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REVIEW

Regulatory roles of sugars in plant growth and development

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Abstract

In recent years, several studies have focused on the factors and mechanisms that regulate plant growth and development, as well as the functioning of signaling pathways in plant cells, unraveling the involvement of sugars in the processes regulating such growth and development. Saccharides play an important role in the life of plants: they are structural and storage substances, respiratory substrates, and intermediate metabolites of many biochemical processes. Sucrose is the major transport form of assimilates in plants. Sugars can also play an important role in the defense reactions of plants. However, it has been shown that glucose, sucrose, or trehalose-6-phosphate (Tre6P) can regulate a number of growth and metabolic processes, acting independently of the basal functions; they can also act as signaling molecules. Changes in the concentration, qualitative composition, and transport of sugars occur continuously in plant tissues, during the day and night, as well as during subsequent developmental stages. Plants have developed an efficient system of perception and transmission of signals induced by lower or higher sugar availability. Changes in their concentration affect cell division, germination, vegetative growth, flowering, and aging processes, often independently of the metabolic functions. Currently, the mechanisms of growth regulation in plants, dependent on the access to sugars, are being increasingly recognized. The plant growth stimulating system includes hexokinase (as a glucose sensor), trehalose-6-phosphate, and TOR protein kinase; the lack of Tre6P or TOR kinase inhibits the growth of plants and their transition to the generative phase. It is believed that the plant growth inhibition system consists of SnRK1 protein kinases and C/S1 bZIP transcription factors. The signal transduction routes induced by sugars interact with other pathways in plant tissues (for example, hormonal pathways) creating a complex communication and signaling network in plants that precisely controls plant growth and development.

Keywords

glucose; receptor; SnRK; sucrose; sugar signaling; TOR; Tre6P

Introduction

The growth and development of plants is regulated by various factors at different levels. Much research has been recently devoted to deciphering the mechanisms of growth, developmental regulation, and interactions between different signaling pathways in plant cells [1–8]. One of the most interesting aspects has been the demonstration of the regulatory function of sugars – molecules known for a long time to be involved in basal cell metabolism, and which are substrates or products of numerous chemical reactions.

The saccharides in plant tissues are primarily produced from triose-phosphates formed during photosynthesis occurring in leaves. Sucrose and starch, the final products of photosynthesis, can be temporarily stored in leaves, but most of the sucrose pool is transported to the acceptor tissues that do not produce this sugar [9–11]. The

basal functions of saccharides in plant tissues are well known. Sugars play structural roles and are substrates in respiratory reactions or intermediate metabolites in many other biochemical processes. They can be transported over long distances and are often storage substances [9–14]. Sugars can also play a protective role against stress factors, for example, as osmoprotectants, donors of carbon skeletons, or signaling molecules in the regulation of many defensive reactions [10–15]. Changes in sugar concentrations, their qualitative composition, and transport occur in plant tissues throughout the day and night, as well as during successive developmental stages [7,12,14]. The assimilation of starch in leaves is most often observed at the end of the light period in the form of starch grains [14]. The shoot and root apical meristems and flower buds have increased sugar demand, followed by that of the developing fruits and seeds [2,9,10]. Sugar accumulation is also observed under cold stress, drought, phosphorus deficiency, or pathogen attack [10,11,13,15]. In contrast, lower sugar levels in tissues are often recorded under reduced oxygen conditions [10,12]. It has been proven that sugars induce several mechanisms in the host plants during pathogen attack [15–18]; for example, oligosaccharides secreted from cell walls are the signals that induce plant defense mechanisms and regulate the expression of "defense genes". Recent research has shown that sugars can regulate a number of growth, developmental, and metabolic processes, acting independently of the basal functions. Sugars, in millimolar concentrations, regulate certain stages of the cell cycle, cell differentiation, vegetative growth, organ formation, flowering, fruit formation, and senescence [2,4–8]. Plants, by monitoring the sugar levels in tissues, have developed efficient systems for perception and transmission of signals caused by lower or higher sugar availability [4,5,7,8]. Sugars induce appropriate reactions at the cellular level, because of their functioning, and affect the expression of numerous genes, as well as metabolic and growth processes. This has been presented in detail in many previous experimental and review articles (e.g., [18–25]).

Sugars can act as signaling molecules; as chemical stimuli they are received by receptors, and the signal is then transferred by specific transmitters, eliciting the proper response of the plant (at the cellular level) (Fig. 1). Different sugars can serve as signaling and regulatory molecules but the effects of glucose, sucrose, trehalose, and some phosphates (Tre6P) have mostly been studied [4,6,15,21,22,24,25]. The experimental works that indicated the regulatory or signaling functions of sugars in plants began to appear in the 1990s (e.g., [26,27]). The signaling and regulatory functions of sugars are extensively documented (viz., in [7,10,15,20,22,24,28–31]). However, despite many advanced studies, the basis of plant response mechanisms and the functioning of signaling pathways (and their possible interactions) are awaiting clarification. The purpose of this article is to review the current reports on the regulatory role of sugars and to select data concerning the regulation of various stages of plant growth in terms of information that would be most useful to botanists. Some of the previously known and extensively described control mechanisms have been included only as outlines.

Fig. 1 Schematic diagram of sugar signals, receptors, and signal transmitting system operative in a typical plant cell. AUX – auxin; BR – brassinosteroid; ET – ethylene; FINS1 – putative fructose sensor; Fru – fructose; Glu – glucose; HXK1 – glucose receptor; JA – jasmonic acid; KIN10/KIN11 – subunits of SnRK1 – sucrose-nonfermentation-related protein kinase1; C/S1 bZIPs – group C/S1 basic leucine zipper transcription factors; RGS1 – regulator of G-protein signaling1 – glucose sensor; Suc – sucrose; SUT2 – sucrose transporter-like protein – putative sucrose sensor; Tre-6-P – trehalose-6-phosphate; TOR kinase – target of rapamycin kinase.

Growth and metabolic processes regulated in plants by sugars

Even small changes in sugar concentrations can affect seed germination and the growth of plant seedlings

[32–37]. It was found that the presence of glucose in the medium (6% and higher) significantly reduced seed germination and the development of *Arabidopsis thaliana* seedlings, regardless of the changes in osmotic potential (because the same concentrations of mannitol did not affect germination) [6,32,36,37]. Mannose and fructose had similar inhibitory effects on the germination and growth of seedlings [36–38]. Another example of the independent interaction of sugars was the inhibitory effect of glucose (25 mM) that reduced the synthesis of the starch degrading enzyme, α-amylase, in the germinating seeds [36,37]. During the next decades, considerable progress was made in understanding the molecular basis of the influence of sugars on germination and early seedling growth [6,8,23,34,35]. Recently, it was also demonstrated that sugars could act as signals that differentially regulate the process of pollen germination in *Arabidopsis*, depending on their structural properties [39].

Sugars affect the growth, development, and metabolism of leaves, shoots, roots, and other plant organs [2,3,5,6,30,36,37]. In leaves, changes in glucose or sucrose levels mainly affect photosynthesis intensity and export of assimilates (high sugar levels often decrease photosynthesis rate), whereas changes in transport and sugar concentrations in roots mainly affect respiratory metabolism and storage [9,28,29]. Depending on other factors, high sugar levels can stimulate the development of leaves (e.g., at optimal nitrogen nutrition) or limit their development (see [36] and studies cited therein). Additionally, the administration of sucrose to leaves affected the morphology, size, and number of chloroplasts in *A. thaliana* rosette leaf cells; for example, smaller and irregular plastids were observed in the mesophyll cells. The results indicated the role of chloroplasts in the regulation of the increase in leaf area, depending on the access to sugars [40]. The effects of sugars on plant aquaporins (and water conductance) have recently been examined; it was observed that glucose reduces the movement of water from the xylem to the mesophyll [41], which could also affect leaf growth. It has also been shown that sugars (such as, glucose and sucrose) can affect the movement of cellular organelles, including chloroplasts [42,43]. Trehalose (at a concentration about 25 mM) inhibited root elongation in *A. thaliana* seedlings, whereas sucrose did not affect this process [44]. Trehalose-6-phosphate (Tre6P) appeared to be essential for the growth of *A. thaliana*, in a study on transgenic plants overexpressing the enzymes involved in trehalose metabolism [44,45]. It was also found that, under stress conditions, the application of glucose stimulated the shoot growth that was restricted by stress [12]. However, under some conditions (for example, low temperature and nutrient deficiency), the growth of plants is limited, despite abundant sugar availability [46]. A few novel studies indicated that sugars are components of the signaling pathways in leaves that mediate changes in vegetative phases (via miR156 decrease) [47,48]. The progress in understanding the mechanisms responsible for the transition from the juvenile to the adult stage, as well as the basis of developmental transitions to the next phases in a plant's life have been previously summarized [48].

Recent studies have indicated the involvement of sugars and their transport as the determinants of lateral shoot development, after the removal of the main shoot [49,50]. Apical dominance is conditioned by the transport of auxins from the production site, the apical meristem of the main shoot, downstream, to the root [51]. However, it appeared that changes in the transport of sucrose to the lateral buds of pea, as well as changes in its content, occurred significantly earlier (4–6 h), before the change in auxin concentration (recorded after about 24 h) [49]. The authors of this study also demonstrated that apical dominance is a result of the increased demand of the main shoot for sugars, which limits the availability of sugars for lateral shoot development. BRC1 (BRANCHED1) is a key transcription factor involved in inhibiting the development of lateral shoots; its expression is dependent on cytokines and strigolactones. It was shown that exogenous sucrose resulted in the inhibition of BRC1 expression, similar to that observed after the decapitation of shoot apex, indicating a key role of sugars in the branching of shoots [49].

Efficient transport of assimilates (sugars) from their production sites (leaves) to the sites of their use (acceptors) is crucial for proper plant growth in all stages of development. Sucrose (and/or raffinose, stachyose) is mainly transported through phloem to farther distances [52]. Some reports indicated that plants from the Ranunculaceae and Papaveraceae families could also transport glucose through phloem (about 80% of all sugars in the phloem) [53]. However, other reports support the previous opinion that

sucrose is a ubiquitous transport sugar, and hexoses are usually absent in the phloem stream [54]. Recently, new membrane transporters of sugar, named SWEET (sugars will eventually be exported transporters), have been discovered, which, among others, are involved in the process of phloem loading, together with H^+/sucrose symporter [55,56]. It was shown that *AtSWEET4* overexpression increased the size of *A. thaliana* rosette leaves. In contrast, knock-down of *AtSWEET4* (by RNAi) reduced plant growth and decreased chlorophyll content in the leaves [56]. Sugars (sucrose) have been found to affect the activity (and expression) of both the sucrose transporters, which are essential for the efficient transport of sugar over long distances. Sugars, as assimilates, are necessary for the initiation of flowering in plants [31,57,58]; however, recent studies have shown the regulatory role of sucrose, along with miRNA156 and Tre6P, in the regulation of the flowering process [24,59]. For example, the delivery of sucrose to the *A. thaliana* mutant, *phyA*, characterized by late flowering, accelerated the formation and flowering of the inflorescence stem [58]. As was recently reported, the crosstalk between sugar signaling and photoreceptors (as well as hormones) is required for proper transmission of the flowering signal [31,57].

Sugars also affect the senescence of plants. Published data indicate that senescence can be induced by sugar deficit or excess [60–62]. It was previously shown that glucose (and fructose) was accumulated and the *SAG12* (*SENESCENCE-ASSOCIATED GENE12*) senescence marker was strongly induced in *A. thaliana* leaves during senescence (yellowing). Moreover, the senescence-accelerating effect of glucose was also stimulated under reduced nitrogen nutrition of plants [61]. The *gin2* mutant (with reduced glucose sensitivity), in turn, did not accumulate hexoses and the senescence was delayed, indicating a relationship of senescence with sugar sensitivity [63]. The senescence of leaves is affected by different environmental factors, including nutrients, light, and abiotic and biotic stresses, which often influence photosynthesis, sugar accumulation, and signaling [62]. Hormones and sugars also participate in a complex signal transduction system operating in the process of reproductive organ abscission in response to environmental stress [64].

Sugars can affect cell division and cell cycle stages, which might be essential for the regulation of plant growth processes. Sucrose deficit leads to the induction of PCP1 and PCP2 (principal control point 1/2) checkpoints that block the cell cycle in the G_1 and G_2 phases [21,65,66]. Cell cycle arrest is a reversible process. Sucrose activates replication and mitotic activity (with some delay), which can be modulated by growth regulators (such as, cytokinins or auxins) [66]. Recent studies have shown that sugars regulate the expression of CYCD (D-type cyclins, associated with CDKA, A-type cyclin-dependent kinase) during G_1 interphase [67]. In addition, the presence of sugars activates the TOR protein kinase, which couples the phosphate residue to S6K (ribosomal S6 kinase), thereby affecting cell growth [67]. The activated S6K affects the CDKA–CYCD and RBR1–E2FB complexes (retinoblastoma-related 1 eukaryotic transcription factor 2B) during the S phase, resulting in elongated cell growth [66–68].

The regulation of growth and metabolic processes with the participation of sugars is most often triggered by changes in gene expression (Fig. 1). Changes in sugar concentrations in plant tissues affect the expression of nuclear and plastid genes, although the latter generally react to sugars quite slowly [10,29,36]. Studies using DNA microarrays demonstrated both the stimulation and inhibition of several hundred different genes in response to exogenously administered glucose and sucrose, or sugar depletion, including regulation of transcription factors [20,22,29,46,69]. Glucose-regulated genes are involved in all the metabolic and growth processes, and in responses to stress factors [23]. Sucrose and glucose often stimulate the expression of the same genes; for example, the expression of the sucrose synthase gene is induced both by glucose and sucrose (especially at higher concentrations). UDP-glucose pyrophosphorylase genes in turn are stimulated mainly by sucrose [70,71]. Recent studies have demonstrated that under reduced UDP-glucose content, the abnormal growth of vegetative and reproductive organs of plants occurred, which could be reversed by providing UDP-glucose. The function of UDP-glucose as a signaling molecule was suggested [72]. It is characteristic that genes encoding the enzymes in the sucrose metabolism are involved in the production of sugar signaling factors, and at the same time they are themselves subject to sugar level-dependent control [10]. The regulation of gene expression by sugars can occur at the transcription level, through posttranscriptional modifications, at the

translational level (for example, the control of bZIP S transcription factor synthesis by sucrose), or by post-translational regulation [4,23,24,28,30]. The influence of sugars on the expression of genes (including those controlling the growth processes) is often modified by environmental factors, such as changes in the intensity of irradiation or in the access to minerals. The sugars accumulated under drought or cold mainly play the role of osmoregulators and cryoprotectans, but also as a stored source of carbon for later use (when the stress factor ceases to exist); they can also act as regulators modulating plant growth under new conditions [10,12,15,17,18,69]. Soluble sugars (such as, disaccharides, raffinose family oligosaccharides, and fructans) are strongly related to the accumulation of reactive oxygen species under stress conditions. Thus, nowadays, some studies have been focused on the role of sugars as scavengers of reactive oxygen species [73]. The regulatory role of sugars during plant development also results from the connections of sugar signaling pathways with other routes, including hormonal pathways, as described in the following subsection, and with nitrogen metabolism [34,37,57,63,74].

"Sugar mutants", especially of *A. thaliana*, were helpful in explaining the mechanisms of the regulation of gene expression and growth and metabolic processes [28,29,33,36,63,74]. The following strategies were used in order to select the appropriate mutants: (*i*) if high sugar concentrations in the medium inhibited germination and seedling development, then the seedlings showing development were nonsusceptible to sugars (for example, *gin – glucose insensitive*, *rsr – reduced sugar response*, *sis – sucrose insensitive*, or *mig – mannose insensitive germination*); (*ii*) seeds incapable of germinating (and growing) on media containing sugar concentrations that did not inhibit the development of other plants were mutants that were excessively sensitive to sugars (for example, *gss – glucose super sensitive*, *sss – sucrose super sensitive*, or *hsr – high sugar-response*). During the last decades, a huge progress has been made in understanding the physiological roles of sugar-metabolizing enzymes or sugar transporters, mainly by using transgenic/ mutational approaches [2,9,18,55,56,75,76]. The use of novel mutants (and transgenic plants) that specifically react to different sugars, as well as hormonal mutants, will certainly be helpful in subsequent studies on the regulatory role of sugars throughout plant development and in the elucidation of crosstalk with other signaling pathways.

Receiving and transmitting the signals triggered by sugars

Stimuli are received by extracellular or intracellular receptors and the signal (after transformation) is further transmitted through specific transporters, including protein kinases/phosphatases. The perception of the signal induced by sugars can involve membrane specific sugar sensors, sugar transporters or their analogs, or receptors within the cells (Fig. 1). *Arabidopsis thaliana* hexokinase1 (AtHXK1) is the best characterized intracellular sugar receptor [23,26,63,77,78]. The AtHXK1 analogs, OsHXK5 and OsHXK6 [79] or OsHXK7 [80], are present in rice, and their roles in sugar signaling and metabolism have been reported. In addition, the hexokinase analog, AtHKL1 (hexokinase-like1 protein), can act as a growth regulator and a factor that integrates sugar signaling pathways with hormonal routes [81,82]. Hexokinase (EC 2.7.1.1; HXK) was previously considered a typical cytosolic enzyme, linked to the glycolysis process. Over the past decade, studies have shown that, in addition to the cytosolic fraction, there are isoforms associated with mitochondria, chloroplast, and cell membrane, and a small fraction is also located in the nucleus [77,81–83]. The diverse cellular localization of this enzyme strongly indicates other functions of HXK than its involvement in glycolysis only [82]. Initially, the participation of HXK in sugar perception and signal transduction was studied by introducing phosphorylated (by HXK) and nonphosphorylated sugar analogs and HXK activity inhibitors, and subsequently by making use of *AtHXK1* overexpressing transgenic plants also, predominantly *Arabidopsis*, or plants in which this gene was expressed in an antisense orientation [26,29,36]. The catalytic functions and roles of HXK as an intracellular glucose sensor were successfully distinguished using *gin2-1* HXK mutants, and transgenic plants constructed from these mutants [63]. The *gin2-1* mutation (nonsense mutation on chromosome IV in the *HXK1* coding region) manifests partial loss of function, i.e., reduced activity and protein level of

HXK1 [63]. The effect of mutation on the phenotype of *Arabidopsis* plants was visible, especially when the plants were exposed to elevated radiation conditions. Under these conditions, the growth of the rosette and the leaf area was reduced, the flowering was delayed, and inflorescence stem was small [63]. Transgenic plants (S177A and G104D) constructed on the basis of *gin2-1*, were characterized by reduced protein levels and hexokinase enzyme activity. However, they exhibited signaling functions manifested as the repression of genes encoding photosynthetic proteins under the influence of glucose [63]. Many pathways of sugar perception and signal transduction involving HXK are currently known; they, for example, result in repression of certain photosynthetic genes (*CAB*, *RBCS*), affect stomatal closure, induce sucrose metabolism and anthocyanin accumulation, affect the growth processes, senescence, and developmental transitions [23,28,29,83,84]. A study by Cho et al. [77] explained the mechanism of hexokinase1 action, as a sensor. HXK1, as part of a specific protein complex located in cell nucleus, may directly affect gene expression. VHA-B1 (vacuolar H^+-ATPase B1) protein and RPT5B (regulatory particle of proteasome subunit 19S), and transcription factors co-operate with HXK1 [77]. A recent structural study provided an explanation for the dual functions of HXK1; experiments with two catalytically inactive mutants of *AtHXK1* revealed a domain rearrangement in HXK1 upon glucose binding and showed similar glucose-binding interactions as in the wild type plants [78].

The perception of the signal induced by altered sugar availability might also occur independently of hexokinase. Sugar transporter proteins or their analogs, such as glucose or sucrose transporters (or SUT2 – sucrose transporter-like protein) located in the plasmalemma might function as membrane sensors (Fig. 1). G-protein coupled receptors could also act as sugar sensors [28,29,85]. G proteins (or their analogs) were previously implicated in the sugar signal transduction pathways in plants [28,85,86], mostly independently of the HXK-mediated pathway. In addition, a model of RGS1 (regulator of G-protein signaling 1) regulatory protein action was presented as a glucose receptor located in the plasmalemma [86,87]. The mechanism of action of RGS1 and plant G proteins is currently being intensively investigated [87,88]. The interactions of *Arabidospis* RGS1 proteins (about 120 identified proteins in AtRGS1 complex) were reported to be dynamically modulated by glucose, and changes in AtRGS1 interactome were observed within minutes of providing glucose [87]. It has also been found that the FINS1/FBP (fructose insensitive1 and putative fructose-1,6-bisphosphatase) protein plays a key role in the signaling pathway induced by fructose [38,83]. Some researchers have suggested the involvement of invertases (EC 3.2.1.26 – β-fructofuranosidase) in the reception of sugar signal [9,89,90]. The participation of invertase could be direct, in which case the signal would be passed directly to cascades of specific kinases. An important role of invertase is definitely the generation and amplification of the signals (glucose) that can initiate the transduction pathways, leading to changes in gene expression (Fig. 1). Therefore, there are several different ways for the perception and transduction of sugar signals. Some signaling pathway components (for example, hexokinase or protein kinases) are the same or are similar to those found in bacteria, yeast, and animal cells. Other elements of the sugar signaling transduction chain function only in plants [4,7,23,28,85].

Various secondary mediators are involved in sugar signal transduction, including specific kinases and protein phosphatases (Fig. 1). This role is attributed to the SnRK serine–threonine kinase complexes (sucrose nonfermenting1-related protein kinases), CDPK (Ca^{+2}-dependent protein kinases), MAP kinases (mitogen-activated protein), and as discovered more recently, to TOR kinases (target of rapamycin), as well [2,5,7,8,25,28,29,36,68,91,92]. Several mechanisms of plant growth regulation have been proposed, depending on sugar availability. For the system that stimulates plant growth processes, the hexokinase (as a glucose sensor), Tre6P (as a signal), and TOR kinases were postulated to be operative [4,8,23,30]. The lack of Tre6P or TOR kinases inhibits growth and transition to the generative phase of the plant (it can be also lethal during embryogenesis) [23,24,30,92]. The other system that inhibits plant growth processes (such as vegetative development and flowering) involves protein kinases, SnRK1, and C/S1 bZIP transcriptional factors (C/S class basic region leucine zipper) [91]. The induction of SnRK1 and C/S1 bZIP most frequently inhibits the growth processes [4,8,91].

Trehalose (a disaccharide composed of two glucoses) was previously known as a sugar that is commonly present in microorganisms and fungi. It was discovered in

plants rather late, and it was thought that it could act in plant tissues only as an osmo-protectant under drought conditions [44]. In the last decade, trehalose-6-P was found to be essential for the normal growth and development of plants and for stable sugar metabolism [25,45,92–94]. Many genes encoding Tre6P synthase and phosphatase in plants have been discovered, however, not all of their products are catalytically active [25,44]. The Tre6P levels increase after sucrose administration; it was suggested that Tre6P could be a sugar signal sensor [24,92]. It was demonstrated that Tre6P can also affect the activity of other components of sugar transduction pathway (for example, SnRK1) [24,25,32]. Plant growth processes, shown to be regulated by Tre6P, range from the early development of embryos through vegetative and generative stages to the senescence of leaves [24,44,48]. Sometimes, such regulation of developmental processes occurs in cooperation with phytohormones [36]. However, lately, a model has been proposed with Tre6P as an essential factor, connecting sugars with plant growth and development [8,24,48,91,92]. The effects of Tre6P on the different stages of plant development and interaction with sugar and mediators of sugar signaling were recently discussed in detail [7,24,48,91–94].

SnRK serine–threonine kinases are plant homologs of previously known yeast SNF1 kinases and animal AMPK kinases (activated by AMP). We have known, for a long time, that the SnRK1 complex participates in the regulation of sugar and nitrogen metabolism, for example, through the phosphorylation of the enzymatic proteins, sucrose synthase and α-amylase [28,29]. The SnRK kinase activity is regulated by phosphorylation, glucose-6-phosphate, and sucrose (at the gene level), as well as by Tre6P, which inhibits the SnRK activity depending on the metabolic status of the cell. The role of SnRK1, and especially their KIN10/KIN11 subunits, has been extensively investigated with regard to sugar transduction in plant cells [8,23,91,94–97]. KIN10 and KIN11 protein kinases are currently considered as essential for coordinating plant responses to sugars and stress factors and they affect cellular energy homeostasis. Energy depletion activates KIN10 and KIN11, which stimulate or inactivate a number of processes in the cell, leading to improved energy management, adaptation of growth, and proper reaction of the plant to the stress factor [3,8,23,37,94–96]. SnRK1 usually inhibits the vegetative growth and flowering of the studied plants. Recent studies have indicated that the regulation of seed maturation and germination by sugars, as well as the transition of plants from the vegetative to the generative stage, takes place with the participation of Tre6P and SnRK1 (or SnRK2) [24,48,91,94,97].

The TOR protein kinase system has previously been well described in yeast and animal cells; its function is to regulate growth, proliferation, cell differentiation, and motility, as well as the translation and transcription processes. TOR functions as a sensor/regulator of the cellular levels of energy-rich compounds and the redox state [68,98–102]. Yeasts and mammals contain two complexes, namely TORC1 and TORC2, but only one complex (TORC1) is known in *A. thaliana* [68,99]. In plants, changes in TOR expression lead to alterations in the growth and development, starting from embryonic development to senescence [48,97,99–101]. The TOR kinases form complexes with other proteins, for example, with RAPTOR1 [99]. It has been demonstrated that signaling pathways involving TOR kinases affect the primary and secondary metabolism of plant cells and growth processes; for example, the stimulation of glucose-induced growth of *A. thaliana* roots is controlled by TOR kinases [68,97,100]. Lately, a pivotal function of TOR kinases in integrating various external signals to control the development of shoot apical meristem and distinct root apical meristem growth was underlined [100]. The involvement of ROP2 (small GTPase Rho-related protein 2) in light-auxin signal transduction, necessary for TOR activation and further promotion of E2F(A, B) transcription factors and for the expression of cell cycle genes in shoot apex was postulated [98–100]. Recent findings on the function of TOR kinases in plants, including the study on genetic connections between SnRK1-TOR and their antagonistic roles in the regulation of plant developmental stages, have been extensively summarized [8,48,68,98,102].

Phytohormones, such as ABA and ethylene, might be involved in the transduction of the sugar signal. It is known that sugars can affect the synthesis and transfer of certain phytohormones (including ABA and gibberellins), whereas hormones might regulate sugar metabolism [5,28,35,36,78]. Glucose has also been shown to increase the concentration of auxin synthesis precursors; furthermore, it affects the transcriptional

factors controlling the synthesis of auxins and the expression of hormone receptor genes [6,66,74]. The isolation and characterization of numerous sugar and hormonal mutants has provided evidence for the interaction of hormonal and sugar signaling pathways [63,66,75,103]. It has been shown that phenotypes of the hormonal mutants are similar or same like those of sugar mutants; for example, the phenotype of the mutant with ethylene overproduction, *eto1*, is the same as that of the *gin1* (glucose insensitivity) mutant or the *gin1*, *isi4*, and *sis4* mutants were found to be allelic to *aba2* (with reduced abscisic acid synthesis), and *gin6* and *sun6* were allelic to *abi4* [28,29,36,74,75]. The participation of ABI3 as well as ABF2 and ABF4 transcription factors has been demonstrated in sugar signal transduction, either dependent or independent of hexokinase [6,28,36,63]. In addition, more recent results indicated the interaction of cytokinins, gibberellins, jasmonic acid, salicylic acid, and brassinosteroids with sugar pathways during plant development [57,103,104]. It was suggested that the function of HXK1 is dependent on the presence of brassinosteroids, which might act downstream of HXK1 to regulate hypocotyl elongation in *A. thaliana* in darkness (in a glucose-dependent reaction) [104]. Recent studies have indicated the involvement of several miRNAs in phytohormone signaling pathways [105] and in sugar responses in plants [106], but more research is needed to fill in some gaps in knowledge.

In conclusion, the signal transduction pathways induced by sugars interact with many hormonal pathways and routes responding to environmental factors, forming a complex communication and signaling network in plant cells. The proper cooperation of different transduction pathways enables efficient regulation of the growth and development of plants. However, further research is required to elucidate the details of regulatory mechanisms, which is important for understanding, and improving, human-induced plant development in future.

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