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REVIEW

Signal transduction during wheat grain development

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Abstract

Main conclusion **This review examines the signaling pathways from the developmental and environmental point of view and the interactions among external conditions, hormonal regulations, and sugarsensing in wheat.**

Grain development is the key phase of reproductive growth that is closely associated with vegetative organ senescence, initiation of grain filling, pre-stored assimilates remobilization, and maturation. Senescence is characterized by loss of chlorophyll and the degradation of proteins, nucleic acids, lipids as well as nutrient exports to the sink. The initiation and progression of vegetative organ senescence are under the control of an array of environmental signals (such as biotic and abiotic stresses, darkness, and nutrient availability) and endogenous factors (including aging, multiple hormones, and sugar availability). This review will discuss the major breakthroughs in signal transduction for the wheat (*Triticum aestivum*) grain development achieved in the past several years, with focuses on the regulation of senescence, reserves remobilization and biosynthesis of main components of the grain. Different mechanisms of diverse signals in controlling different phrases of wheat grain development, and cross talks between different signaling pathways will also be discussed. For perspectives, key signaling networks for grain development remain to be elucidated, including cross talks and the interactions between various environmental factors and internal signals.

Keywords Grain development · Hormones · Senescence · Signal transduction · Wheat (*Triticum aestivum* L)

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Introduction

Cereal grain development is a genetically programmed process that is related to senescence of vegetative organs (source) and remobilization of the degradation products to the reproductive organs (sink). Senescence is characterized by a general dismantling of cellular structures such as chloroplasts (Fig. 1) (Kong et al. 2010), a decrease in photosynthetic performance, and programmed cell death (PCD). However, our observations under TEM suggested that the PCD did not frequently occur in the cells of flag leaves and glumes as revealed by rare occurrence of the chromatin condensation (Fig. 2).

Senescence can be controlled by many internal and external factors and can be accelerated or delayed by alteration of these signals. Nutritional limitation, especially in concerns of N, has been shown to be able to enhance leaf senescence. Sunflower (*Helianthus annuus*) plants grown under low N supply showed a stronger decline of photosynthetic activity and more pronounced senescence symptoms than plants sufficiently supplied with N (Aguera et al. 2010). Gpc-B1, a QTL locus in wheat encodes a NAC transcription factor (*NAM-B1*), accelerates senescence and enhances nutrient remobilization from leaves, and is associated with increased grain protein content (Derkx et al. 2012). RNA interference mediated silencing of multiple

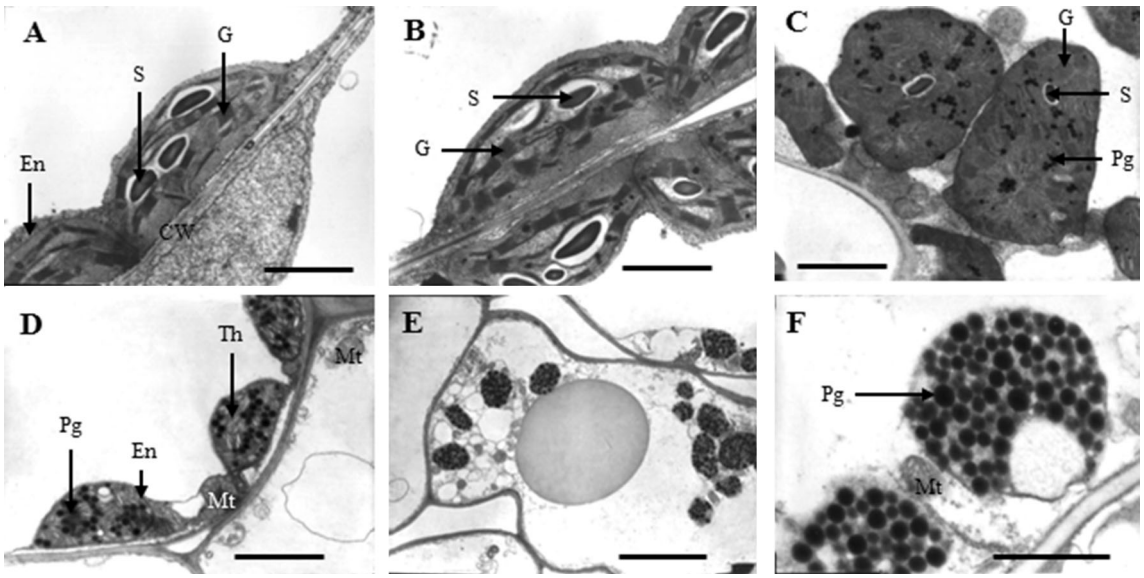

Fig. 1 Transmission electron micrographs showing the ultrastructure of the chloroplast at different stages in flag leaves. At the end of anthesis and milk development stages, chloroplasts are well differentiated, containing fully developed grana with numerous layers and well-developed stroma lamellae with several starch granules (**a**, **b**). The soft-dough development stage is characterized by slightly dilated thylakoid membranes, an irregular arrangement of the thylakoid stacks, and a marked increase in the number of plastoglobuli, indicating the onset of leaf senescence (**c**). At the hard-dough development stage, the chloroplasts were smaller but structurally swollen, and their ultrastructure was characterized by a disintegrating envelope, disrupted and irregularly-shaped thylakoids and irregularly arranged thylakoid grana with fewer stacks (**d**). At the ripening stage, thylakoid membranes is completely disintegrated and the entire structure of the chloroplasts is ruptured (**e**, **f**). *Bars* **a**–**d** 2 μm; **e** 5 μm; **f** 1 μm. *CW* cell wall, *En* envelop, *G* granum, *Mt* mitochondrion, *Pg* plastoglobuli, *S* starch, *Th* thylakoid (Kong et al. 2010)

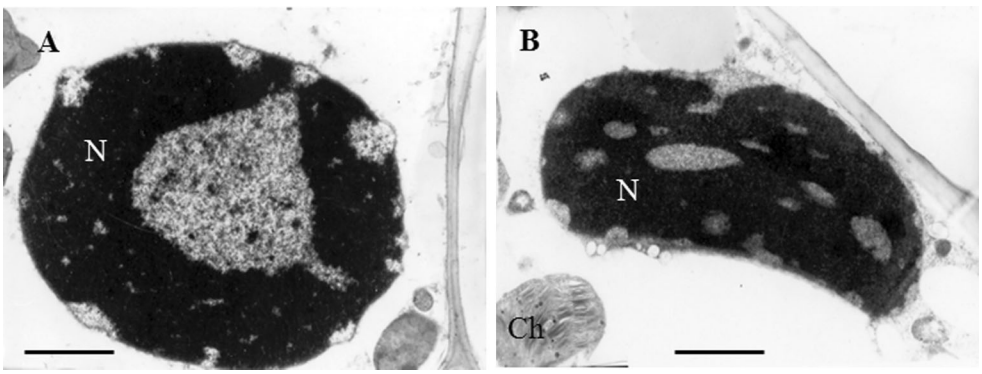

Fig. 2 Transmission electron micrographs of flag leaves (**a**) and glumes (**b**). The chromatin condensation, indicator of the programmed cell death, occurs at the late stages of grain development. *Ch* chlorophyll, *N* nucleus. *Bars* 2 μm

homologues resulted in a delay of leaf senescence by approximately 3 weeks and decreased grain protein, iron and zinc content by more than 30 % (Uauy et al. 2006), indicating that the relation between senescence and nutrient remobilization is complex and cannot be modified as easily as expected (Slimane et al. 2013). The external cues include stresses such as drought, nutrient deficiency, and shading. Among these stresses, limited N availability is one of the main causes promoting proteolysis and N remobilization and, ultimately, senescence in field-grown wheat plants (Crafts-Brandner et al. 1998; Criado et al. 2007; Gan and Amasino 1997), while higher N inhibited both the proteolytic activity and N remobilization (Kong et al. 2013).

Senescence of vegetative organs is essential for reserves remobilization to developing grain. In wheat, 60–95 % of the grain nitrogen (N) comes from the remobilization of N stored in vegetative organs before anthesis depending on the genotypes and environment and their interactions, a minor portion of grain N is derived from N uptake post-flowering (Hirel et al. 2007; Kichey et al. 2007). However, it seems that grains do not regulate their N filling rate themselves. Although half of the mobilized N came from the blades,

grain filling by mobilized N appeared to be largely regulated by stem and/or sheaths; therefore these organs did not behave as a passive transient storage place, but they developed a temporary sink activity with a regulating role at the whole plant level (Slimane et al. 2013). More exactly, the grain-filling rate is largely determined by source/sink relationships; for example, a decrease in grain N sink strength may result in stay-green trait and low reserves remobilization efficiency (Derkx et al. 2012).

In addition, many other compounds influence grain development. Nitrate reductase (NR) activity was highly correlated to N absorbed post-flowering and to grain protein content. Glutamine synthetase (GS) activity was even more highly correlated than NR activity to the amount of N remobilized and grain yield (Kichey et al. 2007). The activity of GS, particularly the cytosolic GS1, is induced during leaf senescence, resulting in an efficient remobilization of amino acids from senescing leaves towards grain filling (Kant et al. 2011). Thus, a significant correlation between GS activity and grain N content was observed in wheat. Serine proteases are the most important family of proteases participating in N remobilization in wheat (Chauhan et al. 2009). Even though the grain development is of importance for getting admired yields in cereal crops and a large number of studies have been conducted at the physiological and molecular levels, to date, signals regulating these processes are as yet poorly understood. This review focuses on the most recent reports on the function of signals involved in wheat grain development. We will in particular address the role of phytohormone and sugar signaling pathways.

Hormone signaling

It is well known that plant hormones are involved in seed development (Yang et al. 2003a; Song et al. 2012). Grain hormone content or exogenous application of hormone is significantly correlated to grain-filling rate by modulating the sink strength of the grains and varies with grain-filling stage (Yang et al. 2000a, b; Travaglia et al. 2010). Grain cytokinin levels are maximal immediately after anthesis, followed by peaks of GA and auxin during the linear growth phase, and then of ethylene and ABA as the grain mature. In addition, complex interactions between environment cues (such as water stress and N availability) and levels of cytokinins, GA, auxin and ABA were observed in a detailed study of developing grains (Yang et al. 2001, 2006).

Cytokinins (CKs)

Cytokinins are plant growth regulators that regulate many developmental and physiological processes in plants, including senescence, reproductive development and grain yield. Exogenous application of CKs causes a delay in senescence in many plant species and the level of endogenous CKs decreases with the progression of tissue senescence (Gan and Amasino 1997; Buchanan-Wollaston et al. 2003). It has also been shown that N supply to the plant resulted in a delayed senescence and protein degradation, which was closely associated with higher CKs concentration (Forde 2002; Yang et al. 2002). In senescent wheat plants induced by N starvation, a sharp fall in isopentenyladenosine occurred as the earliest signal triggering protein degradation, which may subsequently lead to ABA accumulation and oxidative stress (Criado et al. 2007).

This role of vegetative organ CKs in regulating senescence was associated with a delay of proteolytic activity (Noodén et al. 1997), increased NR activity, decreased nitrate concentration and thus inhibiting N remobilization (Criado et al. 2009). Higher CKs in vegetative organs may determine reserve remobilization by inhibiting assimilate exports to the phloem (Criado et al. 2009). Two subtilisin-like proteases (P1 and P2) participated in N remobilization to developing grains during senescence and their induction and functions were regulated by a CKs-mediated mechanism (Roberts et al. 2011).

It is well documented that grain CKs regulate assimilate partitioning, sink strength and source/sink relationships. Hess et al. (2002) reported that the grain CK levels [>30 μmol kg^{-1} dry mass (DM)] in ovules is high during early embryony (0–7 DPA) and significantly higher than ABA and IAA, coinciding with early embryo and endosperm cell divisions (Hess et al. 2002). By initiating rapid cell division, the high level of CKs probably enhances sink strength (Hess et al. 2002; Yang et al. 2002). At the soft-dough stage and thereafter, CKs content gradually decreased (Hess et al. 2002). CKs homeostasis regulated by their gene family members during reproductive development will contribute to grain yield and quality (Song et al. 2012). Rijavec et al. (2009) concluded that grain CKs might promote grain development by enhancing sink strength at early stages of grain filling and, consequently, increasing grain size by up-regulating cell cycle related genes through the action of sugar signaling and by enhancing phloem unloading and sugar import into the endosperm through enzymatic activity of cell wall invertase.

Auxin

Auxin is an important signal in the cereal endosperm and embryo development and this may be due to its ability to establish embryo polarity (Hess et al. 2002), stimulate endoreduplication in endosperm (Lur and Setter 1993), and cell division (Yang et al. 2003b).

Indole-3-acetic acid (IAA) contents in rice grains transiently increased at the early filling stage and coincided with the rapid increase in grain-filling rate (Yang et al.

2001). This result was highly consistent with that observed in wheat where IAA increased rapidly and reached their highest points during the soft-dough stage (Hess et al. 2002). Similarly with CKs, the heights and timings of such peaks were regulated by N nutrition status, with high N being associated with lower peaks and their later appearance, and soil drying hastened decline in grain IAA contents at the late grain-filling stage (Yang et al. 2001). Increased IAA levels in differentiating tissues could enhance the sink capacity of the grain by affecting components of grain growth such as cell enlargement and nutrient accumulation (Hess et al. 2002). Recently, it is supposed that IAA can induce the expression of MADS29 after flowering to regulate the PCD of nucellus and nucellar projection; thus, acting through MADS29 might be as one pathway in auxin regulation of the PCD processes that are required for normal endosperm development and grain filling (Yin and Xue 2012).

ABA

ABA is also generally believed to be one of the major regulators of plant senescence. Generally grain ABA content was low at the early grain-filling stage (1.0 μmol kg^{-1} DM in wheat), reaching a maximum when the grain-filling rate was highest, namely, the ABA peak values were significantly correlated with the maximum grain-filling rates (Hess et al. 2002; Govind et al. 2011). It seems that ABA has little effect on early embryo development; wheat embryos develop normally in ABA-deficient kernels and become dormant if exposed to ABA after embryo differentiation has occurred (Rasmussen et al. 1997; Suzuki et al. 2000). But at the rapid grain filling stages, accumulation of ABA in developing seeds is an important prerequisite for reserves remobilization, efficient grain filling and therefore grain development (Seiler et al. 2011; Yang et al. 2001,2006).

In contrast to CKs, ABA treatment or endogenous ABA often promotes senescence (Yang and Zhang 2006) and remobilization of pre-stored assimilates to the grains, accelerates grain filling, and thus improves yield (Tietz et al. 1981; Yang et al. 2000a, b). ABA was significantly and negatively correlated with the photosynthetic performance and chlorophyll content of the flag leaves in wheat and rice, while CKs were positively correlated with these variables, suggesting that both ABA and CKs are involved in controlling senescence (Yang and Zhang 2006). Moderate soil drying during grain filling can induce senescence, coupled with substantially increases in ABA concentration in the leaves and stems or root exudates, and markedly reduction in CKs (zeatin and zeatin riboside) in the leaves (Yang et al. 2000a, b; Yang et al. 2002, 2003a). A recent study showed that when Arabidopsis plants are exposed to drought conditions, ABA signals trigger ROS accumulation mediated by NTL4/NAC053, resulting in induction of leaf senescence (Lee et al. 2012).

It seems that ABA preferentially promotes starch accumulation in developing seeds. The drought-induced ABA was positively and significantly correlated with carbon remobilization from senescing leaves to grains in wheat plants (Fig. 3) (Yang et al. 2003a; Yang and Zhang 2006). Therefore, exogenous applied ABA to leaves increases carbohydrate accumulation and redistribution to grains, resulting in an increase in yield (Travaglia et al. 2007). It has been also demonstrated that grain ABA homeostasis regulates starch accumulation rate and grain filling in barley under drought (Govind et al. 2011), is involved in regulating the starch biosynthesis as a signaling (Seiler et al. 2011), and probably exerts control over starch biosynthetic genes in the endosperm via SNF1 kinase and several TFs in barley (Sreenivasulu et al. 2006). Novel ABA- and dehydration-responsive *cis*-elements have been found in the promoters of key genes of starch biosynthesis (*HvSUS1*, *HvAGP-L1*) and degradation (*HvBAM1*); spraying of fluridone (an ABA biosynthesis inhibitor) to drought-stressed plants results in severely impaired starch content and thousand grain weight of mature seeds (Seiler et al. 2011). However, spraying ABA only to the spike region resulted in a slight yield loss in barley (Seiler et al. 2011).

The mechanisms that ABA promotes senescence and remobilization events and the regulatory role of ABA within developing grains in regulating starch metabolism may include following cues: (1) ABA along with ethylene pay a key role in controlling PCD in endosperm during grain filling (Sreenivasulu et al. 2006; Young and Gallie 1999; Yang et al. 2001). PCD is the genetically regulated disassembly of cells, and commonly occurs in the endosperm of cereals during grain filling. In developing starchy endosperm of rice, PCD is characterized by the involvement of mitochondrial signaling, probably by releasing signal molecules such as cytochrome c and ROS from mitochondria (Kobayashi et al. 2013). (2) ABA plays a key role in initiating a network of signaling cascades concerning multiple protein kinases, such as ATH1 (a transmembrane histidine kinase receptor), mitogen-activated protein kinases (MAPKs), calcium-dependent protein kinases (CDPKs) and sucrose non-fermenting-1-related protein kinases (SnRKs) (Semenov and Halford 2009 and references cited herein). These kinases play functions signaling proteins in plants. In particular, increasing body of evidence showed that SnRKs have been associated with metabolic regulation and stress responses. They comprise three subfamilies: SnRK1, SnRK2, and SnRK3. SnRK1 plays a major role in the regulation of carbon metabolism, while SnRKs 2 and 3 have been implicated in ABA-mediated signaling pathways. (3) ABA induced the up-

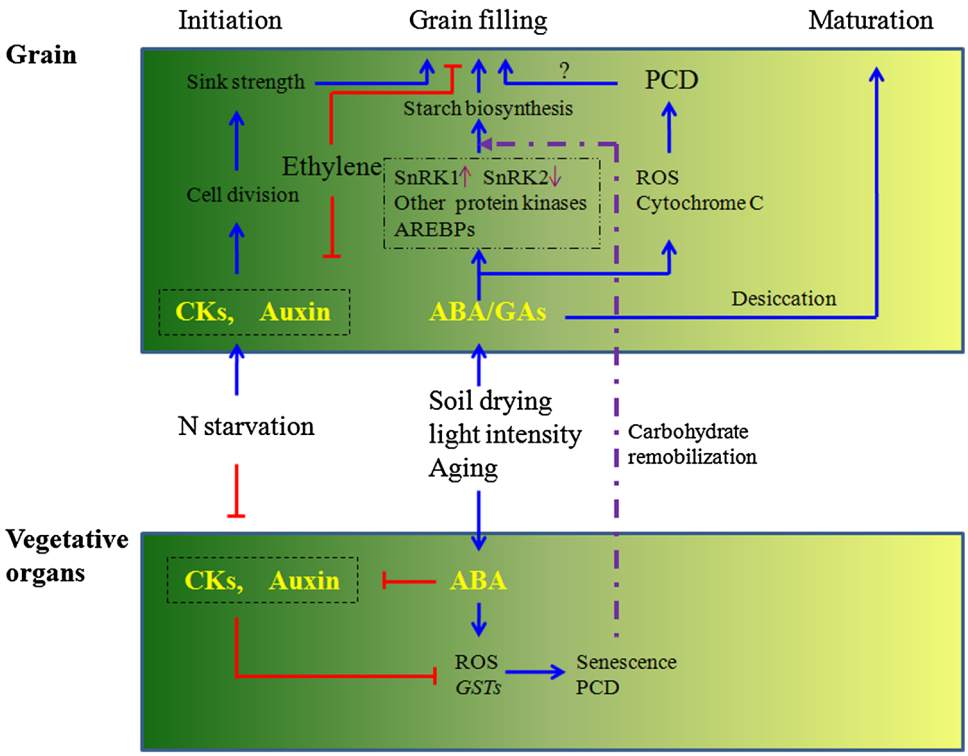

Fig. 3 Diagram summarising a model for the role of hormone signaling and interactions between hormones in the developmental and environmental regulation of wheat grain development. The *blue arrows* indicate the promoting effects. The *red lines* indicate the inhibitory effects. The *dashed line* indicates the carbohydrate remobilization and the relationship between senescence/PCD of vegetative organs and grain starch biosynthesis. *Small colorful arrows* represent SnRKs down-regulated or up-regulated due to the actions of ABA of ABA/GAs interactions

regulation of *TaGSTU1B* and *TaGSTF6* both playing a role in senescence in both shoot and root tissues in *Triticum tauschii* and it was confirmed that the promoter region of *TtGSTUs* contained ABA-, ethylene-, and auxin-responsive elements (Xu et al. 2002; Gallé et al. 2009). These findings indicate ABA signaling regulates plant senescence via *TtGSTUs*. (4) Differential ABA levels in the grains influence the ABA signal transduction complex (*SnRK2.6* and *RCAR/PP2C*) and possibly affect transcriptional regulation of sucrose synthase 1 (*HvSUS1*) and ADP-glucose pyrophosphorylase small subunit (*HvAGP-S1*) (Govind et al. 2011). It seems that ABA regulates SUS in wheat and rice (Yang et al. 2006; Zhu et al. 2011) or SUS, AGPase and BAM together in barley (Govind et al. 2011).

An antagonism between ABA and GAs has been reported in wheat during grain development. A decrease in GAs and an increase in ABA in the grains produced by soil drying enhance the remobilization of pre-stored carbon to the grains and thus, accelerating the grain-filling rate; this process can be modified by N status (Yang et al. 2001). Pre-maturity α-amylase formation in wheat grain was stimulated by GAs but inhibited by ABA at mid-grain development (Kondhare et al. 2014).

Ethylene

Generally, ethylene is considered as another growth regulator that is known to induce senescence in plants (Noodén et al. 1997). An inhibition of ethylene biosynthesis in pea (*Pisumsativum* L.) leaves under senescence-promoting conditions resulted in a slower senescence rate, probably due to the anti-senescence properties of NO (Neill et al. 2003).

However, in contrast to ABA, the grain ethylene concentration was significantly and negatively correlated with the grain-filling rate, very high at the early grain-filling stage and decreased sharply during the linear period of grain growth in rice (Yang et al. 2004). Application of cobalt ion (an inhibitor of ethylene synthesis) or ABA at the early grain-filling stage significantly increased the grain-filling rate. Spraying with ethephon (an ethylene-releasing agent) or fluridone (an inhibitor of ABA synthesis) had the opposite effect. These results indicate that the opposite effects of ethylene and ABA on grain-filling rate depend not only on their concentrations but also on their balance (Yang et al. 2004). Reductions in ethylene and 1-aminocylopropane-1-carboxylic acid (ACC) concentrations in grains increased the grain-filling rate under moderate soil drying conditions (Yang et al. 2006; Yang and Zhang 2006). The balance between ABA and ethylene in the grains is requested for the grain filling and an increase in the ratio of ABA to ethylene increases the grain-filling rate (Yang et al. 2006; Yang and Zhang 2006). Further investigation is needed to confirm the interactions between ethylene and ABA using mutant or transgenic plants with an alteration of hormone action.

MiRNAs-regulated signals

Recently, many biotechnologies have been invented for probe of regulating mechanisms for grain development, including the signal transduction. Plant microRNAs (miRNAs), a class of regulatory small RNAs (sRNAs), down-regulate target genes by mRNA degradation or translational repression and play a critical role in controlling genes involved in basic developmental processes, such as organ development, anthesis time, hormonal signaling, and stress responses. Another way of plant miRNAs in negatively regulating their cognate mRNAs is by fully or partly binding to complementary sites. Recently, a large set of diverse plant miRNAs have been discovered using the high-throughput sequencing technologies. Up to date, thousands of miRNAs have been identified from different tissues or developmental stages in different plant species, rapidly enlarging the identified plant miRNA pool (Meng et al. 2013).

Studies of plant miRNAs have indicated that this group of regulatory molecules plays crucial roles in numerous biological processes, e.g., general plant development and responses to environmental signals (Sunkar et al. 2008; Zhan and Lukens 2010; Sha et al. 2012). The first miRNA was discovered in rice (Reinhart et al. 2002) and many new miRNAs in rice have been identified using high-throughput sequencing technology. Some miRNAs are preferentially expressed during grain development (Zhu et al. 2008; Xue et al. 2009), indicating the regulation of grain development by miRNAs. A rice miRNA, miR167, targeted ARF6 and ARF8, which might be involved in rice grain development through regulation of auxin signaling (Xue et al. 2009). In wheat, Martínez-Barajas et al. (2011) has also reported that SNF1-related protein kinase regulatory subunit beta-1 (TC371426), a potential target of miR1211, has vital roles in a signal transduction cascade that controls gene expression and carbohydrate metabolism in higher plants. Its counterpart in barley is thought to modulate the accumulation of storage products during grain filling (Sreenivasulu et al. 2006). Grain-filling-associated miRNAs might target a set of genes involved in the signal transduction during grain filling (Table 1) (Meng et al. 2013).

Signaling related proteins

Signaling proteins play key roles in signal transduction. Proteomics techniques promise to add greatly to information about patterns of protein accumulation and can provide information about pathways of signal transduction by identifying regulatory modifications of proteins. For example, the nonlinear (NL) 2-DE is a powerful tool for studies on wheat grain proteome. MALDI-TOF and MALDI-TOF/TOF mass spectrometry are commonly used in comparative proteomic analysis during grain development and identified a large number of differentially expressed protein spots in wheat varieties subjected stresses or at deferent developmental stages (Guo et al. 2012; Jiang et al. 2012).

Drought is one of the major factors limiting the yield of wheat particularly during grain filling. Under terminal drought condition, remobilization of pre-stored carbohydrates in wheat stem to grain has a major contribution in yield. The 14-3-3 proteins are highly conserved hydrophilic proteins, capable of binding a multitude of functionally diverse signaling proteins, including kinases, phosphatases, and transmembrane receptors, in a sequence specific and phosphorylation-dependent manner (Chen et al. 2006; Comparot et al. 2003; Fu et al. 2000; Mackintosh, 2004; Nohzadeh Malakshah et al. 2007; Roberts 2003). The 14-3-3 proteins might also functions as components of transcription factor complexes involved in ABA-induced gene expression (Fulgosi et al. 2002) but down-regulated by the ABA treatment (Zhang et al. 2012). Using proteomics comparison, Bazargani et al. (2011) identified three of down-regulated proteins including 14-3-3 protein in two contrasting wheat landraces under a progressive post-anthesis drought stress. Therefore, it is reasonable to conclude that a highly expressed 14-3-3 proteinis detrimental to the starch formation and accumulation and thus causes the poor grain filling (Zhang et al. 2014). However, a study on barley showed that longer presence of 14-3-3 proteins is essential in generating an ABA response (Schoonheim et al. 2007).

A proteomic study by Jiang et al. (2012) showed that among 122 identified differential proteins, the signal transduction-associated proteins accounted for 2 %, including G beta-like protein, WD-40 repeat protein and Os04g0118400. These proteins contain a structurally conserved Trp-Asp motif (the so-called WD-40 repeat), a ~40-amino acid stretch typically ending in Trp-Asp, but exhibiting only limited amino acid sequence conservation (Neer et al. 1994). These WD-40 proteins may play key roles in signal transduction and other processes including drought adaptation (Smith et al. 1999; Krugman et al. 2010). Guanine nucleotide binding protein (G proteins) belongs to a family of WD repeat proteins and is involved in second messenger cascades serving as modulators or transducers in various transmembrane signaling systems (Assmann 2005; Xiong et al. 2002). Jiang et al. (2012) reported that G beta-like protein in grains was correlated with drought resistance in wheat during grain filling.

The ubiquitin–proteasome system (UPS) is one of the most important mechanisms implicated in plant developmental processes and is essential to hormone signaling. In particular, E3 ubiquitin ligases of the UPS have been

Table 1 Grain development-associated miRNAs identified and potential targets involved in signal transduction in wheat

miRNA	Sequence 5′ to 3′	Target description (accession no.)	References
miR1211	AGGGAGGGAUGGAUAGAAGA	SNF1-related protein kinase regulatory subunit beta-1-like (TC371426); Protein phosphatase (TC422862)	Martínez-Barajas et al. (2011), Meng et al. (2013)
miR1508	AGAAAGGAAAUAUCAGUU	Germin-like (CJ625244); Ubiquitin-activating enzyme (TC369936)	Meng et al. (2013)
miR1439	AUUUUGGAACGGAGGGAGUAA	E3 ubiquitin-protein ligase (TC371157)	Meng et al. (2013)
miR168a	UCGCUUGGUGCAGAUCGGGAC	WD repeat protein WRAP73-like (CJ682815)	Meng et al. (2013)
miR825	UUCUAAGACAUGCAUGAAC	Cytokinin-O-glucosyltransferase (BJ262853)	Meng et al. (2013)
miR529a	CGACGCAGAGAGCAAGCCC	WD repeat domain phosphoinositide-interacting protein (BI750979); MAPK (TC390981)	Meng et al. (2013)
miR835	UUGGAAGAUCCAAGAAAG	Receptor protein kinase (CJ937725); CDPK-related (TC398911)	Meng et al. (2013)
miR114	AUCGGUCGGAUCGGGAAGACGU	Calmodulin (CA484949)	Meng et al. (2013)
miR172	UUGAGAAUUUUGUGAUGAUGACAU	Calmodulin-3 (CA620409)	Meng et al. (2013)
miR207	AGAGUUGUAUGAUGUCGAUGACGA	CDPK (TC430574)	Meng et al. 2013
miR171a	UGAUUGAGCCGCGCCAAUAUC	Serine/threonine protein kinase (TC399588)	Meng et al. (2013)
miR1060	UUUGGUCAUAGAUCGCACACG	Protein kinase (TC412491)	Meng et al. (2013)

shown to play critical roles in hormone perception and signal transduction. The differential expression of genes involved in the UPS and plant hormone pathways suggests that phytohormones and UPS crosstalk might play a critical role in the wheat grain developmental process. Some E3 ligase and hormone-related genes seem to be up- or down-regulated during the early and late stages of the grain development (Capron et al. 2012).

Nucleoside diphosphate kinase (NDPK) is a ubiquitous enzyme functioning in intracellular distribution of terminal phosphate bond energy among the various nucleotides used in synthesis pathways and regulatory functions in cells. In a study by Guo et al. (2012), several main groups of grain proteins were identified according to their functions, of which 3.4 % was involved in signal transduction including NDPK. NDPK might play an important role in signal regulation for grain development in wheat, because it was gradually down-regulated during grain development (Guo et al. 2012).

The protein disulfide isomerase (PDI) gene family encodes several PDI and PDI-like proteins. PDI-like proteins would also be involved in signal transduction pathways through their association with transcriptional complexes regulating genes responding to various stimuli. The most expressed genes *TaPDIL1-1*, *TaPDIL2-1* and *TaPDIL8-1* displayed divergent expression patterns during grain development (d'Aloisio et al. 2010). Calmodulin is a Ca^{2+}-binding protein involved in calcium signaling under stress conditions; the calmodulin TaCaM2-2 identified in wheat grain decreased in response to drought (Yang et al. 2011).The functions and properties of recently identified signaling proteins are listed in Table 2. But little information is available by now on how the signaling proteins are finely regulated as a key component of signaling cascades in the grain development.

Sugar signaling

The supply of photosynthate is a major factor that limits accumulation of dry weight. Sugars from the leaves and stems not only serve as substrates for starch synthesis, but also interact to regulate gene expression and metabolic pathways as signals.

Regulation of senescence

As early as in 1997, Buchanan-Wollaston concluded that sugar accumulation in the leaf resulted in an increase in the source/sink ratio and thus induced leaf senescence and N remobilization. Indeed, a decrease in source/sink ratio due to source leaf excision decreases the leaf sugar concentration and delays senescence and N remobilization (Guitman et al. 1991; Buchanan-Wollaston 1997). In sunflower, N starvation caused a strong decline of photosynthetic activity and pronounced senescence symptoms and at the same time, a significant increase in the hexose/sucrose ratio was observed at the beginning of senescence; this indicates that sugar signaling is involved in the N availability induced senescence (Aguera et al. 2010) and may also play a role in light signaling (Wingler et al. 2006). Thus, it could be proposed that higher hexose/sucrose ratio induces leaf senescence (Fig. 4).

Table 2 Signaling proteins associated with grain filling or nutrient remobilization

Accession no.	Protein name	Suggested functions	Score	Theoretical MW (kDa)/pI.	Species	References
P29305	14-3-3 protein	Signaling in stem reserves remobilization; carbohydrate metabolism; play important roles in IS poor grain filling by regulating the activity of starch synthesis enzymes; in response to high temperature and water deficit	279	33/4.9	*T. aestivum; O. sativa*	Bazargani et al. (2011), Tasleem-Tahir et al. (2011), Yang et al. (2011), Zhang et al. (2014)
Q10E23			95	29.2/4.90		
gil40781605			85	33.8/8.13		
AAR89812				29/4.6		
gi257664738						
gi297851506						
TA59247_4565; BE424346	14-3-3-like protein	Signaling in stem reserves remobilization and glucose accumulation in grains	89	32/4.8	*T. aestivum N. tabacum; H. vulgare*	Bazargani et al. (2011), Stamova et al. (2009), Tasleem-Tahir et al. (2011)
gi227473229						
gi2492487						
Q7XTE8	Similar to 14-3-3-like protein GF14-6		246	30.0/4.76	*O. sativa*	Zhang et al. (2014)
Q6YZA9	Germin-like protein 3		354	19.6/8.89	*O. sativa*	Zhang et al. (2014)
	G beta-like protein	Related to drought resistance			*T. aestivum*	Jiang et al. (2012)
gil16903082	Small Ras-related GTP-binding protein	In response to high temperature and water deficit during grain development	133	31.3/5.70	*T. aestivum*	Yang et al. (2011)
TC249217	Fructose-6-phosphate-2-kinase	In response to high temperature and water deficit during grain development	74	70.3/8.17	*T. aestivum; O. sativa*	Yang et al. (2011)
gil1754999	Calmodulin TaCaM2-2	In response to high temperature and water deficit during grain development	76	19.3/5.90	*T. aestivum*	Yang et al. (2011)
	WD-40 repeat protein	Related to drought resistance			*T. aestivum*	Jiang et al. (2012)
BE398510	Putative WD-40 repeat protein	Starch accumulation and B-granule number			*T. aestivum; O. sativa*	Stamova et al. (2009)
	Os04g0118400	Related to drought resistance			*T. aestivum; O. sativa*	Jiang et al. (2012)
	PPDK isoforms	Remains to be elucidated			*T. aestivum*	Jiang et al. (2012)
BE424694	OsCDPK protein	Fructose accumulation in grain involving calcium as a second messenger			*T. aestivum; O. sativa*	Stamova et al. (2009)
Q9M7N5	MFP1 attachment factor 1	MAF1 integrates the responses from convergent nutritional and stress signaling pathways; signaling in stem reserves remobilization		19/4.7	*T. aestivum; Z. mays*	Bazargani et al. (2011)
BE495028	Calmodulin	Glucose accumulation			*T. aestivum*	Stamova et al. (2009)
gil1754999	Calmodulin TaCaM2-2	Associated with high temperature and water deficit stresses		19.3/5.90	*Z. mays*	Yang et al. (2011)
BF429053	Auxin-responsive protein-like	Glucose accumulation			*T. aestivum; O. sativa*	Stamova et al. (2009)

Table 2 continued

Accession no.	Protein name	Suggested functions	Score	Theoretical MW (kDa)/pI.	Species	References
41469575	Putative polyprotein	Signal transduction in drought resistance		106/9.75	*T. aestivum*	Ge et al. (2012)
115463815	Os05g0405000	Signal transduction in drought resistance		103/5.98	*T. aestivum*	Ge et al. (2012)
2104951	MAP kinase-like protein	Signal transduction in drought resistance		26/9.48	*T. aestivum*	Ge et al. (2012)
	PDI-like proteins	Involved in signal transduction pathways through their association with transcriptional complexes regulating genes			*T. aestivum*	d'Aloisio et al. (2010)
	γ-gliadin proteins	Have a typical γ-gliadin structure with a signal peptide			*T. aestivum*	Wan et al. (2013)
gi126517972	Serine/threonine-protein phosphatase PP2A-1 catalytic subunit					Tasleem-Tahir et al. (2011)
gi257672913	Annexin P33					Tasleem-Tahir et al. (2011)

Sugar signaling in the regulation of senescence is likely affected by many factors, and then triggering leaf senescence mechanism. Trehalose 6-phosphate (T6P) is an intermediate of trehalose biosynthesis and is an important signaling metabolite that is involved in the regulation of plant growth and development in response to carbon availability (O'Hara et al. 2013). In wheat, it has been proposed that T6P acts as a signal of sugar availability and the interaction of T6P and SnRK1 has been suggested to play a role in the regulation of senescence by sugar during grain development (Martínez-Barajas et al. 2011) (Fig. 4).

Regulation of grain filling and maturation

In wheat grain, SnRK1 was also under the regulation of T6P (Martínez-Barajas et al. 2011; O'Hara et al. 2013). During early grain development, SnRK1 was inactivated by T6P (Fig. 4), although SnRK1 was expressed in both endosperm and embryo throughout grain development (Coello et al. 2012). Inactivation of SnRK1 may be necessary for carbon biosynthetic processes regulated by the amount of sucrose available; Subsequent development of the pericarp and embryo during grain filling is characterized by cessation of the inhibition of SnRK1 by T6P (O'Hara et al. 2013). Therefore, SnRK1-dependent processes are needed in the later stages of the development. T6P expression is also tissue-dependent and developmentally regulated. During very early embryo development, its level was high in all grain tissues and closely correlated to sucrose levels overall but gradually became restricted to the endosperm with only trace amounts present in the outer and inner pericarp and in the embryo in spite of the presence of sucrose in these tissues (Martínez-Barajas et al. 2011). The data confirm the relationship between sucrose and T6P (O'Hara et al. 2013). However, as of date, it is not yet clear whether T6P responds specifically to sucrose or is a more general signal of sugar availability (Yadav et al. 2014).

ABA is involved in SnRK-related sugar signaling. In the absence of ABA, SnRK2 is kept in an inactive state through the action of protein phosphatase 2C (PP2C). In the presence of ABA, ABA receptors PYR/PYL/RCAR bind to and inhibit PP2C, leading to an activation of SnRK2 (Cutler et al. 2010). In wheat roots, SnRK1 has been shown to be broken down in response to ABA treatment and a putative calcium-dependent SnRK2 is activated (Coello et al. 2012). Similar results have been also observed in barley (Chen et al. 2013). These results suggest differential roles for SnRK1 and SnRK2 in ABA signaling and antagonistic effects of SnRK1 and SnRK2 on target genes. Chen et al. (2013) proposed a possible model in which alteration of ABA levels induces a transition from grain filling stage dominated by endosperm SnRK1 to maturation stage dominated by SnRK2.

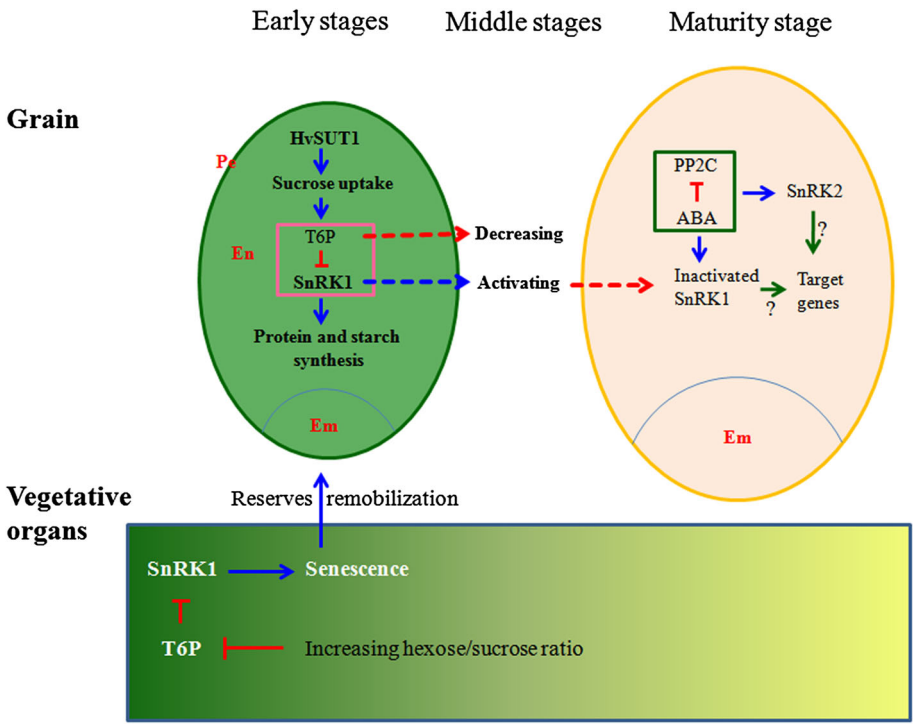

Fig. 4 Model for the function of sugar signaling in wheat grain development. The *blue arrows* indicate the promoting effects. The *red lines* indicate the inhibitory effects. The *red dashed arrow* presents decreasing of T6P level from the early stages to late stages of grain filling or SnRK1 inactivating. The *blue dashed arrow* presents increasing of SnRK1 activity from the early stages to late stages of grain filling. The *square frames* indicate the effect of interactions of the components on the down stream processes. *Em* embryo, *En* endosperm, *Pe* pericarp

Overexpression of barley sucrose transporter HvSUT1 specific in wheat endosperm increases sucrose uptake capacity and increases grain protein content compared with the wild type, probably via a network of sugar and hormonal signals (Weichert et al. 2010). Thiel (2014) has also observed that sucrose levels clearly peak at the early grain-filling stages and may be an indicator for the switch from high to low hexose/sucrose ratios, which might serve as an intracellular signal for the transition of the endosperm into a storage-accumulating organ. Thus, an increased sucrose uptake into the grain should increase sink strength and perhaps, subsequently also, seed protein synthesis (Fig. 4).

Invertase (INV) hydrolyzes sucrose into glucose and fructose, thereby playing key roles in primary metabolism and plant development. INVs are located in cell wall (CWIN), cytoplasmic (CIN), and vacuolar (VIN). The broad importance and implications of INVs in plant development and crop productivity have been reviewed by Ruan et al. (2010). They concluded that INV mediated sugar signaling in hormonal control of development and seed and fruit set. CWIN activity is also required for seed development and size, probably by controlling endosperm and embryo cell division (Ruan et al. 2010).

Based on the work described in this review, the following model is proposed for sugar signaling in the regulation of vegetative organ senescence and grain development (Fig. 4).

Conclusions and perspectives

As of date, some crucial and important signaling pathways in the developing grain have never been explored in wheat (Capron et al. 2012). Much work remains to be done before the precise roles of signals in grain development and the roles of signal transduction pathways that coordinate the response to the environment are understood. More exact models elucidating the signal transduction and should be proposed. Modification of N status, increasing light interception by regulation of row spacing, seeding rate and choice of proper plant type, and application of growth regulators may increase signal sensitivity. Therefore, the role of signals including hormones, sugars, and signaling proteins in the regulation of vegetative organ senescence during grain development should integrate environmental factors.

Genomics and proteomics techniques offer considerable promise for understanding the roles of signals in regulating grain development. Functional genomic and proteomic studies of developing wheat endosperm promise to reveal patterns of gene expression associated with key developmental events. By comparing profiles of gene expression and protein accumulation from endosperm developing under different environmental conditions, it should be possible to uncover basic molecular mechanisms that are influenced by environment and that affect productivity and

quality. Global analyses of gene expression and protein accumulation must rest on a solid foundation of grain developmental studies. Some biotechnologies, such as microarray should be used to study the expression profiles of signaling pathways during grain development. Large-scale transcriptomic analysis of grain development could allow the definition of a number of signaling networks. This approach provides an extensive insight into tissue-specific gene expression patterns that reflects tissue-specific physiological processes (Sreenivasulu et al. 2006).

Temporal changes in signal content have been observed throughout grain development in wheat. Changes in the levels of endogenous signals, such as phytohormones and sugar availability will alter the regulation of many physiological processes. Therefore, by means of genetic and temporal manipulation of signal metabolism and signaling processes, improvement of coordination of signal components of signal synthesis and metabolism genes to artificially manipulate the endogenous signal levels could be of considerable importance for increasing grain sink strength, promoting assimilate uptake capacity and thus, getting a higher promising yield.

Author contribution LAK conceived the idea and wrote the manuscript. HHG prepared the figure and gave many critical suggestions. MZS collected the data listed in the tables and edited the manuscript.

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