turnover and metabolism during flower and early embryo development. Plant Physiol 172:2388–2402. https://doi.org/10.1104/pp.16.00916

Hehenberger E, Kradolfer D, Kohler C (2012) Endosperm cellularization defines an important developmental transition for embryo development. Development 139:2031–2039. https://doi.org/10.1242/dev.077057

Herbers K, Sonnewald U (1998) Molecular determinants of sink strength. Curr Opin Plant Biol 1:207–216. https://doi.org/10.1016/S1369-5266(98)80106-4

Herchi W, Al Hujaili AD, Sakouhi F et al (2014) Flaxseed hull: chemical composition and antioxidant activity during development. J Oleo Sci 63:681–689. https://doi.org/10.5650/jos.ess14006

Hills MJ (2004) Control of storage-product synthesis in seeds. Curr Opin Plant Biol 7:302–308. https://doi.org/10.1016/j.pbi.2004.03.003

Högy P, Fangmeier A (2008) Effects of elevated atmospheric CO_2 on grain quality of wheat. J Cereal Sci 48:580–591. https://doi.org/10.1016/j.jcs.2008.01.006

Hua S, Yu H, Zhang Y et al (2012) Variation of carbohydrates and macronutrients during the flowering stage in canola (*Brasscia napus* L.) plants with contrasting seed oil content. Aust J Crop Sci 6:1275–1282

Huang B, Hennen-Bierwagen TA, Myers AM (2014) Functions of multiple genes encoding ADP-glucose pyrophosphorylase subunits

in maize endosperm, embryo, and leaf. Plant Physiol 164:596–611. https://doi.org/10.1104/pp.113.231605

Huang J, Schols HA, van Soest JJG et al (2007) Physicochemical properties and amylopectin chain profiles of cowpea, chickpea and yellow pea starches. Food Chem 101:1338–1345. https://doi.org/10.1016/j.foodchem.2006.03.039

Huang X, Zhao Y, Wei X et al (2012) Genome-wide association study of flowering time and grain yield traits in a worldwide collection of rice germplasm. Nat Genet 44:32–39. https://doi.org/10.1038/ng.1018

Ingram GC (2010) Family life at close quarters: communication and constraint in angiosperm seed development. Protoplasma 247:195–214. https://doi.org/10.1007/s00709-010-0184-y

Itoh K, Ozaki H, Okada K et al (2003) Introduction of Wx transgene into rice wx mutants leads to both high- and low-amylose rice. Plant Cell Physiol 44:473–480. https://doi.org/10.1093/pcp/pcg068

James MG, Robertson DS, Myers AM et al (2015) Characterization of the maize gene sugary1, a determinant of starch composition in kernels. Plant Cell 7:417–429

Jaynes TA, Nelson OE (1971) Invertase activity in normal and mutant maize endosperms during development. Plant Physiol 47:623–628

Jofuku KD, Omidyar PK, Gee Z, Okamuro JK (2005) Control of seed mass and seed yield by the floral homeotic gene APETALA2. Proc Natl Acad Sci 102:3117–3122. https://doi.org/10.1073/pnas.0409893102

Khan S, Anwar S, Kuai J et al (2018) Alteration in yield and oil quality traits of winter rapeseed by lodging at different planting density and nitrogen rates. Sci Rep 8:634. https://doi.org/10.1038/s41598-017-18734-8

Kim Y, Keogh JB, Clifton PM (2017) Benefits of nut consumption on insulin resistance and cardiovascular risk factors: multiple potential mechanisms of actions. Nutrients 9:1271. https://doi.org/10.3390/nu9111271

Kirchberger S, Leroch M, Huynen MA et al (2007) Molecular and biochemical analysis of the plastidic ADP-glucose transporter (ZmBT1) from *Zea mays*. J Biol Chem 282:22481–22491. https://doi.org/10.1074/jbc.M702484200

Kok S, Ong-Abdullah M, Ee GC, Namasivayam P (2011) Comparison of nutrient composition in kernel of tenera and clonal materials of oil palm (*Elaeis guineensis* Jacq.). Food Chem 129:1343–1347. https://doi.org/10.1016/J.FOODCHEM.2011.05.023

Kondou Y, Nakazawa M, Kawashima M et al (2008) RETARDED GROWTH OF EMBRYO1, a new basic helix-loop-helix protein, expresses in endosperm to control embryo growth. Plant Physiol 147:1924–1935. https://doi.org/10.1104/pp.108.118364

Kunieda T, Shimada T, Kondo M et al (2013) Spatiotemporal secretion of PEROXIDASE36 is required for seed coat mucilage extrusion in arabidopsis. Plant Cell 25:1355–1367. https://doi.org/10.1105/tpc.113.110072

Kunz H-H, Zamani-Nour S, Häusler RE et al (2014) Loss of cytosolic phosphoglucose isomerase affects carbohydrate metabolism in leaves and is essential for fertility of Arabidopsis. Plant Physiol 166:753–765. https://doi.org/10.1104/pp.114.241091

Kurai T, Wakayama M, Abiko T et al (2011) Introduction of the ZmDof1 gene into rice enhances carbon and nitrogen assimilation under low-nitrogen conditions. Plant Biotechnol J 9:826–837. https://doi.org/10.1111/j.1467-7652.2011.00592.x

Lafon-Placette C, Köhler C (2014) Embryo and endosperm, partners in seed development. Curr Opin Plant Biol 17:64–69. https://doi.org/10.1016/j.pbi.2013.11.008

Lalonde S, Wipf D, Frommer WB (2004) Transport mechanisms for organic forms of carbon and nitrogen between source and sink. Annu Rev Plant Biol 55:341–372. https://doi.org/10.1146/annurev.arplant.55.031903.141758

Lee KJD, Dekkers BJW, Steinbrecher T et al (2012) Distinct cell wall architectures in seed endosperms in representatives of the Brassicaceae and Solanaceae. Plant Physiol 160:1551–1566. https://doi.org/10.1104/pp.112.203661

Lee SK, Hwang SK, Han M et al (2007) Identification of the ADP-glucose pyrophosphorylase isoforms essential for starch synthesis in the leaf and seed endosperm of rice (*Oryza sativa* L.). Plant Mol Biol 65:531–546. https://doi.org/10.1007/s11103-007-9153-z

Lee Y, Choi MS, Lee G et al (2017) Sugary endosperm is modulated by starch branching enzyme IIa in rice (*Oryza sativa* L.). Rice 10:33. https://doi.org/10.1186/s12284-017-0172-3

Li G, Pan J, Cui K et al (2017a) Limitation of unloading in the developing grains is a possible cause responsible for low stem non-structural carbohydrate translocation and poor grain yield formation in rice through verification of recombinant inbred lines. Front Plant Sci. https://doi.org/10.3389/fpls.2017.01369

Li J, Baroja-Fernández E, Bahaji A et al (2013) Enhancing sucrose synthase activity results in increased levels of starch and adp-glucose in maize (*Zea mays* l.) seed endosperms. Plant Cell Physiol 54:282–294. https://doi.org/10.1093/pcp/pcs180

Li JY, Wang J, Zeigler RS (2014) The 3,000 rice genomes project: new opportunities and challenges for future rice research. Gigascience 3:8. https://doi.org/10.1186/2047-217X-3-8

Li N, Li Y (2015) Maternal control of seed size in plants. J Exp Bot 66:1087–1097. https://doi.org/10.1093/jxb/eru549

Li S, Wei X, Ren Y et al (2017b) OsBT1 encodes an ADP-glucose transporter involved in starch synthesis and compound granule formation in rice endosperm. Sci Rep 7:40124. https://doi.org/10.1038/srep40124

Lin Q, Huang B, Zhang M et al (2012) Functional interactions between starch synthase III and isoamylase-type starch-debranching enzyme in maize endosperm. Plant Physiol 158:679–692. https://doi.org/10.1104/pp.111.189704

Liu J, Huang J, Guo H et al (2017) The conserved and unique genetic architecture of kernel size and weight in maize and rice. Plant Physiol 175:774–785. https://doi.org/10.1104/pp.17.00708

Locascio A, Roig-Villanova I, Bernardi J, Varotto S (2014) Current perspectives on the hormonal control of seed development in Arabidopsis and maize: a focus on auxin. Front Plant Sci 5:1–22. https://doi.org/10.3389/fpls.2014.00412

Lonien J, Schwender J (2009) Analysis of metabolic flux phenotypes for two Arabidopsis mutants with severe impairment in seed storage lipid synthesis. Plant Physiol 151:1617–1634. https://doi.org/10.1104/pp.109.144121

Luo M, Dennis ES, Berger F et al (2005) MINISEED3 (MINI3), a WRKY family gene, and HAIKU2 (IKU2), a leucine-rich repeat (LRR) KINASE gene, are regulators of seed size in Arabidopsis. Proc Natl Acad Sci 102:17531–17536. https://doi.org/10.1073/pnas.0508418102

Ma W, Kong Q, Mantyla JJ et al (2016) 14-3-3 protein mediates plant seed oil biosynthesis through interaction with AtWRI1. Plant J 88:228–235. https://doi.org/10.1111/tpj.13244

Malinova I, Kunz HH, Alseekh S et al (2014) Reduction of the cytosolic phosphoglucomutase in Arabidopsis reveals impact on plant growth, seed and root development, and carbohydrate partitioning. PLoS ONE 9:e112468. https://doi.org/10.1371/journal.pone.0112468

Matsushima R, Maekawa M, Kusano M et al (2014) Amyloplast-localized SUBSTANDARD STARCH GRAIN4 protein influences the size of starch grains in rice endosperm. Plant Physiol 164:623–636. https://doi.org/10.1104/pp.113.229591

McDonald R, Wang HL, Patrick JW, Offler CE (1995) The cellular pathway of sucrose transport in developing cotyledons of *Vicia faba* L. and *Phaseolus vulgaris* L.: a physiological assessment. Planta 196:659–667. https://doi.org/10.1007/BF00197329

Melkus G, Rolletschek H, Fuchs J et al (2011) Dynamic 13C/1H NMR imaging uncovers sugar allocation in the living seed. Plant Biotechnol J 9:1022–1037. https://doi.org/10.1111/j.1467-7652.2011.00618.x

Mendel G (1865) Versuche uber Pflanzen-Hybriden. Verh. Naturforsch. Ver Brunn 4:3–47

Meng L-S, Wang Y-B, Loake GJ, Jiang J-H (2016) Seed embryo development is regulated via an AN3-MINI3 gene cascade. Front Plant Sci 7:1073. https://doi.org/10.3389/fpls.2016.01645

Mentzen WI, Peng J, Ransom N et al (2008) Articulation of three core metabolic processes in Arabidopsis: fatty acid biosynthesis, leucine catabolism and starch metabolism. BMC Plant Biol 8:76. https://doi.org/10.1186/1471-2229-8-76

Morley-Smith ER, Pike MJ, Findlay K et al (2008) The transport of sugars to developing embryos is not via the bulk endosperm in oilseed rape seeds. Plant Physiol 147:2121–2130. https://doi.org/10.1104/pp.108.124644

Mudgil D, Barak S, Khatkar BS (2014) Guar gum: processing, properties and food applications—a review. J Food Sci Technol 51:409–418. https://doi.org/10.1007/s13197-011-0522-x

AQ8 Muhammad C, Umar A, Birnin-Yauri UA, Musa A (2011) Proximate composition and mineral analysis of *Nymphaea lotus* seeds Proximate composition and mineral analysis of *Nymphaea lotus* seeds. Afr J Food Sci Technol 3:20–30

Müller K, Tintelnot S, Leubner-Metzger G (2006) Endosperm-limited Brassicaceae seed germination: Abscisic acid inhibits embryo-induced endosperm weakening of *Lepidium sativum* (cress) and endosperm rupture of cress and *Arabidopsis thaliana*. Plant Cell Physiol 47:864–877. https://doi.org/10.1093/pcp/pcj059

Nakamura Y (2002) Towards a better understanding of the metabolic system for amylopectin biosynthesis in plants: rice endosperm as a model tissue. Plant Cell Physiol 43:718–725. https://doi.org/10.1093/pcp/pcf091

Nakamura Y, Ono M, Sawada T et al (2017) Characterization of the functional interactions of plastidial starch phosphorylase and starch branching enzymes from rice endosperm during reserve starch biosynthesis. Plant Sci 264:83–95. https://doi.org/10.1016/j.plantsci.2017.09.002

Nehdi IA, Sbihi HM, Tan CP et al (2018) Chemical composition of date palm (*Phoenix dactylifera* L.) seed oil from six Saudi Arabian cultivars. J Food Sci. https://doi.org/10.1111/1750-3841.14033

Niittylä T, Messerli G, Trevisan M et al (2004) A previously unknown maltose transporter essential for starch degradation in leaves. Science 303:87–89. https://doi.org/10.1126/science.1091811

Nishinari K, Takemasa M, Zhang H, Takahashi R (2007) Storage plant polysaccharides: Xyloglucans, Galactomannans, Glucomannans. In: Kamerling JP (ed) Comprehensive glycoscience: from chemistry to systems biology, 1st edn. Elsevier, Amsterdam, pp 613–652

Nonogaki H, Gee OH, Bradford KJ (2000) A germination-specific endo-β-mannanase gene is expressed in the micropylar endosperm cap of tomato seeds. Plant Physiol 123:1235–1246. https://doi.org/10.1104/pp.123.4.1235

Ohto M-AA, Fischer RL, Goldberg RB et al (2005) Control of seed mass by APETALA2. Proc Natl Acad Sci USA 102:3123–3128. https://doi.org/10.1073/pnas.0409858102

Onda Y, Mochida K (2016) Exploring genetic diversity in plants using high-throughput sequencing techniques. Curr Genomics 17:356–365. https://doi.org/10.2174/1389202917999160304160040

Orozco-Arroyo G, Paolo D, Ezquer I, Colombo L (2015) Networks controlling seed size in Arabidopsis. Plant Reprod 28:17–32. https://doi.org/10.1007/s00497-015-0255-5

Patron NJ (2004) The lys5 mutations of barley reveal the nature and importance of plastidial ADP-Glc transporters for starch synthesis in cereal endosperm. Plant Physiol 135:2088–2097. https://doi.org/10.1104/pp.104.045203

Paul MJ, Oszvald M, Jesus C et al (2017) Increasing crop yield and resilience with trehalose 6-phosphate: targeting a feast–famine mechanism in cereals for better source–sink optimization. J Exp Bot 68:4455–4462. https://doi.org/10.1093/jxb/erx083

Peng C, Wang Y, Liu F et al (2014) FLOURY ENDOSPERM6 encodes a CBM48 domain-containing protein involved in compound granule formation and starch synthesis in rice endosperm. Plant J 77:917–930. https://doi.org/10.1111/tpj.12444

Perdomo FA, Acosta-Osorio AA, Herrera G et al (2013) Physicochemical characterization of seven Mexican *Ricinus communis* L. seeds & oil contents. Biomass Bioenerg 48:17–24. https://doi.org/10.1016/j.biombioe.2012.10.020

Periappuram C, Steinhauer L, Barton DL et al (2000) The plastidic phosphoglucomutase from arabidopsis. a reversible enzyme reaction with an important role in metabolic control. Plant Physiol 122:1193–1200. https://doi.org/10.1104/pp.122.4.1193

Pfister B, Zeeman SC (2016) Formation of starch in plant cells. Cell Mol Life Sci 73:2781–2807. https://doi.org/10.1007/s00018-016-2250-x

Pirone C, Gurrieri L, Gaiba I et al (2017) The analysis of the different functions of starch-phosphorylating enzymes during the development of *Arabidopsis thaliana* plants discloses an unexpected role for the cytosolic isoform GWD2. Physiol Plant 160:447–457. https://doi.org/10.1111/ppl.12564

Pommerrenig B, Popko J, Heilmann M et al (2013) SUCROSE TRANSPORTER 5 supplies Arabidopsis embryos with biotin and affects triacylglycerol accumulation. Plant J 73:392–404. https://doi.org/10.1111/tpj.12037

Poschet G, Hannich B, Raab S et al (2011) A novel Arabidopsis vacuolar glucose exporter is involved in cellular sugar homeostasis and affects the composition of seed storage compounds. Plant Physiol 157:1664–1676. https://doi.org/10.1104/pp.111.186825

Pouvreau B, Baud S, Vernoud V et al (2011) Duplicate maize Wrinkled1 transcription factors activate target genes involved in seed oil biosynthesis. Plant Physiol 156:674–686. https://doi.org/10.1104/pp.111.173641

Rachwa-Rosiak D, Nebesny E, Budryn G (2015) Chickpeas—composition, nutritional value, health benefits, application to bread and snacks: a review. Crit Rev Food Sci Nutr 55:1137–1145. https://doi.org/10.1080/10408398.2012.687418

Radchuk V (2006) Jekyll encodes a novel protein involved in the sexual reproduction of barley. Plant Cell Online 18:1652–1666. https://doi.org/10.1105/tpc.106.041335

Radchuk V, Borisjuk L (2014) Physical, metabolic and developmental functions of the seed coat. Front Plant Sci 5:510. https://doi.org/10.3389/fpls.2014.00510

Reidel EJ, Turgeon R, Cheng L (2008) A maltose transporter from apple is expressed in source and sink tissues and complements the Arabidopsis maltose export-defective mutant. Plant Cell Physiol 49:1607–1613. https://doi.org/10.1093/pcp/pcn134

Ritchie RJ, Fieuw-Makaroff S, Patrick JW (2003) Sugar retrieval by coats of developing seeds of *Phaseolus vulgaris* L. and *Vicia faba* L. Plant Cell Physiol 44:163–172. https://doi.org/10.1093/pcp/pcg022

Rolletschek H (2005) Ectopic expression of an amino acid transporter (VfAAP1) in seeds of vicia narbonensis and pea increases storage proteins. Plant Physiol 137:1236–1249. https://doi.org/10.1104/pp.104.056523

Rolletschek H, Grafahrend-Belau E, Munz E et al (2015) Metabolic architecture of the cereal grain and its relevance to maximize carbon use efficiency. Plant Physiol 169:1698–1713. https://doi.org/10.1104/pp.15.00981

Ruan Y-L, Chourey PS (2006) Carbon partitioning in developing seeds. In: Basra AS (ed) Handbook of seed science and technology. Food Products Press, New York, pp 125–152

Ruan YL, Llewellyn DJ, Liu Q et al (2008) Expression of sucrose synthase in the developing endosperm is essential for early seed development in cotton. Funct Plant Biol 35:382–393. https://doi.org/10.1071/FP08017

Ruuska S, Girke T (2002) Contrapuntal networks of gene expression during Arabidopsis seed filling. Plant Cell 14:1191–1206. https://doi.org/10.1105/tpc.000877.teins

Satoh H (2003) Starch-branching enzyme I-deficient mutation specifically affects the structure and properties of starch in rice endosperm. Plant Physiol 133:1111–1121. https://doi.org/10.1104/pp.103.021527

Satoh H, Shibahara K, Tokunaga T et al (2008) Mutation of the plastidial α-glucan phosphorylase gene in rice affects the synthesis and structure of starch in the endosperm. Plant Cell Online 20:1833–1849. https://doi.org/10.1105/tpc.107.054007

Scott PT, Pregelj L, Chen N et al (2008) *Pongamia pinnata*: an untapped resource for the biofuels industry of the future. BioEnergy Res 1:2–11. https://doi.org/10.1007/s12155-008-9003-0

Scott RJ, Spielman M, Bailey J, Dickinson HG (1998) Parent-of-origin effects on seed development in *Arabidopsis thaliana*. Development 125:3329–3341

Shahid S, Begum R, Razzaque S et al (2016) Variability in amylose content of Bangladeshi rice cultivars due to unique SNPs in Waxy allele. J Cereal Sci 71:1–9. https://doi.org/10.1016/J.JCS.2016.07.006

Shannon JC, Pien FM, Cao H, Liu KC (1998) Brittle-1, an adenylate translocator, facilitates transfer of extraplastidial synthesized ADP-glucose into amyloplasts of maize endosperms. Plant Physiol 117:1235–1252. https://doi.org/10.1104/pp.117.4.1235

Shen B, Allen WB, Zheng P et al (2010) Expression of ZmLEC1 and ZmWRI1 increases seed oil production in maize. Plant Physiol 153:980–987. https://doi.org/10.1104/pp.110.157537

AQ9 Shewry PR, Piironen V, Lampi AM et al (2008) Phytochemical and fiber components in oat varieties in the healthgrain diversity screen. J Agric Food Chem 56:9777–9784. https://doi.org/10.1021/jf801880d

Shewry PR, Underwood C, Wan Y et al (2009) Storage product synthesis and accumulation in developing grains of wheat. J Cereal Sci 50:106–112. https://doi.org/10.1016/j.jcs.2009.03.009

Solís-Guzmán MG, Argüello-Astorga G, López-Bucio J et al (2017) *Arabidopsis thaliana* sucrose phosphate synthase (sps) genes are expressed differentially in organs and tissues, and their transcription is regulated by osmotic stress. Gene Expr Patterns 25–26:92–101. https://doi.org/10.1016/j.gep.2017.06.001

Song Y, He L, Wang X-D et al (2017a) Regulation of carbon partitioning in the seed of the model legume *Medicago truncatula* and *Medicago orbicularis*: a comparative approach. Front Plant Sci 8:2070. https://doi.org/10.3389/fpls.2017.02070

Song Y, Wang XD, Rose RJ (2017b) Oil body biogenesis and biotechnology in legume seeds. Plant Cell Rep 36:1519–1532. https://doi.org/10.1007/s00299-017-2201-5

Stadler R (2005) Cell-to-cell movement of green fluorescent protein reveals post-phloem transport in the outer integument and identifies symplastic domains in Arabidopsis seeds and embryos. Plant Physiol 139:701–712. https://doi.org/10.1104/pp.105.065607

Stein O, Avin-Wittenberg T, Krahnert I et al (2017) Arabidopsis fructokinases are important for seed oil accumulation and vascular development. Front Plant Sci 7:1–16. https://doi.org/10.3389/fpls.2016.02047

Streb S, Zeeman SC (2014) Replacement of the endogenous starch debranching enzymes ISA1 and ISA2 of arabidopsis with the rice orthologs reveals a degree of functional conservation during starch synthesis. PLoS ONE 9:e92174. https://doi.org/10.1371/journal.pone.0092174

Sullivan TD (1991) Analysis of maize brittle-1 alleles and a defective suppressor-mutator-induced mutable allele. Plant Cell Online 3:1337–1348. https://doi.org/10.1105/tpc.3.12.1337

Sun Y, Jiao G, Liu Z et al (2017) Generation of high-amylose rice through CRISPR/Cas9-mediated targeted mutagenesis of starch branching enzymes. Front Plant Sci 8:298. https://doi.org/10.3389/fpls.2017.00298

Taliercio EW, Kim JY, Mahé A et al (1999) Isolation, characterization and expression analyses of two cell wall invertase genes in maize. J Plant Physiol 155:197–204. https://doi.org/10.1016/S0176-1617(99)80007-8

Tang XJ, Peng C, Zhang J et al (2016) ADP-glucose pyrophosphorylase large subunit 2 is essential for storage substance accumulation and subunit interactions in rice endosperm. Plant Sci 249:70–83. https://doi.org/10.1016/j.plantsci.2016.05.010

Tausz M, Norton RM, Tausz-Posch S et al (2017) Can additional N fertiliser ameliorate the elevated CO_2-induced depression in grain and tissue N concentrations of wheat on a high soil N background? J Agron Crop Sci 203:574–583. https://doi.org/10.1111/jac.12209

Tetlow I, Emes M (2017) Starch biosynthesis in the developing endosperms of grasses and cereals. Agronomy 7:81. https://doi.org/10.3390/agronomy7040081

Thiel J, Weier D, Sreenivasulu N et al (2008) Different hormonal regulation of cellular differentiation and function in nucellar projection and endosperm transfer cells: a microdissection-based transcriptome study of young barley grains. Plant Physiol 148:1436–1452. https://doi.org/10.1104/pp.108.127001

Turbant A, Fournet F, Lequart M et al (2016) PME58 plays a role in pectin distribution during seed coat mucilage extrusion through homogalacturonan modification. J Exp Bot 67:2177–2190. https://doi.org/10.1093/jxb/erw025

Umemoto T, Aoki N, Lin H et al (2004) Natural variation in rice starch synthase IIa affects enzyme and starch properties. Funct Plant Biol 31:671–684. https://doi.org/10.1071/FP04009

van Bel AJE, Helariutta Y, Thompson GA et al (2013) Phloem: the integrative avenue for resource distribution, signaling, and defense. Front Plant Sci. https://doi.org/10.3389/fpls.2013.00471

Vilhar B (2002) Cytometrical evidence that the loss of seed weight in the miniature1 seed mutant of maize is associated with reduced mitotic activity in the developing endosperm. Plant Physiol 129:23–30. https://doi.org/10.1104/pp.001826

Wan H, Wu L, Yang Y et al (2017) Evolution of sucrose metabolism: the dichotomy of invertases and beyond. Trends Plant Sci 23:163–177. https://doi.org/10.1016/j.tplants.2017.11.001

Wang A, Garcia D, Zhang H et al (2010a) The VQ motif protein IKU1 regulates endosperm growth and seed size in Arabidopsis. Plant J 63:670–679. https://doi.org/10.1111/j.1365-313X.2010.04271.x

Wang AY, Kao MH, Yang WH et al (1999) Differentially and developmentally regulated expression of three rice sucrose synthase genes. Plant Cell Physiol 40:800–807. https://doi.org/10.1093/oxfordjournals.pcp.a029608

Wang J, Hu P, Chen Z et al (2017a) Progress in high-amylose cereal crops through inactivation of starch branching enzymes. Front Plant Sci 8:469. https://doi.org/10.3389/fpls.2017.00469

Wang L, Ruan Y-L (2012) New insights into roles of cell wall invertase in early seed development revealed by comprehensive spatial and temporal expression patterns of GhCWIN1 in cotton. Plant Physiol 160:777–787. https://doi.org/10.1104/pp.112.203893

Wang L, Ruan Y-L (2013) Regulation of cell division and expansion by sugar and auxin signaling. Front Plant Sci 4:163. https://doi.org/10.3389/fpls.2013.00163

Wang N, Fisher DB (1994) The use of fluorescent tracers to characterize the post-phloem transport pathway in maternal tissues of developing wheat grains. Plant Physiol 104:17–27

Wang X (2010) The dawn angiosperms: Uncovering the origin of flowering plants. Springer, New York

Wang X, Pang Y, Wang C et al (2017b) New candidate genes affecting rice grain appearance and milling quality detected by genome-wide and gene-based association analyses. Front Plant Sci. https://doi.org/10.3389/fpls.2016.01998

Wang X, Xue L, Sun J, Zuo J (2010b) The Arabidopsis BE1 gene, encoding a putative glycoside hydrolase localized in plastids, plays crucial roles during embryogenesis and carbohydrate metabolism. J Integr Plant Biol 52:273–288. https://doi.org/10.1111/j.1744-7909.2010.00930.x

Wang XD, Harrington G, Patrick JW et al (1995) Cellular pathway of photosynthate transport in coats of developing seed of *Vicia faba* L. and *Phaseolus vulgaris* L. II. Principal cellular site(s) of efflux. J Exp Bot 46:49–63. https://doi.org/10.1093/jxb/46.1.49

Weber H (1995) Seed coat-associated invertases of fava bean control both unloading and storage functions: cloning of cDNAs and cell type-specific expression. Plant Cell Online 7:1835–1846. https://doi.org/10.1105/tpc.7.11.1835

Weber H, Borisjuk L, Wobus U (2005) Molecular physiology of legume seed development. Annu Rev Plant Biol 56:253–279. https://doi.org/10.1146/annurev.arplant.56.032604.144201

Weber H, Borisjuk L, Wobus U (1996) Controlling seed development and seed size in *Vicia faba*: a role for seed coat-associated invertases and carbohydrate state. Plant J 10(5):823–834

Wei X, Jiao G, Lin H et al (2017) GRAIN INCOMPLETE FILLING 2 regulates grain filling and starch synthesis during rice caryopsis development. J Integr Plant Biol 59:134–153. https://doi.org/10.1111/jipb.12510

Weichert N, Saalbach I, Weichert H et al (2010) Increasing sucrose uptake capacity of wheat grains stimulates storage protein synthesis. Plant Physiol 152:698–710. https://doi.org/10.1104/pp.109.150854

Weickert MO, Pfeiffer AF (2018) Impact of dietary fiber consumption on insulin resistance and the prevention of type 2 diabetes. J Nutr 148:7–12. https://doi.org/10.1093/jn/nxx008

Weigelt K, Küster H, Radchuk R et al (2008) Increasing amino acid supply in pea embryos reveals specific interactions of N and C metabolism, and highlights the importance of mitochondrial metabolism. Plant J 55:909–926. https://doi.org/10.1111/j.1365-313X.2008.03560.x

Weschke W, Panitz R, Gubatz S et al (2003) The role of invertases and hexose transporters in controlling sugar ratios in maternal and filial tissues of barley caryopses during early development. Plant J 33:395–411. https://doi.org/10.1046/j.1365-313X.2003.01633.x

Weselake RJ, Taylor DC, Rahman MH et al (2009) Increasing the flow of carbon into seed oil. Biotechnol Adv 27:866–878. https://doi.org/10.1016/j.biotechadv.2009.07.001

Wobus U, Weber H (1999) Sugars as signal molecules in plant seed development. Biol Chem 380:937–944. https://doi.org/10.1515/BC.1999.116

Wu AC, Ral JP, Morell MK, Gilbert RG (2014) New perspectives on the role of α- and β-amylases in transient starch synthesis. PLoS ONE 9:e100498. https://doi.org/10.1371/journal.pone.0100498

Xiao Q, Wang Y, Du J et al (2017) ZmMYB14 is an important transcription factor involved in the regulation of the activity of the ZmBT1 promoter in starch biosynthesis in maize. FEBS J 284:3079–3099. https://doi.org/10.1111/febs.14179

Xie G, Li Z, Ran Q et al (2017) Over-expression of mutated ZmDA1 or ZmDAR1 gene improves maize kernel yield by enhancing starch synthesis. Plant Biotechnol J 16:234–244. https://doi.org/10.1111/pbi.12763

Xu J-J, Zhang X-F, Xue H-W (2016) Rice aleurone layer specific OsNF-YB1 regulates grain filling and endosperm development by interacting with an ERF transcription factor. J Exp Bot 67:6399–6411. https://doi.org/10.1093/jxb/erw409

Xu W, Bobet S, Le Gourrierec J et al (2017) TRANSPARENT TESTA 16 and 15 act through different mechanisms to control proanthocyanidin accumulation in Arabidopsis testa. J Exp Bot 68:2859–2870. https://doi.org/10.1093/jxb/erx151

Yan D, Duermeyer L, Leoveanu C, Nambara E (2014) The functions of the endosperm during seed germination. Plant Cell Physiol 55:1521–1533. https://doi.org/10.1093/pcp/pcu089

Yang S, Johnston N, Talideh E et al (2008) The endosperm-specific ZHOUPI gene of *Arabidopsis thaliana* regulates endosperm breakdown and embryonic epidermal development. Development 135:3501–3509. https://doi.org/10.1242/dev.026708

Yin L-L, Xue H-W (2012) The MADS29 transcription factor regulates the degradation of the nucellus and the nucellar projection during rice seed development. Plant Cell 24:1049–1065. https://doi.org/10.1105/tpc.111.094854

Ying R, Rondeau-Mouro C, Barron C et al (2013) Hydration and mechanical properties of arabinoxylans and β-D-glucans films. Carbohydr Polym 96:31–38. https://doi.org/10.1016/J.CARBPOL.2013.03.090

Yu T-S, Zeeman SC, Thorneycroft D et al (2005) alpha-Amylase is not required for breakdown of transitory starch in Arabidopsis leaves. J Biol Chem 280:9773–9779. https://doi.org/10.1074/jbc.M413638200

Zeeman SC (2004) Plastidial α-glucan phosphorylase is not required for starch degradation in Arabidopsis leaves but has a role in the tolerance of abiotic stress. Plant Physiol 135:849–858. https://doi.org/10.1104/pp.103.032631

Zhang H, Lu Y, Zhao Y, Zhou D-X (2016) OsSRT1 is involved in rice seed development through regulation of starch metabolism gene expression. Plant Sci 248:28–36. https://doi.org/10.1016/J.PLANTSCI.2016.04.004

Zhang WH, Zhou Y, Dibley KE et al (2007) Review: nutrient loading of developing seeds. Funct Plant Biol 34:314–331. https://doi.org/10.1071/FP06271

Zhou H, Wang L, Liu G et al (2016) Critical roles of soluble starch synthase SSIIIa and granule-bound starch synthase Waxy in synthesizing resistant starch in rice. Proc Natl Acad Sci 113:12844–12849. https://doi.org/10.1073/pnas.1615104113

Zhou X, Yang J, Qu G (2007) Study on synthesis and properties of modified starch binder for foundry. J Mater Process Technol 183:407–411. https://doi.org/10.1016/j.jmatprotec.2006.11.001

Zhu F (2018) Triticale: nutritional composition and food uses. Food Chem 241:468–479. https://doi.org/10.1016/j.foodchem.2017.09.009