Chapter

Seed Filling

Sercan Önder, Sabri Erbaş, Damla Önder, Muhammet Tonguç and Murat Mutlucan

Abstract

The synthesis of seed storage reserves occurs during seed filling, and many seeds contain large and characteristic levels of polymeric reserves. Storage reserves are found in the endosperm of cereal seeds and in the endosperm and/or cotyledons of dicot seeds depending of the plant crop species. Recently progress has been made in understanding the complex network of genetic regulation associated with seed filling. These advances in storage reserve quantity and nutrient quality contribute to a comprehensive understanding of reserve composition, synthesis, and regulation. Phytohormones such as abscisic acid (ABA), cytokinin, gibberellic acid, Indole-3-acetic acid (IAA), ethylene and their interactions play critical roles in seed filling and development. At different stages of seed development, the levels of different hormones such as ABA, IAA zeatin and zeatin riboside changes gradually from the beginning of the process to maturity. In addition, the quality and yield of seed storage reserves are significantly affected by the environmental conditions before and during the synthesis of the reserves. Given the fateful importance of seed storage reserves for food and feed and their use as sustainable industrial feedstock to replace dwindling fossil reserves, understanding the metabolic and developmental control of seed filling will be an important focus of plant research.

Keywords: early maturation, environmental factors, genetic regulation, plant hormones, storage reserves

1. Introduction

Seed development is divided into three stages: embryogenesis, which includes embryo development, early maturation, or seed filling, which includes the accumulation of storage reserves; and late maturation, which includes seed desiccation and the transition to dormancy. After seed filling and desiccation, seed longevity increases up to 30-fold and places the embryo in a dormant state. The seed filling period accounts for between 10 and 78% of the total seed development period, but its importance during seed filling is still overlooked. Seed filling is a crucial stage for all seed plants, involving the synthesis of carbohydrates, lipids, and proteins, as well as the mobilization and accumulation of various components in the developing seeds. Although the metabolic pathways responsible for the synthesis of storage molecules are well known, their regulation is not well understood. Although seed filling is under genetic control, these developmental processes are influenced by the environmental factors, such as heat and drought stress. Therefore, environmental factors have major impacts on the qualitative and quantitative characteristics of seed development and

yield. Optimizing the rate and duration of seed filling could provide high and stable yields by reducing the potential negative effects of late maturation and maximizing the assimilation of metabolites formed by photosynthesis. Therefore, the rate and duration of seed filling are important determinants of seed quality and yield in many plants. In addition, understanding the complex processes during seed filling could help develop high-yielding cultivars under stress conditions.

In this chapter, we will attempt to summarize recent developments in the following areas: synthesis of storage reserves, genetic regulation, role of phytohormones, and effects of environmental factors to expand our understanding of these processes during seed filling. Given the emergence of new approaches to the study of seed filling and the tremendous growth of this topic in recent years, our discussion will inevitably be largely incomplete, and we apologize in advance to our colleagues.

2. Synthesis of storage reserves during seed filling

The main carbon source for biosynthesis and nutrient accumulation in seeds is sucrose, which is produced by the products of photosynthesis in plants. Sucrose is transported from the vegetative parts where photosynthesis occurs to the developing seeds. In cereals and legumes, nitrogen is transported to seeds mainly in the form of asparagine and glutamine; in some species, alanine may also serve as a nitrogen source [1]. Cerelas obtain nitrogen from organic or chemical fertilizers. Ureides, allantoin, and allantoic acids are the major forms of organic nitrogen transport in legumes [2, 3], and about 10–15% of organic nitrogen is transported as ureides in soybean and cowpea. Nitrogen-fixing symbiotic *Rhizobium* in nodules produce ammonium used for purine and uric acid synthesis, and uric acid is transported to neighboring uninfected cells to synthesize allantoin in peroxisomes [4].

During seed filling, carbohydrates are constantly transported from vegetative parts, so the conversion and accumulation of photosynthetic products varies greatly among plant species. In wheat and barley, the net photosynthetic activity in the flag leaf and spike is quite high, while the sugar produced in the leaves below the tassel makes a lower photosynthetic contribution to the grain in maize. However, sugars produced in the leaves enveloping the cob are efficiently transported to the developing seeds. In legumes, sucrose is deposited in the form of starch in the leaves and pods, and nitrogen is stored in the leaves and remobilized to the developing seeds.

Vascular tissues transport nutrients and water and terminate in the placentochalazal region and seed coat of monocotyledons and dicotyledons, respectively. Nutrients are transported and released into the apoplast and taken up by the developing endosperm and embryo during seed filling. Vascular tissues across the developing grain facilitate the transport of nutrients to the endosperm in winter cereals. Specialized transfer cells facilitate the transport of nutrients from the pedicel to the endosperm in warm-season cereals. In legumes, reserves are accumulated in the cotyledons and nutrients are transported via vascular tissue to the funiculus, from where they enter the apoplast space and are then redistributed in the developing seed.

Seeds must have long-term energy stores in the form of starch, lipids, or hemicellulose to ensure successful germination and seedling development. These carbon sources are stored in the cotyledons or endosperms of most plant species. The conversion of assimilated carbon, usually in the form of sucrose, into various storage compounds in different tissues is regulated by complex interactions of gene expression and metabolic activity during seed development [5–7]. Starch is present in most

plant tissues as a carbon storage compound and can account for up to 70% of the dry weight of seeds in many cereal grains [8].

The structure and composition of starch, which is inert and insoluble in water, makes it an ideal storage material that allows large amounts of sugars to be stored in cells without negatively affecting the dissolution potential in seeds. Starch accumulation begins in endosperm cells shortly after fertilization and rapid cell division [9, 10]. The number of endosperm cells can be used as an indicator of yield. The cell division phase is completed within 2–6 days after pollination (DAP), but cell volume continues to increase until maturity (~35–40 DAP) [11]. Accumulation of storage reserves usually occurs between 10 and 35 DAP [1].

2.1 Starch synthesis

There are at least four groups of enzymes involved in starch synthesis in plants. They are ADP-glucose pyrophosphorylases (AGPase), starch synthases (SS), starch branching enzymes (SBE) and starch debranching enzymes (DBE) (**Figure 1**). Plants usually have several isozymes of each group, 14 forms of these enzymes (2 AGPase, 5 SS, 3 SBE ve 4 DBE) are involved in starch synthesis and 13 of them show varying degrees of homology in all plans [13]. Sucrose is used as a substrate for starch formation to produce straight-chain amylose and branched amylopectin in seeds (**Figure 1A**). In cell cytosols, sucrose is converted to fructose (Fru) and uridine diphospho glucose (UDPG1c) by sucrose-UDP glucosyltransferase.

Fructose is phosphorylated by hexose phosphate isomerase to Glc-6-P and to Fru-6-P, which is converted to G1c-1-P by phosphoglucomutase. UDPG1c is also converted to Glc-1-P by UDPG1c pyrophosphorylase (UGPase). The first step of starch synthesis is the formation of ADP-glucose by AGPase [14]. The reaction catalyzed by AGPase is the first stable step in the biosynthesis of both temporarily stored starch in chloroplasts and chromoplasts and starch stored in amyloplasts. This enzyme is located in the plastids of photosynthetic tissue and has different forms in seeds, therefore its cellular location may vary in different plants. While most of the AGPase is found in the plastids of potato and pea, it is mainly located in the cytoplasm in maize, barley, and rice [15]. The enzyme carries out the following reaction: Plastid alkaline conversion of inorganic pyrophosphate (PPi) to inorganic phosphate (Pi) maintains the balance in favor of ADP-glucose synthesis through the action of inorganic pyrophosphatase [16], which can be transported through the plastid envelope [17]. The conversion of ADP-glucose occurs in the amyloplasts of storage cells of dicotyledons (**Figure 1**), while it occurs in the cytosols and plastids of endosperm cells of cereals (**Figure 1**). APGase is a heterotetrameric protein consisting of two large (APG-L) and two small (APG-S) subunits encoded by two different genes [18]. Plastidial AGPase is found in all starch-synthesizing tissues, but there are at least two different AGPases, corresponding to plastidial and cytosolic isoforms of AGPase present in the developing endosperm of maize [19], barley [20], rice [21], and wheat [22]. Starch synthesis by cytosolic AGPase depends on PPi-consuming reactions catalyzed by fructose-6-phosphate, 1-phosphotransferase, and UDP-glucose pyrophosphorylase for starch biosynthesis [23, 24]. The cytosolic AGPase isoform is responsible for 65–95% of the total AGPase activity in the developing cereal endosperms. Consequently, most starch biosynthesis occurs through the import of ADP-glucose in exchange for ADP, which is a byproduct of starch synthase in plastids [25, 26]. Starch biosynthesis in non-graminaceans depends on plastidial AGPase and the import of ATP and hexose phosphates from the cytosol (**Figure 1**). The forms and activity of APGases can vary in different parts of the

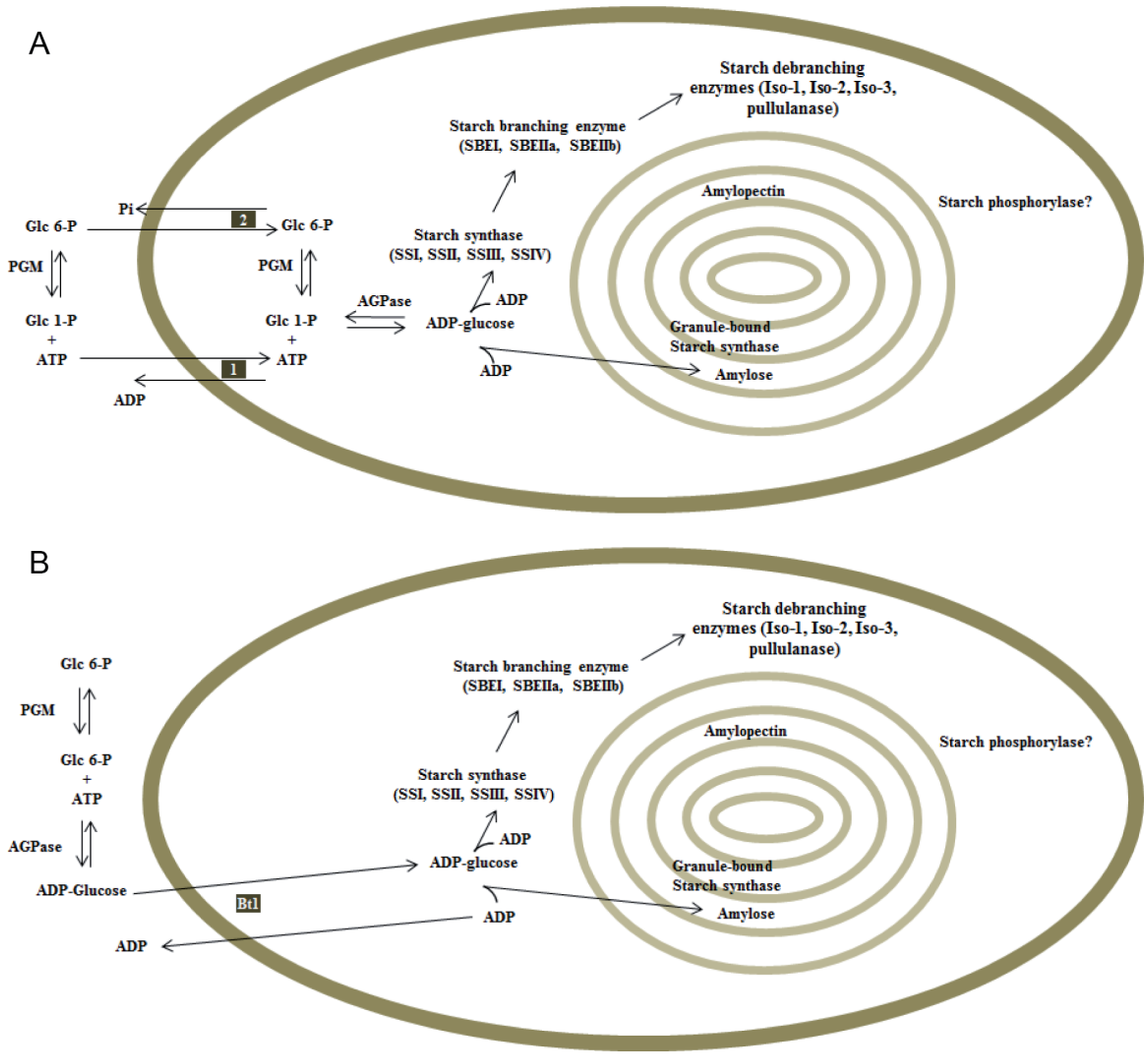

Figure 1.
Biosynthesis of starch in monocotyledons (A) and dicotyledons (B). (A) Monocotyledons have the cytosolic form of AGPase. ADP-glucose is taken up from the cytosol via the ADP-glucose/ADP transporter pathway (Bt1). (B) Hexose-phosphates and ATP are transferred from the cytosol into the plastid via the Glc 6-P/Pi antiporter (1) and the ATP/ADP transporter (2), which are located in the plastid inner envelope membrane. Cytosolic and plastidial isoforms of phosphoglucomutase (PGM) convert Glc 1-P and Glc 6-P into each other. Pi produces the pyrophosphate produced by AGPase. ADP is produced as a byproduct of starch synthase activity (SS). The starch synthases use ADP-glucose to form amylopectin with starch branching and debranching enzymes [12].

same plant because there are several genes encoding large and small subunits of APGases [27–29]. The APG-L subunits have specific expression patterns in different tissues, such as leaves, roots and endosperm of cereals [28, 30–32], or their expression levels are regulated under specific conditions, such as sugar content in potato [33, 34].

Starch synthases catalyze ADP-glucose to glucans and these are eventually used to synthesize water-insoluble amylose and amylopectin. Granule-bound starch synthases (GBSSI and GBSSII) produce and extend the amylose chain [35, 36]. Plants carrying a mutant form of GBSS corresponding to the waxy gene in cereals, do not produce amylose. They may also be involved in the elongation of glucans in various plants such as rice [37]. Another group of starch synthase enzymes (SSI-SSIV) is encoded by several genes and plays different roles in the formation of amylopectin in different tissues and developmental stages [38]. SSI produces short glucan (Glc) chains (<10). The first synthesized amylopectin is water-soluble and is elongated by SSII and SSIII to form water-insoluble amylopectin. Besides starch, there are other types of carbohydrates in the seeds of cereals

and legumes, such as glucans and arabinoxylans. However, their amounts in the seeds does not exceed 10%, which is why they are not considered storage carbohydrates.

2.2 Lipid synthesis

Sucrose in seeds is used as a carbon source for the synthesis of triacylglycerols (TAGs). Lipid synthesis occurs in three steps: glycerol skeleton formation, fatty acid synthesis, and esterification of fatty acids and glycerol to complete lipid synthesis.

2.2.1 Glycerol synthesis

Glycerol synthesis reactions can occur in more than one way in plants, with the most common pathway being the fructose diphosphate (FDP) pathway. It is also known as the EMP pathway, after Emden-Meyerhof-Parnas, who discovered the pathway. Glucose is converted to fructose and enriched in energy by phosphorylation, then fructose-1,6-diphosphate is cleaved by aldolase to produce dihydroxyacetone phosphate (DHAP) and glyceraldehyde-3-phosphate (GAP), each with 3 carbons (**Figure 2**). The

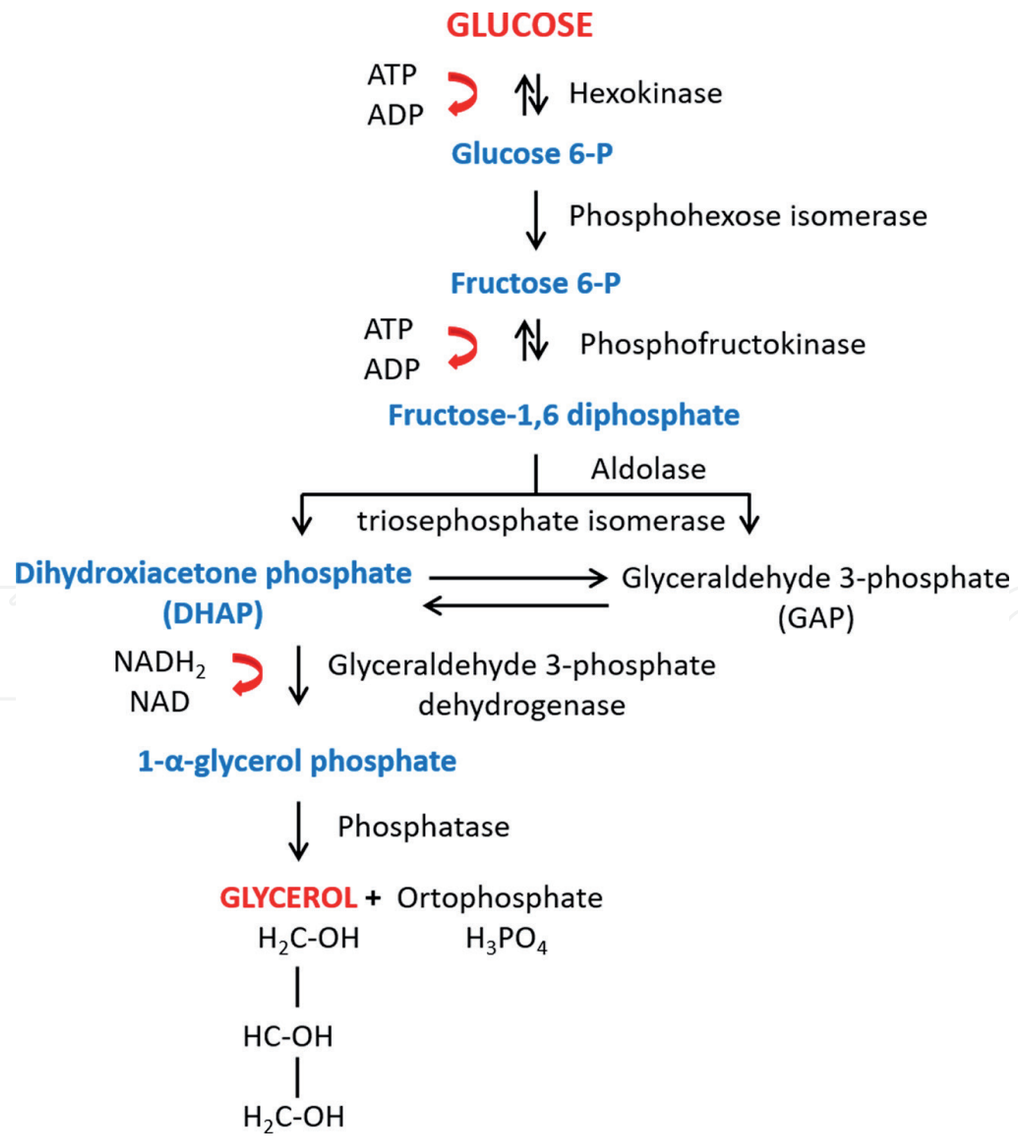

Figure 2.
Production of gylecerol from glucose [39].

two triose-phosphates are in equilibrium with each other and the equilibrium is maintained by triose-phosphate-isomerase. DHAP is converted to glyceraldehyde phosphate by 3-phospho-glyceraldehyde dehydrogenase, and glyceraldehyde phosphate is further converted by phosphotosis to yield glycerol and orto-phosphate [39].

2.2.2 Fatty acid synthesis

Acetyl-CoA is used as a starting material for fatty acid synthesis. Glucose produced by photosynthesis is first converted to pyruvic acid and then to acetyl-CoA. Saturated fatty acids such as palmitate, stearate and oleate are produced from acetyl-CoA by acetyl-CoA carboxylase and fatty acid synthase (FAS) in the chloroplast of plants. The elongation of fatty acids to longer-chain fatty acids is catalyzed by elongases, and fatty acid desaturases (FAD) produce unsaturated fatty acids by inserting double bonds (desaturation) between carbon atoms (**Figure 3**) [40].

2.2.3 Lipid (triacylglycerol) synthesis

Lipids (triglycerides) are formed by combining a glycerol with three fatty acids via ester linkages. Glycerol and free fatty acids do not combine to form lipids, and glycerol-3-phosphate (G-3-P) and fatty acids bind to coenzyme A (fatty acyl-CoA) or acyl-bearing protein (ACP). The precursor of all fatty acids in seeds is acetyl-CoA, which is

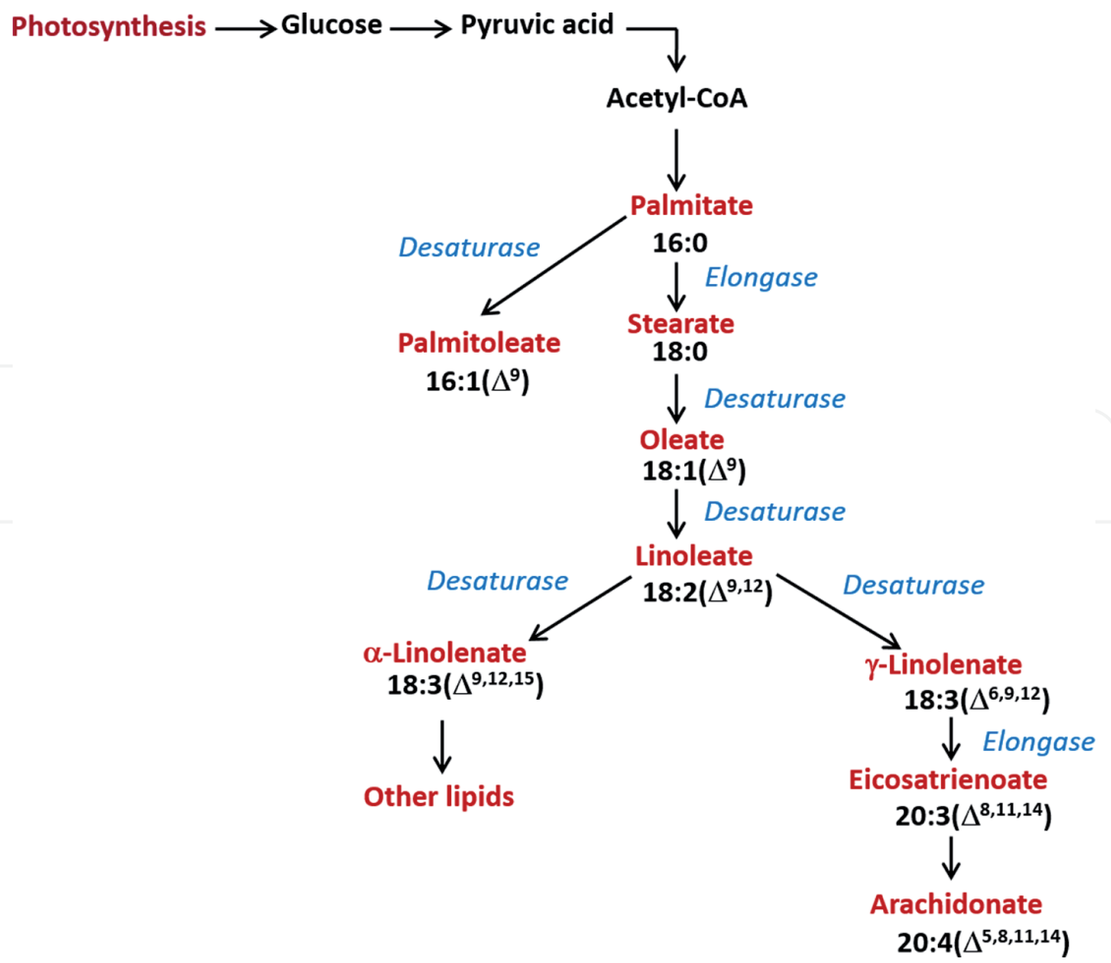

Figure 3.
Production of fatty acids from glucose in plants [40].

derived from sucrose in plants. After sucrose is transported into the developing seed, it is converted to hexose phosphate (Glc-6-P) and triose phosphate (Triose-P) in the plastids. The dihydroxyacetone phosphate is then reduced to yield glycerol-3-phosphate (G-3-P) in the cytosol. G-3-P is then esterified with three fatty acids in the endoplasmic reticulum to form triglycerides. Accumulation of G-3-P is an important limiting factor for the formation of new triglycerides. Glc-6-P is usually transferred to the plastids, but in some species it may also be converted to other intermediates in the cytosol or mitochondria. The first product for fatty acid synthesis is acetyl-CoA, which provides the 2C-acyl groups for the fatty acid chain. The first coupling step in fatty acid biosynthesis is the carboxylation of acetyl-CoA carboxylase (ACCase) to form malonyl-CoA. It is then converted to malonyl-ACP by addition of ACP with malonyl transacylase. Several enzymes are involved in a FAS complex that adds 2C to the extended chain and increases the length of the fatty acid at each cycle. Fatty acids are released from the ACP complex by acyl-ACP trioesterase (FAT) (**Figure 4**) [1, 40–44].

2.3 Protein synthesis

The synthesis and accumulation of storage proteins in seeds can vary due to genetic and environmental factors during seed filling. Synthesis of storage proteins occurs in specific tissues and depending on the stage of cell expansion during seed filling. During seed filling, endosperm, cotyledons, and embryo accumulate various proteins, including storage proteins, acid hydrolases, plant defense proteins and other reserve materials or metabolites. Vacuoles are the major storage organelles in seeds. Seed storage proteins undergo various modifications, including cleavage of signal peptides, glycosylation, folding, disulfide bond formation, and other proteolytic processes. These post-translational modifications are essential for seed protein functions (e.g., hydrolytic enzyme activity) and often have profound effects on seed protein accumulation in parenchymal storage cells (e.g., storage proteins). Proteins are transported simultaneously or shortly thereafter to the plastids, mitochondria, nucleus, and peroxisome/glyoxisome within plant cells by direct recognition through specific targeting signals. In contrast, transport to the vacuole and cell surface occurs through the endomembrane system with the endoplasmic reticulum, golgi complex, and transport vesicles. Proteins transported through the endomembrane system are synthesized on polyribosomes associated with the endoplasmic reticulum and first migrate into the lumen and enter the secretory system. In addition to seed storage proteins, other seed proteins are also transported via the secretory pathway during seed development, including those destined for the tonoplast (vacuolar membrane), plasma membrane, and cell wall matrix [45].

2.3.1 Cleavage of signal peptides

In most cases, the signal peptide is cleaved from the nascent polypeptide chain upon leaving the endoplasmic reticulum by a protease (signal peptidase) located on the inner surface of the membrane. The cleavage usually occurs in the C-terminal region, which allows further processes such as folding and assembly of the protein [46].

2.3.2 Protein folding and assembly

In order to have a three-dimensional structure and function, all proteins must undergo protein folding. With few exceptions, protein folding and assembly occur in the lumen of the endoplasmic reticulum and contribute to protein stability and efficient

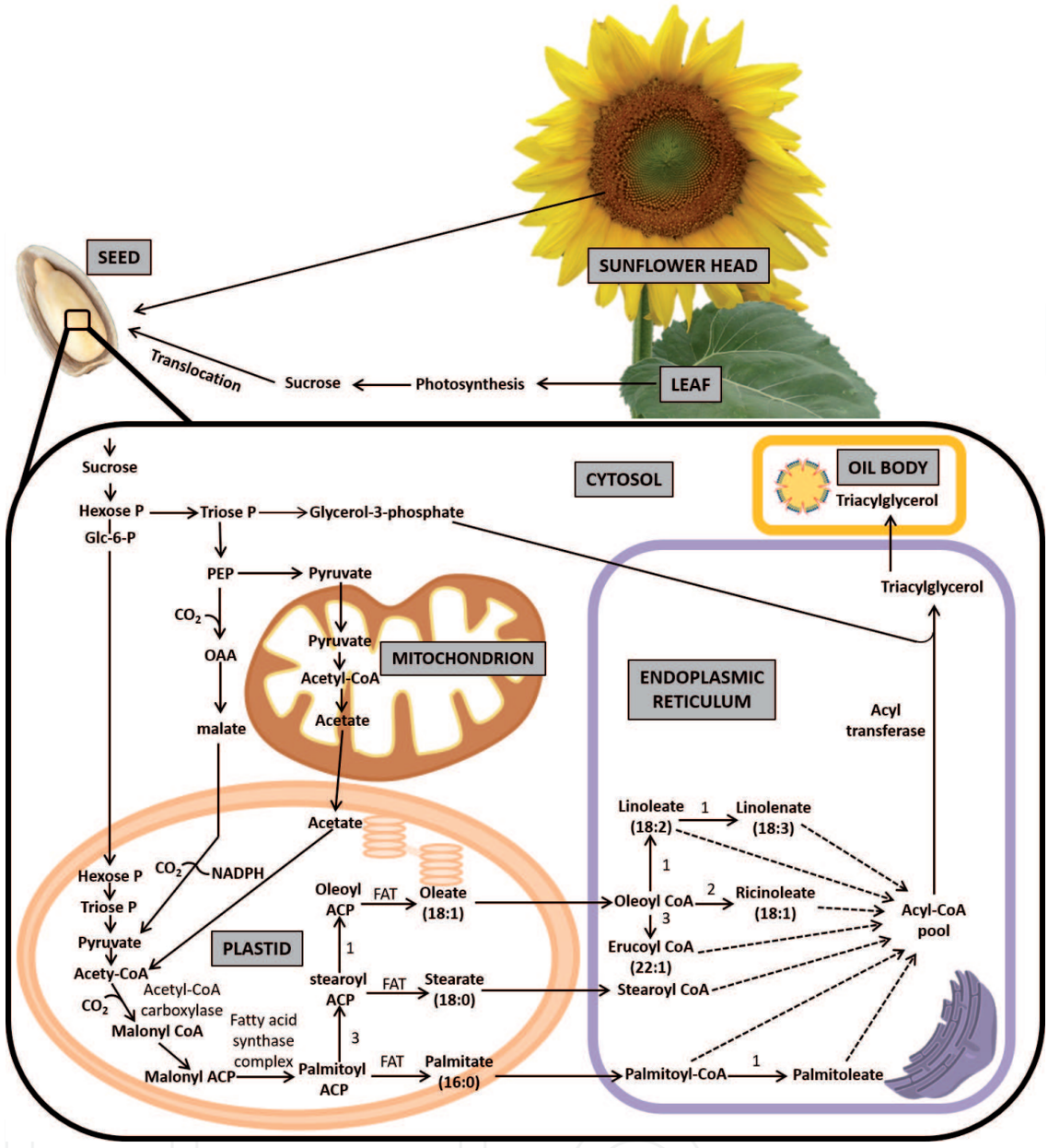

Figure 4.
Synthesis of fatty acids and oils in intracellular organelles during the seed filling period after fertilization. 1: FAD enzymes, 2: hydroxylase enzymes, 3: elongase complex enzymes, FAD: fatty acid desaturases, Glc-6-P: glucose-6-phosphate, PEP: phosphoenol pyruvate, OAA: oxaloacetate, ACP: acyl carrier protein, CoA: coenzyme A, FAT: fatty acyl thioesterase [1].

transport [1, 45–49]. Many plant vacuolar proteins, including storage proteins are oligomers, most of which are oligomerized in the endoplasmic reticulum. Chaperone proteins in the endoplasmic reticulum promote proper folding of polypeptides, and protein disulfide isomerase (PDI) forms disulfide bonds within and/or between peptides using the -SH groups of cysteines. The function of chaperones depends on their ability to recognize a variety of nascent polypeptides that do not share unique similarities, while accurately discriminating between properly folded and unfolded structures [50].

2.3.3 Glycosylation

Glycosylation is a commonly used modification of vacuolar proteins in seeds. The asparagine residue is used for N-linked glycosylation, and vacuolar glycoproteins

usually have both high mannose content and complex N-linked glycans [46, 48, 49]. This process occurs in the lumen of the endoplasmic reticulum because the polypeptide is still in translation and contains a lipid carrier molecule (dolichol phosphate). There are two main types of oligosaccharide side chains: simple or mannose-rich oligosaccharides, which consist of mannose and N-acetyl-glucosamine, and complex or modified oligosaccharides, which are usually rich in mannose but also contain other residues such as fucose, xylose, and galactose. These oligosaccharide side chains may be found on the same polypeptide [45]. Glycosylation is thought to increase the stability of proteins and assist them in folding and assembly [1].

2.3.4 Proteolytic cleavage

Seed proteins transported by the secretory pathway are often subject to post-translational proteolytic cleavage, including storage proteins, seed defense proteins, and various vacuolar enzymes (α-mannosidase and thiol proteases). For seed storage proteins, the process begins during the transition to the vacuole and is completed in the vacuole [51]. Polypeptides can be split into two or three smaller peptides, some peptide chains can be removed, and the N- or C-terminus of peptides can be truncated [51, 52]. These modifications, together with glycosylation, could lead to a heterogeneous pool of mature proteins derived from a single polypeptide. Among storage proteins, 2S albumins undergo the largest posttranslational modifications [1, 45].

2.3.5 Formation of disulfide bonds

Many seed proteins must have disulfide bonds to stabilize their tertiary and quaternary structures. Disulfide bond formation occurs through disulfide isomerase, which promotes disulfide formation, isomerization or reduction, in newly formed proteins [53]. The enzyme interacts with unfolded proteins in the endoplasmic reticulum and catalyzes thiol oxidation and disulfide exchange reactions.

3. Genetic regulation during seed filling

Filling occurs when embryonic development is complete in the seed. Seed filling is under genetic control and is tied to changes in storage reserves. Seed filling is regulated by a network of signals mediated by various hormones [54, 55]. Basic research and information on differentiation, growth, and signal transduction related to seed filling and development is derived from studies in *Arabidopsis thaliana*, and there are sufficient reports to suggest that the major mechanisms regulating filling and development are similar in all plant seeds [55–57]. Recent developments in molecular genetics and genomics have led to a better understanding of the processes that occur during seed filling and development and offer opportunities to control and modify seed quality as well [58]. In addition, understanding the genetic factors that influence seed development could help breeders manipulate filling rate and duration to obtain higher yielding varieties.

Plotting phenotypic values on the growth curve throughout the duration of seed filling and analyzing the results using quantitative genetic approaches is a good strategy for exploring a time-dependent trait [59] to understand seed filling. Gene expression regulating storage reserves during seed filling is interrelated [54, 55, 60]

and many known genes are expressed in the endosperm of flowering plants (**Table 1**). In *Arabidopsis*, four major regulators (ABSCISIC ACID INSENSITIVE3 [ABI3], FUSCA3 [FUS3], LEAFY COTYLEDON1 [LEC1], and LEC2) control many aspects of seed development, such as the accumulation of storage molecules, cotyledon identity, and the transition to desiccation tolerance and dormancy [66]. The ABI3, FUS3, LEC1, and LEC2 network of regulators has the common phenotypic effect of reduced expression of seed storage proteins. In addition, the main role of the LEC2 regulatory network is to up-regulate *FUS3* and *ABI3.* In *Arabidopsis*, several genes have been identified, such as the *FERTILIZATION INDEPENDENT SEED* (*FIS*) genes *MEDEA* (*MEA*) [67, 68], *FERTILIZATION INDEPENDENT ENDOSPERM* (*FIE*) [69], *FIS2* and *MULTI-COPY OF IRA1* (*MSI1*) [70, 71], *MEA* homologs *CURLY LEAF* (*CLF*) or *SWINGER* (*SWN*) [72], and *MATERNALLY EXPRESSED PAB C-TERMINAL* (*MPC*) [73] and *FLOWERING WAGENINGEN* (*FWA*). These genes are all involved in seed filling and early seed development in plants [74, 75].

DNA methylation is also one of the first recognized epigenetic modifications that affect gene expression by determining chromatin structure and compartmentalization of DNA during seed filling [55, 76]. *METHYLTRANSFERASE1* (*MET1*) is the major methyltransferase gene in *Arabidopsis* [77] and DNA methylation by *MET1* is involved in epigenetic control of seed size [78]. Transcriptome dynamics during seed filling have been described in several crops. As observed in barley and wheat seeds, the transition from cellular differentiation to filling in rice seeds is associated with changes in gene expression patterns [79, 80]. Using microarray technology, more than 20.000 genes associated with seed filling have been identified in rice, many of them related to metabolic pathways of carbohydrates and fatty acids [81]. The results of cluster and correlation analysis of these genes revealed 269 genes associated with seed filling [81]. In alfalfa, cluster analysis identified 5165 genes involved in seed filling, and most of these genes were associated with metabolic pathways of proteins for seed storage [58, 82]. The major regulators of gene expression are miRNAs and their expression has been studied in some crops [83], including rice, wheat, and maize [83–85]. Members of the miR156 family are specifically expressed during seed filling in rice by targeting genes of the squamosal promoter-binding protein-like (*SPL*) family. One of these genes, *SPL16,* controls cell proliferation during seed filling, and increased expression of *SPL16* correlates positively with grain yield in rice [86]. miR397 enhances brassinosteroid signaling by down-regulating the *laccase* (*LAC*) gene, which increases grain yield in rice [87]. Also, the expression levels of miR156, miR164, miR166, miR167, and miR1861 suggest that they play regulatory roles in rice during seed development and filling [84].

The major storage reserves accumulated during seed filling are storage proteins, lipids (generally TAGs), and carbohydrates (generally starch). Regulatory networks controlling seed filling are repressed prior to germination to prevent the accumulation of reserves during the vegetative development. Therefore, studies of gene expression during seed filling in tissues at the vegetative developmental stage may provide insight into the regulatory mechanisms underlying seed filling. The transcription factor WRINKLED1 (WRI1) plays an important role in fatty acid accumulation during seed development in *A. thaliana* [88]. Genetic and molecular studies suggest that WRI1 is a target of *LEC2*, *ABI3, FUS3*, and *LEC2* to regulate oleosin expression and lipid accumulation [88]. In *Arabidopsis*, mutations in *LEC1, LEC2* and *FUS3* resulted in decreased accumulation of storage proteins and TAGs [89, 90]. Synthesis of fatty acids in lipid metabolism during seed filling occurs through stimulation of fatty acid synthase or acyl carrier protein genes [58].

Plant	Gene full name	Gene symbol	Proposed gene function/ description	References
Pisum sativum	*TRYPTOPHAN AMINOTRANSFERASE RELATED2*	*TAR2*	Expression of the auxin biosynthesis gene (TAR2) is promoted by trehalose 6-phosphate, and affects auxin concentration by mediating the activation of storage processes in seed filling	[61]
Glycine max	*WRINKLED1*	*WRI1*	Regulates fatty acid accumulation and hormone signaling	[62]
Zea mays	—	*ZmABI19*	Acts as a seed filling start regulator. Also, involved in the accumulation of starch and fatty acids, and in signal transduction of plant phytohormones	[63]
Oryza sativa	*SUPER STARCHY1/ ONAC025*	*SS1/ONAC025*	Seed-specific gene in rice that promotes seed filling and adversely affects vegetative growth	[64]
Triticum urartu	Storage protein repressor	*SPR*	TuSPR expressed in endosperm during seed filling, suppresses the synthesis of seed storage proteins	[65]

Table 1.
Some genes involved in seed filling regulation.

Sugar molecules can act as signaling molecules that regulate genes expressed in photosynthesis and metabolism. High sugar content promotes starch biosynthesis, while it has a negative effect on photosynthesis. Low sugar content increases the expression of genes related to photosynthesis and promotes the transport of seed reserves, while it limits the metabolic processes of carbohydrates [91]. Sucrose content controls cell differentiation and filling processes in seeds by altering gene expression and enzyme activities [92]. In faba bean, pea, and barley seeds, sucrose initiates gene expression regulating seed storage reserves and triggers the transition from embryogenesis to seed filling [93, 94]. Sucrose induces gene expression of globulin and albumin proteins, and *LEC1*, *LEC2* and *FUS3* are important regulators of sucrose in *Arabidopsis* [95]. Sucrose is also imported and converted to starch in endosperm during seed filling [96]. In *Arabidopsis*, mutations in sucrose transporter gene (*AtSUC5*) delayed the conversion of sugars to lipids, and the *AtSUC5* gene is involved in seed filling [97]. In rice, *AGPS2/shrunken2* (starch synthesis gene) is upregulated during the period of increasing seed dry weight [98]. Two rice sucrose synthase (*SUS*) genes are expressed, one at the early stage of seed filling and the other during seed filling, but not in the endosperm [81]. The *GRMZM2G391936* and *GRMZM2G008263* genes are involved in starch and sucrose metabolism during seed filling in maize [59]. The gene *GRMZM2G008263* is the starch synthase gene responsible for the production of amylose and is found only in starch grains [59]. The *GRMZM2G391936* gene encodes the large subunit of ADP-glucose pyrophosphorylase (AGPase). Alteration

of AGPase activity can increase the yield of starchy plants [99–101]. *Trehalose-6-phosphate synthase1* (*tps1*) mutants demonstrated the importance of sugar signaling molecules during seed filling by down-regulating genes for starch-sucrose degradation and up-regulating genes for lipid mobilization to produce glucose [102]. Therefore, sugars as signaling molecules are important regulators during seed filling.

The amino acid content and the composition of the seed storage proteins influence the nutritional value of the seeds. Storage proteins are synthesized during seed filling and deposited in endosperm tissues. The rate of amino acid synthesis controls the rate and yield of storage protein synthesis. The phosphoenol pyruvate carboxylase (PEPC) enzyme is a critical factor in the biosynthesis of storage proteins in soybean, pea, faba bean, and wheat. Therefore, PEPC can be used to increase the protein content of seeds. Overexpression of PEPC in bean seeds results in up to 20% higher protein content per gram dry weight due to increased sugar/starch and free amino acid content [103], which led to the identification of an important marker for the transition from seed filling to the drying stage. Up-regulation of genes involved in amino acid metabolism (such as the amino-transferase gene) during seed filling in alfalfa results in increased amino acid synthesis, which is required for the production of seed storage proteins [58]. In maize, the expression level of marker genes for amino acid synthesis during seed filling has been studied [104]. One of these genes, *ZmAS1,* was expressed in both cobs and kernels, while others, *ZmAS2* and *ZmAS3,* were expressed in kernels. In alfalfa seeds, most of the storage reserves accumulate between 14 and 36 DAP in the embryo at the seed filling stage [105]. The *stress-associated protein 1* (*MtSAP1*) gene of alfalfa directly regulates the accumulation of seed storage proteins [106]. Phaseolin is the major seed storage protein in bean and the phaseolin (*phas*) gene is not expressed during the vegetative phase of plant development [107].

Genes responsible for the accumulation of storage proteins and lipids during seed filling are controlled by cis-acting elements in promoters. Well-characterized cis-elements are the RY repeats (CATGCA), the ACGT box (CACGTG), and the AACA motifs, controlled by the B3, bZIP, and MYB domain transcription factors, respectively [55]. For example, silencing of the *phas* gene in vegetative tissues has been associated with the presence of TATA boxes in the *phas* promoter [108].

Abscisic acid (ABA) is a key hormone involved in the regulation of several processes of seed development, such as maturation and reserve accumulation [109]. In *Arabidopsis*, barley and bean seeds *CYP707A* genes regulate ABA degradation in the embryo and endosperm [110–112]. In addition, gibberellins (GA) and ABA are also involved in cell differentiation and grain filling processes [112, 113]. While the level of GA is suppressed during seed filling, the level of ABA increases. In *Arabidopsis*, the biosynthesis of GA is controlled by the expression of the *AtGA2ox6* gene, but its expression is controlled by ABA levels [114]. Auxin is also involved in the seed filling process and interacts with the transcription factors LEC2 and FUS3 [55, 115]. The transcription factor ABI3 is involved in auxin signaling [116]. Expression of *LEC2* activates auxin-related genes [117] and auxin activates the expression of *FUS3* [118].

Flavonoids such as proanthocyanidins and anthocyanins are accumulated in seeds during seed filling. In alfalfa, several genes such as *MtWD40-1* [119], *MtMYB5* and *MtMYB14* [120], *MtPAR* (a regulator of proanthocyanidin accumulation through its effect on *MtWD40-1*; [121]) have been identified to be involved in the proanthocyanidin biosynthetic pathway during seed filling. In addition, genes for flavonoid biosynthesis have been identified, including chalcone synthases (*Mtr.42237.1.S1_at*), chalcone isomerases (*Mtr.40331.1.S1_at*), and flavonol synthases (*Mtr.45897.1.S1_at*) in alfalfa [58]. These enzymes cause the accumulation of isoflavones in the embryo

[122], but may also be involved in the accumulation of proanthocyanidins in the seed coat and tannins in the bark tissues [123]. Other genes involved in the accumulation of proanthocyanidins have been identified, such as glycosyltransferase (*UGT72L1*) and the proanthocyanidin transporter *MATE1* [124], which is responsible for the synthesis and modification of proanthocyanidin precursors [125]. *MATE2* transports anthocyanin by diverting flavonoid precursors into the anthocyanin pathway [126]. In addition, glycosyltransferase (*UGT78G1*) is required for the modification and accumulation of anthocyanins [127]. All of these genes are involved in the control of anthocyanidin reductase, one of the major enzymes responsible for the production of proanthocyanidins.

4. Role of phytohormones during seed filling

Seed development is divided into two main phases: the cellular phase and maturation [128]. The cellular phase includes all the processes involved in the formation and development of the different parts of a seed. In this stage, storage reserves for the embryo are synthesized and seed filling takes place. Phytohormones regulate signaling between the embryo and the endosperm. Most studies on seed filling and development have used *Arabidopsis* and maize as model plants for dicotyledons and monocotyledons. Although monocotyledonous and dicotyledonous plants share common seed characteristics, seed filling and developmental processes differ significantly between the two groups. In developing seeds, precise coordination is required to organize cell distribution in tissues and organs, and to control seed filling. The cells in the seeds can control all these activities by producing and sensing signals. The synthesis and regulation of phytohormones in the process of seed filling is essential for seed development [129, 130]. Seed filling is a highly coordinated and complicated process involving hormonal control and constant exchange of signals between different parts of the embryo [128].

Many studies have shown that hormone levels change during seed development and filling. Phytohormones, such as ABA, GA, cytokinins, Indole-3-acetic acid (IAA), and ethylene regulate seed filling processes (**Figure 5**) [132, 133]. Phytohormone gradients are synthesized in distinct seed sections, and their ratio controls signals that activate or inhibit specific seed filling processes. Among the hormones, ABA plays a central role as it accumulates at high levels from fertilization to seed maturation. Therefore, ABA functions as a signaling molecule and is important for seed filling, seed growth, dormancy, and plant stress responses [134]. Seed filling rate was positively associated with the concentration of ABA, and higher concentration of ABA resulted in higher seed filling rate [135]. In maize, the concentrations of ABA were associated with seed filling rate and kernel weight [136, 137]. Seed filling in barley, wheat, rice, and sorghum is closely related to senescence and the senescence-related hormone ABA, which affects nutrient mobilization and grain filling time [138] and is involved in the expression of senescence-related genes in barley [139]. High ABA levels increase remobilization of previously stored carbon in grains and accelerate grain filling rate [140] and have significant effects on seed filling in upper and lower grains [141]. ABA also inhibits cell cycle while accelerating seed maturation by upregulating inhibitors of cyclin-dependent kinases, which are important regulators of the cell cycle. [142, 143]. While ABA has a positive effect on stomatal activity, seed dormancy, and plant response to abiotic and biotic stresses, it has a negative effect on seed germination [144]. Other plant hormones, such as gibberellins, ethylene, cytokinins,

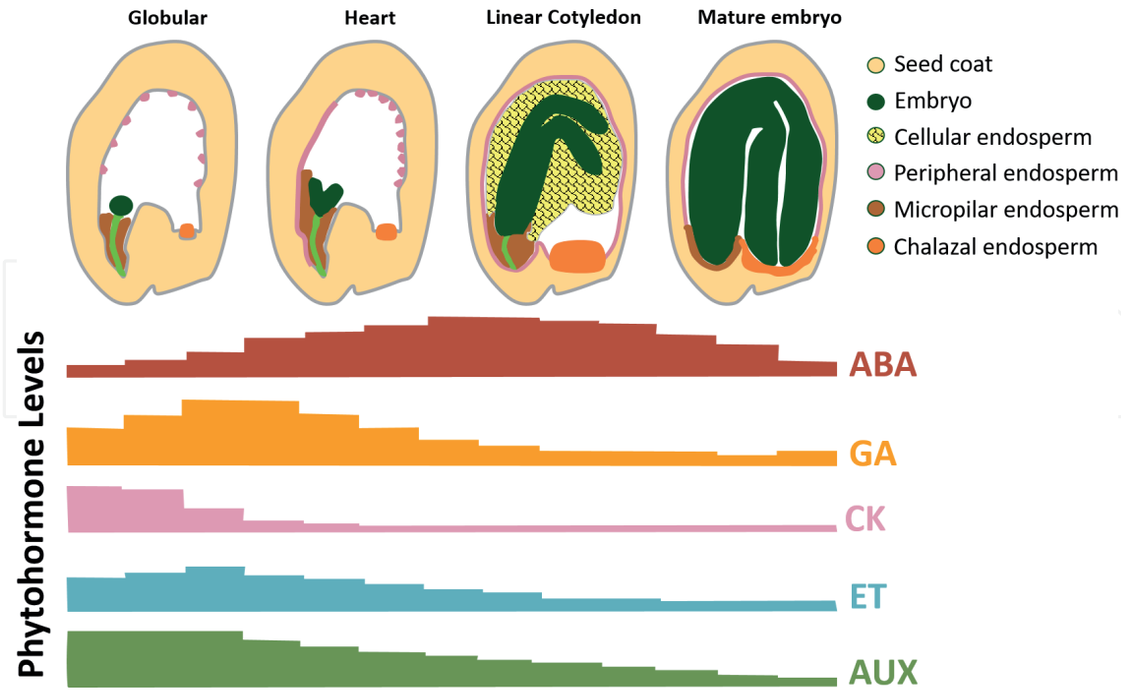

Figure 5.
Schematic representation of phytohormone accumulation during seed development. (A), represents the stages from late seed development to seed maturity of a dicot plant. (B) Shows the changes in specific phytohormone levels from top to bottom. Longer bars indicate higher levels. Three types of endosperm are formed during maturation: unicellular stratified endosperm, micropylar endosperm, and chalazal endosperm. High concentrations of abscisic acid, present at all stages of seed development, are thought to play a key role in seed filling. Gibberellins are synthesized in the differentiation stage of the embryo to promote cell growth and expansion, and in the late maturation stage to activate proteolytic enzymes. Accumulation of abcisic acid inhibits all processes induced by gibberellins. The accumulation pattern of cytokinins is opposite to that of abscisic acid. Cytokinins play an important role in cell division and their levels gradually decrease during the cell enlargement phase. Ethylene production increases during the early stage of seed development. Auxin controls grain filling by regulating invertase activity. An increase in auxin levels improves sink capacity and nutrient uptake [131].

brassinosteroids, and their antagonistic interactions with ABA could improve seed germination. ABA can stimulate sucrose storage in the seed coat and accelerate sucrose transport to the cotyledons during seed filling [145]. Gibberellins are also involved in cell differentiation and seed filling. Gibberellin concentration in seeds was not significantly related to seed filling rate or seed weight [146], but GA content had a negative effect on seed filling rate in rice seeds [140]. These studies showed that ABA and GA have antagonistic effects during seed filling [147]. The amount of bioactive GA decreased at the stages when ABA peaked with inactivation reactions to ensure normal seed filling and growth [148].

Cytokinins are involved in cell division, chloroplast formation, senescence, and stress tolerance in plants [149]. Cytokinins also play an important role in seed filling by inducing rapid cell division of endosperm cells [131]. In addition, zeatin (Z) and zeatin riboside (ZR) are biologically important cytokinins in higher plants [150]. Zeatin and ZR contents increase fertilization, kernel set, and endosperm growth in cereals [151]. High Z and ZR contents are necessary for seed filling, endosperm development, and cell division in wheat [151]. Higher Z and ZR contents in seeds can improve seed filling rate in the early and middle stages of seed filling and are associated with seed filling rate in rice and maize [152, 153]. Zeatin and ZR increase simultaneously with the peak of endosperm mitotic activity during seed filling [154]. Exogenous application of GA in maize improved the degree of grain filling by

increasing the levels of auxin, GA, Z and ABA in the grains [155]. It was also found that auxin, GA and Z content in grains was positively associated with grain mass and filling degree of grains. Cytokinin oxidase decreases cytokinins content in the later stages of seed development [58]. Cytokinin content is related to flower development, grain filling and endosperm growth in rice [152]. Grain seeds also have high cytokinin contents during endosperm development, and cytokinins promote cell division in the early stages of seed filling [152]. In addition, cytokinins and GA have antagonistic effects on various processes of seed development [156]. The levels of Z, ZR, ABA, and IAA in maize were positively correlated with seed filling rate and negatively correlated with the GA levels [157]. In wheat, the levels of Z, ZR, ABA, and IAA were positively correlated with seed filling rate and seed mass, but the ethylene content was negatively correlated [158, 159]. In maize, ABA, Z, and ZR contents were also positively related to seed mass and seed filling rate, but GA content was not. Seed filling rate was dramatically increased when ABA and Z content were higher and GA content was lower [153]. ABA, IAA and ZR contents in maize seeds increased dramatically during the early stages of seed filling and decreased gradually until maturity [160]. Similarly, Z and ZR contents of maize gradually increased during the early stages of seed filling, while the GA content decreased [153]. Moreover, the fluctuations in ZR and IAA contents were similar, they briefly increased in the early stages of grain filling and then decreased in the kernels [155]. The contents of IAA and Z + ZR affect the seed filling rate of maize and are normally located in the endosperm, as they are required for cell division [161]. IAA has been proposed as a correlative signal from seeds that regulates the development of other organs [162]. In maize seeds, high IAA and low ethylene content were significantly associated with grain filling rate [129] and high IAA content in seeds increased cytokinins content [163]. These observations were confirmed by Ahmad [164] who reported that IAA and cytokinin content play an important role in grain filling of maize at early stages by regulating endosperm cell division and thereby increasing seed filling rate. In soybean, IAA concentration and seed filling rate were independent [145]. Seed filling in maize appears to be dependent on IAA synthesis and cell wall invertase activity [128]. The absence of endogenous auxin in the embryo could be lethal [128], indicating the critical functions of the phytohormones in seed development and germination. Invertase activity, together with auxin transport, is important in regulating pathways of carbon cleavage during early development. Sugar signaling is thought to increase phloem transport and sugar import into endosperm cells via invertase activity [165]. Ethylene is also involved in cell division and grain filling [112]. Higher ethylene concentration leads to lower cell division, grain filling, and starch concentration, and higher ethylene concentration leads to higher soluble sugar content in growing rice endosperm [166]. Since cytokinin is known to regulate cell number and cell division activity of rice endosperm, the deleterious effects of ethylene on grain filling and cell division could be mediated by its antagonistic effect with cytokinin [166]. Apart from rice, there are studies reporting that the effect of ethylene is antagonistic to cytokinin [167], because ethylene production in plant tissues promotes cytokinin inactivation [168]. The ratio of ABA to ethylene regulates grain filling rate in wheat [112].

These studies show the importance of phytohormones during seed development. Therefore, seed filling is determined by the content and interactions of various plant hormones that regulate different metabolic processes related to the synthesis and accumulation of seed reserves [169].

5. Effect of environmental factors during seed filling

Stress in plants was described by Hans Selve in 1936 as "unfavorable conditions and environmental constraints in plants". This general definition can be applied to all organisms, but the definition of stress in plants differs from that in animals and humans. Plants are sedentary and live in fixed locations. Therefore, they cannot escape abiotic stress conditions when exposed to them and are constantly exposed to these conditions without protection. Animals, on the other hand, are mobile and can avoid and escape these conditions when needed. Since plants are sedentary, they need mechanisms to protect themselves from stressful conditions so that they can continue their vital activities [170].

Global warming and drought in the world have become important inhibitors of agricultural production in recent years. The process of seed filling, which is affected by environmental factors, is becoming increasingly important for agricultural production because the potential heat and drought affect the, and rate and duration of seed filling. To overcome these adverse conditions, plant breeders are developing new varieties that are resistant to biotic and abiotic stress conditions while ensuring efficient water and nutrient use and good yields. After pollination and fertilization, seed development begins with cell division for embryo and endosperm development in the ovule and continues with cell expansion and differentiation to form seeds. Seed formation continues with the accumulation of storage reserves such as carbohydrates, proteins, and lipids. After accumulation is complete, desiccation occurs, during which the seeds lose moisture.

Flowering plants reproduce by the production, dispersal and germination of seeds. The cellular stage includes all processes involved in the formation and development of the various parts of a seed. At this stage, the storage reserves for the embryo are synthesized and seed filling takes place. Many factors influence seed production and seed content. The position of seeds on the inflorescence can affect the duration and rate of seed filling. Seeds farthest from the transport source, such as seeds on a cob, may remain small because they do not receive sufficient nutrients for optimal seed growth. In the early stages of seed development, a constant and adequate supply of nutrients is required for seed production. Seeds that do not receive an adequate supply of nutrients during the generation stage may fail to develop or develop poorly and have a smaller seed mass. Plants can be affected by abiotic stress at any stage of development, but the generative stage is the most critical period when plants respond to stress conditions. Stress conditions during the generative stage adversely affect pollen formation, pollination and fertilization rates, and reduce fruiting and seed set, resulting in yield losses. The generative stage is highly susceptible to drought, cold, and heat, and these stress factors reduce fertilization, seed development, and the filling process [171]. Heat stress has significant negative effects on meiosis during pollen development and could greatly reduce pollen fertility, pollen quantity and quality, pollen germination, and pollen tube development on the stigma [172, 173]. Heat stress can also significantly affect seed development during the seed filling stage due to reduced assimilate supply and reduce seed yield in many crops including cereals and legumes [174, 175]. The seed filling period is also closely related to the development of plant senescence [129]. Heat and drought stress during the seed filling period cause early senescence and also shorten the seed filling time [176, 177].

5.1 Effects of drought stress during seed filling

Drought stress limits vegetative growth by reducing leaf water content and stomatal conductance [178] in various crops such as cereals [179, 180] and legumes [181]. Decreased stomatal conductance increases leaf temperature, and both events

lead to wilt symptoms [182, 183]. Drought stress damages cell membranes [184, 185], decreases chlorophyll content, photosynthesis, and reserve synthesis [178, 186–188]. Drought stress also impairs plant nutrient uptake [189, 190] and significantly reduces nitrogen fixation in legumes such as soybean [191] and pea [192]. The overall negative effects of drought stress reduce the production of assimilates and reduce the transport of reserves to the developing seeds of plants [193–195].

The generative phase of plants is more sensitive to drought stress than the vegetative phase. Drought stress reduces the number of flowers, fruits, and seed set and therefore could reduce seed yield [196, 197]. Decreased water content in tissues leads to a reduction in the activity of the acid invertase enzyme, which in turn prevents sucrose uptake into developing seeds [198]. Low sucrose and high ABA levels lead to poor seed development in cereals under drought stress [199]. Wheat plants subjected to drought stress during the seed filling period showed a significant decrease in cell wall and soluble invertase activities, and glucose, fructose, and sucrose contents of the drought-sensitive genotype were significantly lower [200]. Drought in the early stages of seed development leads to a reduction in seed size due to reduced number of endosperm cells. Seed yield was significantly reduced in plants subjected to drought stress during the seed filling stage [186, 201, 202]. Drought stress in the early stages of seed filling reduced germination percentage in soybean by up to 9% compared to the control [203]. Similarly, in chickpea, medium-sized seeds produced under drought stress had lower germination percentage and viability than control seeds [204].

Drought stress during embryogenesis and seed filling reduces the number of endosperm cells formed and thus the size and weight of the seeds [205]. At this stage, the duration and amount of seed storage reserves, such as starch accumulation in the endosperm decrease, and so does seed weight [206]. Drought stress during seed filling reduces the number and size of starch granules in endosperm cells [206]. Drought stress affects the composition of seed reserves. The starch content of wheat seeds subjected to drought stress during seed filling is significantly reduced [207]. Drought stress negatively affects phthosynthesis, and low phthosynthesis product content inhibits starch biosynthesis [208] and related activities such as reduced endosperm cell number and starch granule size [206] and lower starch amylase content [209].

Lipid content and fatty acid composition change due to lower content of soluble sugars such as glucose, fructose, and sucrose and reduced transport of sugars from the phloem to endosperm cells under drought conditions [210]. In peanuts, the content of linoleic and behenic acids decreased, while the content of stearic and oleic acids increased under drought stress [211]. In maize, drought stress resulted in a significant decrease in oil content, while the content of linolenic and oleic acids in the seeds increased. In addition to the oil content, the total tocopherol, flavonoids, and oil-soluble phenolics contents also decreased [212, 213]. In soybean, drought stress decreased the oil content and oleic acid content of seeds [214]. While drought stress reduced the starch and oil content of seeds, the protein content of soybean seeds grown under drought stress increased. Seed nitrogen supply depends on remobilization of nitrogen from vegetative tissues, while starch and oil biosynthesis depends on sugars from photosynthesis, which decreases under drought stress. For this reason, seed viability may also be affected by drought during late maturation and seed desiccation.

5.2 Effects of heat stress during seed filling

Heat stress affects all stages of plant development from germination to senescence. Different plants have different sensitivities to heat stress during seed filling [215,

216]. Seed filling rate and potential seed mass are generally used as two selection criteria for heat stress tolerance [217]. High temperature stress could accelerate seed filling rate by shortening the duration of seed filling and could lead to yield reductions [216, 218]. Heat stress during seed filling significantly reduces seed weight, seed number and seed yield in legumes [219–221], cereals [222], and other crops [223]. In chickpea [224] and lentil [183] increased seed filling rate resulted in smaller seed size. Similarly, a reduction in seed filling time resulted in smaller seed sizes in soybean, pea, and white lupin [225]. Temperature also affects seed filling rate and duration. An increase in ambient temperature from 15.5°C to 26.6°C decreased seed filling duration in cowpea from 21 days to 14 days [226]. A 1.7°C increase in temperature shortened the duration of seed filling and accelerated maturation, but decreased seed yield in chickpea [227].

Starch accounts for more than 65% of the dry weight of cereal seeds [228]. Therefore, the main reason for yield reduction is mainly the reduction in starch accumulation. Heat stress during the seed filling period reduces seed size and mass in wheat [229] and rice [230], and also impedes starch biosynthesis and accumulation by altering the expression of genes in starch biosynthetic pathways [231]. As a result of altered gene expression, the amount of non-structural carbohydrates decrease, altering the balance between soluble sugars and starch [232]. Heat stress decreases the content of sugars such as fructose and hexose phosphate in wheat [233]. In some cases, up-regulation of starch hydrolyzing enzymes such as α-amilaz under heat stress is thought to be responsible for the increased sugar content during seed filling [234, 235]. Thus, heat stress negatively affects starch accumulation by altering gene expressions in metabolic pathways. These changes may vary depending on the duration of heat stress, the growing season, and the plant species.

Oil content and quality are severely affected by heat stress in oliferous crops [236]. The effects of heat stress may vary depending on location, altitude, precipitation, and differences between day and night temperatures during the seed filling period. Because oleic acid and linoleic acid are produced by the same pathway through desaturation, there is a strong and negative correlation between them, and temperature and precipitation during the flowering and seed filling periods have significant effects on the fatty acid composition of plants [237]. Growth experiments conducted at different temperatures (10, 16, 21, 26.5°C) with canola, flax, sunflower, safflower and castor bean during the seed filling period have shown that the fatty acid composition changes and the amount of unsaturated fatty acids is reduced, with the exception of safflower and castor bean [238, 239]. High temperatures during seed filling reduce linoleic acid content and increase oleic acid content in seeds, while palmitic and stearic acid content change insignificantly [240–242]. The fatty acid composition of rapeseed also changes depending on location and year. While low temperatures and precipitation decreased oleic acid content, high temperatures and low precipitation did not cause significant changes in linoleic and linolenic acid content [243]. The activities of oleayl-PC desaturase and linoleayl-PC desaturase, which catalyze the synthesis of linoleic and linolenic acids from oleic acid, are decreased by high temperatures [244]. Consequently, high temperatures have negative effects on linoleic and linolenic acids synthesis, whereas high temperatures have positive effects on oleic acid synthesis [240, 241, 245]. Linolenic acid is the major fatty acid in flaxseed, and increasing temperatures (15, 20, 25, 30°C) during seed filling reduced the oleic and linolenic acids content in flaxseed [246]. Increasing the growth temperature from 29°C to 35°C during seed filling in sunflower and soybean resulted in a 2.6% reduction in oil content in the seeds of these plants [214, 247].

Heat stress reduces the duration of seed filling, the amount of protein accumulation and protein quality, but has no effect on the rate of accumulation [248]. The composition and quality of storage proteins change due to changes in nitrogen mobilization during seed filling in wheat under heat stress [228, 249]. A decrease in high molecular weight glutenins and increased gliadin accumulation decreased dough quality in wheat under heat stress [248]. Similarly, high temperatures caused denaturation and aggregation of several storage proteins (globulins, legumin, and vicilin) in pea [250] and loss of enzyme activities in protein synthesis in lupin [251].

6. Conclusion

Effects of climate change and the growing world population along with reduced natural resources pose a major challenge for crop production and food security, especially in the developing countries. In this chapter, we have provided an overview of genetic regulation and synthesis of seed reserves, the role of phytohormones, and the influence of environmental factors on metabolic processes during seed filling in different plant species. To increase crop productivity, it is necessary to understand seed development processes together with reserve synthesis and accumulation under normal and stress conditions, and the control and regulation at the molecular and hormonal levels in seeds during seed filling. We have summarized recent studies on seed filling processes by highlighting the effects of phytohormones on the seed filling process and their interactions the effects of abiotic stress conditions on seed reserve quality and yield during the seed filling process.

7. Future perspectives

Future work should be directed toward investigating various signaling and metabolic pathways during seed filling, and developing a feasible system for delimitating roles of different genes, their regulation and interactions during seed development to better understand roles of these reserve metabolites and their interactions. In addition, future studies could process RNAs, proteins, and metabolites as quantitative traits, offering new insights into the integration of omics tools and how these traits may regulate seed filling as well. In the future, these new insights will help to understand the biochemistry and physiology of the seed filling process at the molecular level and manipulate metabolic pathways to improve valuable seed traits through metabolic engineering. The duration of seed filling is under genetic control and influenced by environmental factors. Therefore, it could be used as a selection criterion in plant breeding programs that focus on yield enhancement. There is a need for multidisciplinary studies to delimitate steps in the synthetic pathways leading to seed storage compounds, and their regulation. In recent years, progress has been made in understanding the various aspects of seed development including seed filling, maturation, acquisition of desiccation tolerance, and post-maturation stages. Identification of important genes and regulatory pathways related to seed filling processes will provide useful tools for developing better strategies to improve seed production. New omics studies will expand our understanding of the processes associated with seed filling. Modeling the stages associated with seed filling, and seed quality will provide insights into seed development and lead to improved seed yield and quality.

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Conflict of interest

The authors declare no conflict of interest.

Author details

Sercan Önder[1*], Sabri Erbaş[2], Damla Önder[3], Muhammet Tonguç[1] and Murat Mutlucan[2]

1 Department of Agricultural Biotechnology, Faculty of Agriculture, Isparta University of Applied Sciences, Isparta, Turkey

2 Department of Field Crops, Faculty of Agriculture, Isparta University of Applied Sciences, Isparta, Turkey

3 Department of Biology, Faculty of Arts and Sciences, Suleyman Demirel University, Isparta, Turkey

*Address all correspondence to: sercanonder@isparta.edu.tr

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