

Sugars and CKs in seeds

Subjects: Plant Sciences

Contributor: Philippe Grappin

Plants adjust their growth and development through a sophisticated regulatory system integrating endogenous and exogenous cues. Many of them rely on intricate crosstalk between nutrients and hormones, an effective way of coupling nutritional and developmental information and ensuring plant survival. Sugars in their different forms such as sucrose, glucose, fructose and trehalose-6-P and the hormone family of cytokinins (CKs) are major regulators of the shoot and root functioning throughout the plant life cycle.

Keywords: nutrient ; hormones ; development ; seeds ; flowering ; branching senescence ; meristem ; source–sink relationship

1. Introduction

The regulation of plant growth and development is crucial for yield and resistance to abiotic and biotic constraints, which relies on fine-tuned interactions between nutrients and hormones, influenced by environmental inputs. Among these central regulators, sugars and cytokinins (CKs) play predominant roles while operating synergistically, antagonistically and sometimes independently to shape the final reaction of the plant. Sugars growth-related metabolic activity and as signaling entities that drive a wide array of mechanisms throughout the plant life cycle ^{[1][2][3][4][5]}. Briefly, sugar signaling is intimately linked to developmental stages, hormonal signaling and environmental conditions, and thereby is an integrative part of plant growth control ^{[6][7][8][9][10][11]}. Plants can sense a diversity of soluble sugars such as sucrose, glucose, fructose and trehalose-6-phosphate (T6P). Sophisticated sugar sensing networks have been identified, including hexokinase (HXK), Regulator of G-protein signaling (RGS1), and two main sensors of nutrients and energy status: sucrose-nonfermentation1-related protein kinase1 (SnRK1) and target of rapamycin (TOR) kinase ^{[12][13][14][15][16][17][18]}.

CKs are a group of adenine derivatives involved in many central processes in plants, such as development of vasculature, differentiation of embryonic cells, maintenance of meristematic cells, shoot formation and leaf senescence delay ^{[19][20][21][22][23]}. There are two types of CKs: adenine-type cytokinins represented by kinetin, zeatin, and 6-benzylaminopurine, and phenylurea-type cytokinins like diphenylurea and thidiazuron. Most adenine-type cytokinins are synthesized in roots. Cambium and other actively dividing tissues also synthesize CKs. CKs are viewed as one of the major long-distance root-to-shoot messengers ^[24]. Their biosynthesis depends on the activity of adenosine phosphate-isopentenyltransferases (IPTs). Trans-zeatin is the most abundant form of CK in plants ^[25]. Initially identified in rice, Lonely Guy (LOG), cytokinin nucleoside 54-monophosphate phosphoribohydrolases, are involved in direct CK production ^{[26][27]}. CKs primarily regulate gene expression through a phosphotransfer signaling cascade. This cascade is initiated by histidine kinase cytokinin receptors, Arabidopsis Histidine Kinase2 (AHK2), AHK3 and AHK4, that located in the endoplasmic reticulum membrane, and completed by cytosolic histidine phosphotransfer proteins (AHP) ^[28]. AHPs shuttle between the cytosol and the nucleus and transfer phosphate to nuclear response regulators (Arabidopsis Response Regulators, ARRs) ^[23] that fall into two classes: type-A and type-B ARRs are negative and positive regulators of CK signaling, respectively.

Sugars and CKs are individually viewed as major players in many aspects of plant biology. Yet, their crosstalk has not been systematically investigated, hence many gaps in current knowledge. Moreover, the available results underline that the crosstalk is very complex and varies at least according to the nature of the organ and the physiological process. This review aims to underline the interactions between sugars and CKs based on their individual and combined roles in the regulation of key developmental processes throughout the plant life cycle. Based on the results derived from different plant species, sugars and CKs seem to act synergistically to take over the seedling emergency, shoot meristem activity, shoot branching and flowering while doing antagonistically as strongly suggested for seed germination, root meristematic activity, and even demonstrated for root branching and leaf senescence (Figure 1). Here, the main results are discussed, potential integrators of this crosstalk are proposed, and further lines of research are highlighted.

Figure 1. Relationship between sugars and cytokinins (CKs) in the main plant developmental processes, including seed development, germination, seedling establishment, root and shoot branching, leaf senescence, and flowering. The black arrows indicate stimulation or positive effect, and the red lines mean repression or negative effect. This model results from a compilation of studies carried out on different model plants (see references and description in the text).

2. Seed Development, Germination and Seedling Establishment

Seed formation, as well as the seed-to-young-seedling transition through germination, involves sugar and hormone signaling [29][30]. Even though common key players have been identified in the seed response to sugars and CKs, their molecular interaction remains speculative.

2.1. Seed Development

Seed development covers morphogenesis phases characterized by active cell division and embryonic organ formation and a maturation phase during which storage nutrients accumulate in cotyledons and/or endosperm tissues, with a transfer of reserves between these two compartments [31]. In this latter phase, the embryo acquires tolerance to desiccation and a dormancy state before dispersal in the environment. Dormancy allows the seed to cope with its adverse environment and secures the transition to a new life cycle. Previous works have reported the contribution of sugars and CKs in the control of seed development [32][33]. In cotyledons of *Vicia faba*, a high glucose-to-sucrose ratio is correlated with cell division during the morphogenesis phase, whereas an increasing sucrose-to-glucose ratio marks the sink–source transition to the storage phase [34]. The high glucose gradient is related to both high cell-wall-bound invertase (*CWINV*) expression in the maternal seed coat and hexose transporter (*VfSTP1*) expression in the embryonic epidermal cells [35][36]. Analyses of the *CWINV*-deficient mutant *miniature1 (mn1)*, impaired in endosperm development in maize caryopses, provide evidence that *CWINV* also contributes to CK-dependent cell proliferation during the developmental transition to the storage phase [37][38][39]. Such a CK effect may operate directly on cell cycle-related genes (*CycD3*) and indirectly through (*CWINV2*)-mediated sugar signaling [40][41]. Nevertheless, the seemingly contradictory phenotype of the CK-receptor-defective triple mutant *ahk2 ahk3 cre1* exhibiting greater seed size points to the complexity of the regulatory network [42]. Understanding how CKs contribute to seed development will require considering the different levels of regulation of CK metabolisms, such as the spatiotemporal accumulation and transport of CKs in seed tissues, the dynamics of their biosynthesis (*IPT*) and inactivation (*CKX*), and their perception. The transition from cell division and expansion (seed morphogenesis) to storage activity (seed maturation phase) is associated with downregulated *CWINV* and *IPT* expression [43][44]. At this stage, sugars serve for seed storage accumulation by mediating sucrose synthase induction for starch biosynthesis in maize kernels [45] or gibberellic acid (GA) dependent alpha-amylase induction for storage remobilization in barley embryos [46]. Such sugar-dependent regulation takes place at the transcriptional and post-transcriptional levels. The role of sugars in seed maturation could be complex and partially mediated through T6P, considered as a proxy for sucrose availability in plants [47], and SnRK1 [48]. Sucrose positively regulates T6P accumulation in wheat at the seed pre-filling stage [49], and its exogenous application stimulates seed filling and yield [50]. Accordingly, *Arabidopsis* seeds of the mutant *tps1* (Trehalose-6-phosphate synthase 1) fail to proceed towards the maturation phase [51][52]. In pea, SnRK1 deficiency hinders the maturation and storage activity [53][54]. Accordingly, SnRK1 induces abscisic acid (ABA) synthesis and signaling and the C/S1-group bZIP signaling pathways associated with carbon starvation [55][56]. This regulation is mediated by pFUS3 (The *Arabidopsis* B3-domain transcription factor FUSCA3) phosphorylation, known to control ABA responses during seed maturation and dormancy [57]. Transcriptomic comparison of CK metabolism and signaling in dormant and non-dormant wheat seeds [58][59] highlights that CK controls the activity of many genes involved in seed dormancy. The interactions of CKs with ABA metabolism and signaling during seed maturation need to be further investigated and compared with sugar signaling mediated at least by the T6P and SnRK1 pathways.

2.2. Seed Germination and Seedling Establishment

The carbon stored in the mature seed will be remobilized during germination to ensure seedling establishment before becoming heterotrophic. Seed germination is accomplished when the radicle protrudes through the outer layers of the embryo, i.e., the endosperm and the teguments [60]. The related cellular and metabolic events are orchestrated by complex signaling crosstalk involving the hormones ABA and GA, well known for their role in inhibiting and inducing germination, respectively [61]. Sugars released from the GA-mediated hydrolysis of storage compounds and cell wall loosening serve as osmotically active solutes for radicle cell expansion. These sugars are potentially used as central signals of the seed's C status and are also a source of C for seedling growth during the transition to autotrophy. Genetic and molecular analysis revealed a possible control of germination by glucose based on HXK1-dependent and independent pathways and the T6P pathway, interacting with different hormonal pathways. Many reports also showed that CKs contribute to the control of seed germination. However, their interactions with glucose are poorly documented. On the

whole, glucose and CKs are likely to operate antagonistically at different steps of the ABA biosynthesis and signaling pathways (Figure 2). The contribution of glucose to the control of seed germination has long been established and proven to be a concentration-dependent signal [62][63][64]. Exogenous supply of high glucose contents delays seed germination through positive regulation of ABA synthesis, accumulation and signaling [65][66][67][68]. At lower concentrations, glucose stimulates germination by inducing ABA catabolism [69]. In germinating seeds, high glucose supply upregulates two ABA biosynthesis genes (*NCED3* and *ABA2*) through the G Protein Alpha subunit *AtGPA1* and the Regulator of G-protein Signaling *AtRGS1*, via an *HXK1*-independent channel [70][71][72]. Glucose also repressed– the positive regulator of seed germination *AtGASA6* via an *HXK1*-dependent pathway [73][74]. *AtGASA6* acts as an integrator of *ABI5*-dependent ABA signaling and *RGL2*-dependent GA signaling [73]. Therefore, a high level of T6P promotes seed germination by decreasing seed sensitivity to glucose and ABA [75][76][77]. In sum, the inhibition of seed germination under excessive glucose supply conditions may be due to the activation of the ABA signaling pathway and an imbalance in sugars/T6P.

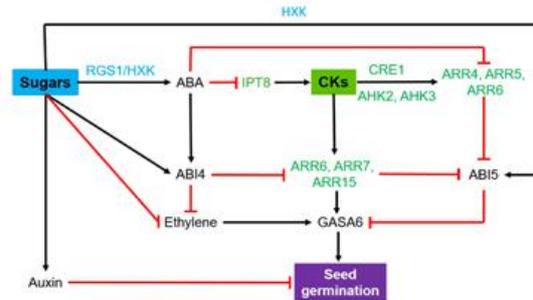


Figure 2. Antagonistic effect of sugars and cytokinins (CKs) on seed germination. Blue stands for players of sugar signaling pathways, and green highlights genes involved in CK synthesis or signaling pathways. Black arrows and red lines indicate stimulatory and inhibitory effects, respectively. ABI, abscisic acid insensitive; AHK, *Arabidopsis* histidine kinase; ARR, *Arabidopsis* response regulator; CRE, cytokinin response; GASA, gibberellic acid-stimulated *Arabidopsis*; HXK, hexokinase; IPT: isopentenyl transferase; RGS, regulator of G-protein signaling. This model results from a compilation of studies carried out on different model plants (see references and description in the text).

The CKs are described to stimulate seed germination by an antagonistic effect on ABA signaling [78][79][80]. In germinating seeds, increasing levels of CKs induce the expression of type-A ARRs (ARR4, ARR5 and ARR6) that inactivate the *ABI5*-mediated inhibition of germination [81][82] whereas glucose enhances *ABI5* transcription [83] (Figure 2). In turn, ABA intake represses CK biosynthetic genes such as *AtIPT8* and CK signaling genes such as type-A ARRs, and during seed dormancy, ABA signaling, including ABA receptor Pyrabactin Resistance (*PYR/PYL*), *SnRK2s* and *ABI4*, downregulates type-A ARRs [84]. In dormant seeds, high ABA levels positively regulate *ABI4*, which inhibits the expression of *ARR6*, *ARR7* and *ARR15*. Either, *Arabidopsis* CK-receptor mutants exhibit a reduced dormancy phenotype, and distinct CK-mediated seed germination regulation pathways seem to exist. In germinating seeds, many other regulatory pathways respond to different forms of sugar signals. The exogenous sugar-dependent inhibition of seed germination is also regulated by the sucrose transporter *SUT4/Cyb5-2*-mediated signaling pathway, independently of the ABA (*ABI2/ABI4/ABI5*)-mediated signaling pathway [85]. CK biosynthesis is noticeably concomitant with *SUT* gene expression during pea seed germination. Therefore, we may wonder whether sugar transporters could be a convergent target of sugars and CKs during this process [86].

Interestingly, promoters of the senescence-associated genes *SAG12* and *SAG13* are inducible in the tomato seed micropylar endosperm [87], suggesting that a senescing mechanism known to be stimulated by *HXK1*-dependent sugar signaling (see leaf senescence section) could facilitate radicle protrusion. Ectopic expression of the *IPT* gene through *SAG12* and *SAG13* promoters delayed endosperm senescence and germination, suggesting that potential CK synthesis in the endosperm can antagonize the *HXK*-dependent sugar senescing mechanism to negatively control germination. Therefore, CKs could be perceived differently in a tissue-dependent manner during seed germination.

The crosstalk between sugars and CKs in the control of germination remains very partially documented, and available results foresee very intricate mechanisms. All the present results support antagonistic effects of glucose and CKs throughout the germination process, which precedes seedling growth considered as a post-germinative phase.

2.3. Seedling Development

Upon radicle protrusion through the seed coat, the first post-germinative events initiate seedling growth through hypocotyl elongation and root meristem development before the activation of the photosynthesis machinery. Hypocotyl elongation occurs in darkness and is fueled by C issued from the hydrolysis and mobilization of seed storage compounds. The shoot

apical meristem (SAM) is characterized by a heterotrophic metabolism, while the development of the root apical meristem (RAM) occurs only under light conditions and is controlled by cotyledon-derived photosynthetic sucrose that acts as a long-distance signal [88].

CK and glucose signaling are involved in controlling different aspects of seedling growth and development, with auxin signaling components as downstream targets. From a physiological point of view, both glucose and CKs could control radicle growth in light conditions, hypocotyl length in darkness, chlorophyll and anthocyanin contents [89]. CKs interact with glucose via an HXK1-dependent pathway for the control of radicle and hypocotyl elongation [90]. SnRK1 overexpression can delay seed germination and increases sensitivity to glucose and ABA during seedling establishment [91]. When glucose is supplied to seedlings, T6P acts antagonistically to SnRK1 by inhibiting ABA synthesis and signaling and, in turn, the seed sensitivity to glucose [92]. Noteworthy, CKs antagonize ABA signaling by inhibiting SnRK2 activity via type-B ARRs and thus promote seedling establishment [93].

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