Sugar Signaling in Plant Growth and Development

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Abstract

Sugars are the primary energy sources produced by green plants via the life-sustaining process of photosynthesis. The metabolic role of sugars as energy compounds and essential metabolites in living organisms has long been recognized. However, genetic and molecular (mutational) studies during the last decade have highlighted the role of sugars as signaling molecules in controlling diverse aspects of plant growth and development. The review focuses on specific signaling roles of various sugars particularly hexoses (glucose and fructose), sucrose, trehalose, and small glycans. Moreover, the sugar-specific regulations of various genes and the diverse signaling cascades involved have been discussed. The role of hexokinase–kinase-dependent and hexokinase-independent signals (like G proteins) in sugar signal transduction pathways has also been documented. The evidences generated from the analyses of sugar-insensitive mutants and hormone-insensitive mutants have also demonstrated a complex interplay of factors regulating the common signaling capabilities of sugar/hormone interactions. Characterization of sugar-signaling mutants in *Arabidopsis* has unraveled a complex signaling network that links sugar responses to two plant stress hormones, abscisic acid and ethylene, in opposite ways. Similar cross talk between sugar and other plant hormones in their signaling capabilities has been discussed.

Keywords

Abscisic acid • G proteins • Hexokinase • Hormones • Signaling • Sugars • Trehalose

5.1 Introduction

Sugars, the molecules of fundamental importance for life, act as the primary carriers of captured energy from the sun. They have been found to modulate a range of vital processes of plant

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K.R. Hakeem et al. (eds.), *Plant signaling: Understanding the molecular crosstalk*,
DOI 10.1007/978-81-322-1542-4_5, © Springer India 2014

growth and development including seed germination, seedling development, root/leaf differentiation, floral transition, fruit ripening, embryogenesis, and senescence, as well as regulation of responses to light, stress, and pathogens. During germination and early seedling development, sugars are known to repress nutrient mobilization, hypocotyl elongation, cotyledon greening/expansion, and shoot development (reviewed in Leon and Sheen 2003) and that sugar starvation in plants activates lipid mobilization, fatty acid transfer, and peroxisomal β-oxidation (Hooks et al. 1995). Using transcriptome profiling analysis in *Arabidopsis*, it has been shown that sucrose (a sugar source) plays an important role in the activation of oxidative-stress genes, such as catalase (Contento et al. 2004). As it is a well-known fact that plant growth and development is under the tight regulation of the environmental conditions that in turn influence the availability of photosynthetic carbon in the form of carbohydrates. These developmental processes are however required to meet the carbon or energy demands of the system, and as such, the production, utilization, mobilization, and allocation of these photosynthates (carbohydrates) in various tissues at different stages of development are therefore highly regulated.

Sugar production in plants mainly involves photosynthetic conversion of light energy into chemical bond energy of organic molecules, utilizing the conventional photosynthetic pathway, and as such, the process of photosynthesis carries the vital importance to plants. The sugar status of a plant has been found to coordinate internal regulators and external environmental cues that in turn govern vital processes of growth and development (Koch 1996; Sheen et al. 1999; Smeekens 2000). Moreover, sugar metabolism is a dynamic process as sugar concentrations have been found to alter dramatically during development and in response to environmental signals, diurnal changes, and biotic/abiotic stress (Rolland et al. 2006). Sugars serve both as an energy source and as signaling components, e.g., sucrose serves as a main transport carbohydrate in plants and also as a signal molecule that can regulate gene expression and plant development (Baier et al. 2004). Similarly in *Vicia faba* embryos, gradients of sugars have been reported to correlate spatially with mitotic activity (Borisjuk et al. 1998), and in *Arabidopsis*, D-type cyclin gene expression has also been found to be regulated by sugars (Riou-Khamlichi et al. 2000) which points out that sugars provide positional information to the cell cycle machinery and different developmental programs. As far as the effect of sugars on floral transition is concerned, studies have revealed that increased leaf carbohydrate export and starch mobilization are required for flowering (Corbesier et al. 1998) and that the addition of sugar source (sucrose at optimum concentrations) can rescue the late-flowering phenotype of several mutants and even promotes leaf morphogenesis and flowering in the dark (Araki and Komeda 1993; Zhou et al. 1998; Roldan et al. 1999). Ohto et al. (2001) has reported that sugars may control floral transition by positively and negatively regulating the expression of floral identity genes. Thus, sugars, in addition to their essential roles as substrates of carbon and energy metabolism, have important hormone-like functions or as primary messengers in plant signal transduction. Sugars have been reported to affect the expression of many genes involved in photosynthesis, glycolysis, nitrogen metabolism, sucrose and starch metabolism, defense mechanisms, and cell cycle regulation, and therefore, studies have been and are being made to reveal the sugar-sensing and signal transduction pathways (Rolland et al. 2006; Bolouri-Moghaddam and Van den Ende 2012). In the present review, we attempt to consolidate the information regarding the role of sugars as signaling molecules in plants and to discuss the different dimensions of the sugar signal transduction pathway.

5.2 Sugars as Signaling Molecules

Sugars such as glucose, fructose, or sucrose have been recognized as important signaling molecules in plants, in addition to their typical roles as carbon and energy sources (Koch 2004; Rolland et al. 2006; Bolouri-Moghaddam et al. 2010). Of the various sugars, sucrose is the most important

Fig. 5.1 Role of sugars in plant growth and development

metabolite in resource allocation system of plants and is the predominant form of carbon transported to the heterotrophic tissues (Chiou and bush 1998). Although it has been reported to regulate plant growth and development, differential gene expression, and stress-related responses, at the same time it is also emerging as a candidate signaling molecule in plant innate immunity (Gómez-Ariza et al. 2007; Birch et al. 2009; Wind et al. 2010). In many cases, the effects of sucrose have been shown to be completely mimicked by hexoses (glucose and fructose) as is reported in case of photosynthesis genes where hexoses at lower concentrations have been found to mimic their sucrose repression (Sheen et al. 1999). It is also indicative of the fact that in such a case sucrose is not the direct signaling molecule instead its hydrolysis products (glucose or fructose) might have the signaling capabilities. It has been reported that some plant families even use raffinose-family oligosaccharides and small fructans as their main transport sugars (Keller and Pharr 1996; Wang and Nobel 1998; Zuther et al. 2004). There has also been a growing recognition that free glycans (oligogalacturonides, chitosan, or chitin oligosaccharides) are also used as signals for the initiation of a wide variety of biological processes involving growth, development, and defense responses of plants and animals (Etzler and Esko 2009) (Fig. 5.1).

5.2.1 Hexose Signaling

The pivotal role of sugars as signaling molecules is illustrated by the variety of sugar-sensing and signaling mechanisms discovered in microorganisms (bacteria and yeast) and plants (*Arabidopsis*) (Rolland et al. 2001; Moore et al. 2003; Yanagisawa et al. 2003). Sugar signals have been reported to be generated either by carbohydrate concentration or by relative ratios to other

metabolites, such as C:N or by flux through sugar-specific sensors and/or transporters (Coruzzi and Bush 2001; Palenchar et al. 2004; Buttner 2010). To activate signal transduction pathways, a signaling molecule first has to be sensed. Nevertheless, dual function of sugars (as a nutrient and a signaling molecule) complicates the analyses of the mechanisms involved and the elucidation of the initial sugar sensor involved in signaling. However, the involvement of transporters like glucose sensors (Snf3 and Rgt2), a G protein-coupled receptor (Gpr1), and more importantly hexokinase (HXK) function has been reported (Rolland et al. 2001, 2002). Multiple sugar sensors/receptors are known to exist, with hexokinase (HXK) being the first to be documented in plants (Jang and Sheen 1997). Hexokinase is a multifunctional protein being both an enzyme, which catalyzes the first step of glycolysis (conversion of glucose to glucose-6-phosphate), and a glucose sensor. The sensing function of the protein has been found to be dependent on the enzymatic function in a similar manner as its yeast counterpart. The difference, however, being that overexpression of the yeast hexokinase in plants only enhances its catalytic activity (Rolland et al. 2006) and not the signaling capability. Hexose phosphorylation by hexokinases has been considered to be an essential step in sugar metabolism, involving at least two classes of glucose- and fructose-phosphorylating enzymes (hexokinases and fructokinases). Using transgenic and mutational approach, the functions of several *HXK* and *FRK* genes have been investigated wherein the sensing roles of HXK and developmental roles of FRK have been documented (Granot et al. 2013). Much progress has been made to reveal the molecular mechanisms underlying sugar sensing and signaling in plants, particularly the demonstration of hexokinase (HXK) as a glucose sensor (Sheen et al. 1999; Smeekens 2000). The isolation and characterization of the *Arabidopsis gin2* mutants have clearly identified hexokinase (AtHXK1) as a core component in plant sugar sensing and signaling. Interestingly, these mutants were found to have partial glucose kinase activity. Uncoupling of metabolic and signaling activity has been confirmed by the analysis of two catalytically inactive *AtHXK1* alleles (one deficient in ATP binding and the other deficient in phosphoryl transfer). Both these alleles have been reported to sustain wild-type growth, repression of photosynthetic gene expression, and hormone (auxin and cytokinin) responsiveness when expressed in a *gin2* background (Moore et al. 2003). These findings suggested the existence of other hexokinases (AtHXK2) and hexokinase-like proteins (AtHXL). In the *Arabidopsis* genome, six *HXK* and *HXK* like (*HXKL*) genes have been identified. One of the hexokinase-like proteins has been found to have detectable kinase activity and was therefore named as AtHXK3. More complex functions of HXK are being anticipated in rice, in which ten functional *HXK* homologs have been identified. The role of hexokinase as a glucose sensor has also been revealed by the use of various glucose analogs (2-deoxyglucose, mannose, 6-deoxyglucose, and 3-O-methyl glucose). 2-Deoxyglucose and mannose act as substrates for hexokinase and were found to mimic glucose signaling in the regulation of photosynthetic and glyoxylate genes, while non-metabolizable 6-deoxyglucose and 3-O-methylglucose were found to be effective in mimicking the signaling response in the regulation of invertase and patatin genes. These findings support the existence of both hexokinase and non-hexokinase sugar sensors (Sheen et al. 1999). The identification of two hexose transporter-like sensors, SNF3 and RGT2, that mediate glucose regulation of glucose transporter genes in yeast has suggested that similar hexose sensors might exist in plants (Johnston 1999; Lalonde et al. 1999). In *Arabidopsis*, three glucose transporter-like proteins have been identified as potential candidates and it has been suggested that distinct hexose sensors might be used for diverse hexose signaling pathways in plants. Hohmann et al. (1999) proposed that hexokinase undergoes a conformational change after binding to its substrate glucose or other hexoses, and this regulation might be an essential mechanism of the sensing process. This conformational change of HXK might resemble the analogous ligand-induced conformational change of a typical receptor that allows modification of protein–protein interactions to trigger a signaling

cascade. It has been also postulated that altered ATP/ADP ratios or altered cytosolic phosphate ion concentration, as a result of hexokinase activity, might have a signaling function, but the experimental verifications are still pending (Sadka et al. 1994).

HXK and HKL protein localization has been suggested to play an important role in their functions as has been evidenced from the association of different hexokinase or hexokinase-like proteins with different cell organelles (particularly chloroplast and mitochondria; Borchert et al. 1993; Galina et al. 1995; Wiese et al. 1999), whether it being the HXK protein association with mitochondria in *Arabidopsis* and maize or an inner-plastidic HXK in tobacco (Galina et al. 1995, 1999). Moreover, AtHXK1 has been reported to translocate to nucleus as well. Here it is important that the involvement of cytosolic hexokinases as hexose sensors has not been observed in the cytoplasm, and it has been proposed that hexoses are sensed only when produced in the endomembrane system (Golgi–endoplasmic reticulum). The apoplastic and vacuolar targeted invertases are thought to play an important role as they are enzymatically active in these compartments and result in the generation of monosaccharides which are then sensed. Hexoses generated in either the endomembrane system or in plastids are then transported into the cytosol with concomitant phosphorylation by signaling hexokinases. Therefore, these transport-associated hexokinases are capable of signaling, while the hexoses produced in the cytosol are not (Halford et al. 1992; Koch 1996). Plant hexokinases have been grouped into two types: type A kinases (such as PpHXK1 and two *Arabidopsis* HXLs), which have a predicted chloroplast transit peptide, and type B kinases (such as AtHXK1 and AtHXK2), which have a membrane anchor. In addition to HXKs, plants are also reported to contain several fructokinases, some of which have been implicated in sugar sensing. Three fructokinase (*FRK*) genes and several *FRK*-like genes have been identified in *Arabidopsis*. In tomato, fructokinase transcripts, *FRK1* and *FRK2*, have been found to be induced by exogenous application of sugars (glucose, fructose, as well as sucrose; Kanayama et al. 1998). Although it is generally believed that FRKs play metabolic roles, the identification of an *frk2* null mutation in *mig* mutant suggests that FRK might be involved in sugar sensing (Pego and Smeekens 2000). This is also confirmed from the fact that glucose-insensitive (*gin*) mutants in Arabidopsis showed glucose insensitivity but were sensitive to fructose and sucrose. The role of fructose as signaling molecule has been demonstrated in *Arabidopsis* where it induces seedling developmental arrest and interacts with plant hormones (abscisic acid and ethylene) in a similar manner to that of glucose. Although earlier studies have suggested the role of fructokinase (an enzyme which phosphorylates fructose in the same manner as hexokinase phosphorylates glucose) in fructose signaling (Pego and Smeekens 2000; Odanaka et al. 2002; German et al. 2003), recent studies have demonstrated the role of fructose insensitive1 (FINS1) or fructose-1,6-bisphosphatase (F6BP) as a putative signaling component. It has been reported that role of FINS1 as a signaling component is independent of its catalytic activity and that fructose signaling is independent of HXK function (Cho and Yoo 2011).

Hexokinase 1 (HXK1) has been implicated to be an evolutionarily conserved glucose sensor that integrates nutrient and hormone signals to govern gene expression and plant growth in response to environmental cues (Cho et al. 2006). Based on the role of hexokinases, three distinct glucose signal transduction pathways have been identified in plants (Xiao et al. 2000).

1. Hexokinase dependent and metabolism independent
2. Hexokinase dependent and metabolism dependent
3. Hexokinase independent

The regulation of photosynthetic genes by hexokinase 1 (HXK 1) provides an excellent example of hexokinase-dependent (metabolism-independent) pathway. Inside the nucleus, HXK1 has been found to interact with the vacuolar H^+-ATPase B1 (VHA-B1) and the 19S regulatory particle of proteasome subunit (RPT5B) in a glucose-dependent manner to form an HXK1-nuclear complex that directly binds to promoters

of glucose-regulated genes (Cho et al. 2006). The second pathway is glycolysis dependent and has been found to be sustained by the heterologous yeast HXK2 activity, e.g., the glucose induction of *PR1* and *PR5* gene expression or the sugar-induced expression of senescence-associated gene *SAG21* (Noh and Amasino 1999; Xiao et al. 2000). The third pathway, i.e., hexokinase-independent pathway, is represented by glucose induction of *CHS*, *PAL1*, and genes encoding AGPase as well as by glucose repression of aspartic synthase (*ASN1*). Ryu et al. (2004) also reported that the induction of carotenoid biosynthesis genes by glucose also involves hexokinase-independent pathway. This pathway has been reported to involve (cyclic AMP-protein kinase) cAMP–PKA signaling. cAMP synthesis by adenylate cyclase via glucose activation involves a dual function. Evidences have suggested that multiple hexose kinases (hexokinases, HXK1 and HXK2, or glucokinase, GLK1) on one hand play a regulatory role through activation of small Ras G proteins (required for adenylate cyclase activity), while on the other hand, these extracellular sugars (glucose or sucrose) are sensed by the G protein-coupled receptor (GPCR) system consisting of GPR1 receptor, GPA2 (a heterotrimeric Gα-protein) and RGS1/RGS2, negative regulators of G protein signaling (Chen et al. 2003; Chen and Jones 2004; Lemaire et al. 2004). Mutants in G protein-interacting membrane protein (*RGS1*) gene have been generated and found to have impaired glucose sensing and that the mutants in G protein α-subunit gene GPA1 were found to have impaired glucose sensitivity (Huang et al. 2006; Grigston et al. 2008). Like *Saccharomyces cerevisiae*, G protein signaling elements have also been identified in *Arabidopsis*, which contained a G_{α} subunit (AtGPA1), a G_{β} subunit (AGB1), one or two G_{γ} subunits, and a regulator of G-signaling protein (AtRGS1). The *Arabidopsis* heterotrimeric GPA1 complex (consisting of G_{α}, G_{β}, and G_{γ} subunits) has been implicated to play an important role in abscisic acid signaling, in biotic/abiotic stress, in germination and early development, as well as in glucose signaling (Tuteja and Sopory 2008). Moreover, AtRGS1 has been reported to comprise a *C*-terminal RGS domain coupled to an *N*-terminal domain with a predicted seven-transmembrane topology which interacts with the AtGPA1 at the plasma membrane and functions as a GTPase activating protein (GAP) for AtGPA1 (Ritchie et al. 2002; Choi et al. 2005; Finkler et al. 2007). Recently, Grigston et al. (2008) have demonstrated that AtRGS1, a putative extracellular receptor for D-glucose aided with the heteromeric G protein complex, mediates the steady-state level of transcripts of some sugar-related genes in a G protein-coupled signaling network in *Arabidopsis*.

5.2.2 Sucrose Signaling

In addition to hexoses (glucose and fructose), other sugars like sucrose, trehalose, some rare sugars (psicose and D-allose), and the sugar-analogs 2,5-dideoxy-2,5-imino-D-mannitol (DMDP, a fructose analog) are reported to have signaling capabilities (Lalonde et al. 1999; Smeekens 2000). These have been found to stimulate the plant immune system and upregulate various genes involved in plant growth and development. Moreover, it has been suggested that these compounds act as signals through hexokinase-dependent/independent pathways (Birch et al. 1993; Vaughn et al. 2002; Derridj et al. 2009; Kano et al. 2011). Compared to hexose signaling, sucrose signaling is far more complex. Sucrose can readily be hydrolyzed to the corresponding hexoses (fructose and glucose), and as such, it becomes difficult to separate the signaling function of sucrose from its hydrolysis products, and thus, the nature of sucrose signaling can often be attributed to the hexose-dependent pathways. However, the identification of some sucrose-specific genes (whose expression is specifically regulated by sucrose and not by hexoses) points to an HXK-independent sucrose-specific signaling pathway, e.g., sucrose-specific expression of a gene encoding a proton–sucrose symporter in sugar beet (Vaughn et al. 2002), the sucrose-mediated translational inhibition of the ATB2/bZIP11 transcription factor in *Arabidopsis* (Wiese et al. 2004; Rosa et al. 2009),

and the posttranscriptional control of a leucine zipper transcription factor (Rook et al. 1998). In addition, studies on starch synthesis in potato tubers and on seed development in transgenic *Vicia narbonensis* also support the involvement of sucrose-specific signals in the differentiation and synthesis of storage products (Geiger et al. 1998; Weber et al. 1998). Nevertheless, Loreti et al. (2001) have reported that the expression of α-amylase gene in barley embryos is modulated by both glucose and sucrose independently. Therefore, sucrose can be sensed as a signal directly or, alternatively, a signal can arise via its hexose cleavage products, i.e., glucose or fructose (Chiou and Bush 1998; Li et al. 2011; Eveland and Jackson 2012). It is also obvious that sucrose could have a signaling mission distinct from that of hexoses and therefore could be perceived by different types of sensors/receptors. The nature of sucrose sensor involved in sucrose signaling is still obscure; however, sucrose transporter SUT2/SUC3 has been proposed to act as a sensor in analogy to SNF3 and RGT2 glucose sensors in yeast (Eckardt 2003). Two sucrose transporter cDNAs (*CitSUT1* and *CitSUT2*) have been isolated and characterized from citrus. They have been reported to encode putative proteins (CitSUT1 and CitSUT2) of 528 and 607 amino acids, respectively, and that both proteins contain 12 predicted transmembrane domains. The expression of *CitSUT1* in mature leaf discs has been found to be repressed by exogenous sucrose, glucose, mannose, and the glucose analog 2-deoxyglucose, but not by another glucose analog 3-O-methylglucose, indicating a hexokinase (HXK)-mediated signaling pathway, while *CitSUT2* expression has been found to be unaffected by exogenous importing sugars, suggesting different physiological role for this sucrose transporter. The expression patterns of citrus sucrose transporters also showed temporal regulation as *CitSUT2* has been found to be expressed in young leaves and *CitSUC1* in the mature leaves (Li et al. 2003). Remarkably, the S1 group bZIP transcription factors (bZIP1, bZIP2, bZIP11, bZIP44, and bZIP53) have been found to be translationally repressed by sucrose, and this repression has been reported to be dependent on an upstream open reading frame (uORF) present in the 5′ leader of the bZIP mRNAs (Rahmani et al. 2009; Weltmeier et al. 2009) that encodes a highly evolutionary conserved sucrose control peptide (SC peptide). The translational repression of bZIP transcription factors by sucrose has recently been reported to depend on conditional stalling of a ribosome translating the SC peptide wherein the stalled ribosomes on the mRNA have been found to inhibit translational initiation of the bZIP encoding ORF. In general, hexoses are considered to have greater signaling potential in promoting organ growth and cell proliferation, while sucrose has been suggested to be typically associated with differentiation and maturation. It has also been postulated that relative ratios of hexoses to sucrose are perceived and maintained by sucrose metabolic enzymes, for which different isoforms act in a spatio-temporal manner to control and coordinate the fine-tuning of growth during different phases of development (Xu et al. 1996; Borisjuk et al. 2002; Koch 2004).

5.2.3 Trehalose Signaling

Trehalose is another important sugar with signaling capabilities. It normally acts as an osmoprotectant which counters the effects of dessication from drought, salt, or low-temperature stress (Crowe et al. 1992). In *Arabidopsis*, T6P accumulation has been found to be associated with increased anthocyanin accumulation during later stages of leaf development (Wingler et al. 2012). Since anthocyanins accumulate under high carbon supply, it has been suggested that T6P signals high sugar availability and thereby stimulating the anthocyanin biosynthetic pathway. Moreover, plants overexpressing microbial trehalose biosynthetic genes have been reported to have altered carbohydrate metabolism and morphological defects like stunted growth (Romero et al. 1997; Garg et al. 2002; Schluepmann et al. 2003, 2004). These phenotypes are thought to result from changes in carbon allocation between sink and source tissues and it has been speculated that trehalose might be

involved in sugar signaling (Paul et al. 2008). In plants, trehalose biosynthesis occurs in two steps. In the first step, trehalose-6-phosphate (T6P; an intermediate) is formed from UDP-glucose and glucose-6-phosphate by trehalose-6-phosphate synthase (TPS). The second step involves the conversion of T6P to trehalose by trehalose-6-phosphate phosphatase (TPP) (Cabib and Leloir 1958). About 11 trehalose phosphate synthase (*AtTPS1-11*) genes and 10 trehalose-6-phosphate phosphatase (*AtTPPA-J*) genes have been identified in *Arabidopsis* (Leyman et al. 2001). AtTPS proteins have been reported to carry both trehalose-6-phosphate synthase (TPS)- and trehalose-6-phosphate phosphatase (TPP)-like domains. Among the Arabidopsis TPSs, only AtTPS1 is reported to have demonstrable TPS activity, while other TPSs lack both TPS and TPP activities (Ramon et al. 2009). Similarly in rice, two active isoforms of TPS1 (*OsTPS1a* and *OsTPS1b*) have been identified (Zang et al. 2011). Based on the homology of Arabidopsis TPSs with the yeast trehalose-6-phosphate synthases (ScTPS), they have been classified into two distinct subfamilies (Ponnu et al. 2011).

Class I Subfamily: It involves AtTPS1–AtTPS4 which are characterized by highest overall symmetry to ScTPS1, and in them, the TPP-like domain is only weakly conserved. AtTPS1 differs from the other class I TPSs in that it contains an auto-inhibitory *N*-terminal extension that restricts its activity in vivo.

Class II Subfamily: It involves AtTPS5 to AtTPS11 which displays more similarity to ScTPS2. These are reported to contain conserved TPP motifs. On the other hand, all trehalose-6-phosphate phosphatases (TPPs) lack the *N*-terminal TPS-like domain and contain only the conserved TPP domain with significant similarity to the highly conserved phosphatase box in the *C*-terminal part of ScTPS2 (Lunn 2007). Out of the ten TPPs in *Arabidopsis*, only *AtTPPA* and *AtTPPB* genes have been shown to encode active TPP enzymes (Vogel et al. 1998). Similarly, rice *TPP2a* and maize *RAMOSA3* (Habibur Rahman Pramanik and Imai 2005; Satoh-Nagasawa et al. 2006; Shima et al. 2007) have also been shown to encode active TPPs.

Evidences accumulated so far support the fact that T6P, rather than trehalose itself, has signaling capabilities. Developmental processes that are regulated by T6P range from embryo development to leaf senescence. Some of these processes have been found to be regulated in interaction with phytohormones, such as auxin (ÓHara et al. 2013). T6P has been found to regulate starch synthesis via redox activation of ADP-glucose phosphorylase (which catalyzes the first step in starch biosynthesis) and has recently been shown to inhibit the KIN10/11 regulatory kinase (Lunn et al. 2006; Zhang et al. 2009; Wingler et al. 2012). The direct regulation of KIN10/11 by T6P has not been demonstrated, and hence, unknown additional signaling steps are thought to be involved. KIN10/11 proteins have been found to regulate gene expression through specific transcription factors of which a small group of bZIP G-box binding transcription factors are of particular importance. The transcription factors have been reported to bind to the promoters of genes regulated by the KIN10/11 signaling pathway. More importantly, bZIP proteins have been found to harbor conserved motifs for phosphorylation by AMPK/SNF1-like kinases which make them vulnerable to direct phosphorylation that might regulate the activity of these transcription factors (Baena-Gonzalez et al. 2007; Hanson et al. 2008). However, more experimental details are required to substantiate the conclusion.

T6P, as a signaling molecule, allows yeast hexokinase to perceive carbon status (Paul et al. 2001) where, as in Arabidopsis, no direct link between hexokinase inhibition and T6P has been observed (Eastmond et al. 2002). It has been suggested that a protein kinase, sucrose non-fermenting-related kinase-1 (SnRK1), might serve as a link between the two (Schluepmann et al. 2004). The role of SnRK1 in regulating plant metabolism has been well established. It has been demonstrated to play an important role in starch breakdown as the expression of α-amylase in wheat and rice embryos during sugar starvation requires the SnRK1 activity. However, overexpression of SnRK1 in potato tubers has been reported to increase the expression of sucrose synthase and

AGPase genes (resulting in increased starch content) which demonstrates that SnRK1 is also involved in activating starch synthesis (Laurie et al. 2003; McKibbin et al. 2006; Lu et al. 2007). It has been reported to bring direct phosphorylation leading to inactivation of various metabolic enzymes including 3-hydroxymethyl-glutaryl-CoA reductase, sucrose phosphate synthase, nitrate reductase, and trehalose-6-phosphate synthase (Polge and Thomas 2007; Halford and Hey 2009). Zhang et al. (2009) have reported that T6P inhibits the catalytic activity of SnRK1 in vitro at physiological concentrations in *Arabidopsis* seedlings, but not in mature leaves. Such a variation in the regulation of SnRK1 by T6P has also been reported during wheat grain development (Martínez-Barajas et al. 2011). It has been speculated that a protein factor, present only in growing tissues like seedlings and young leaves of *Arabidopsis* and in cauliflower florets, underlies these developmental changes in the inhibition of SnRK1 by T6P. The regulation of SnRK1 itself in response to the availability of metabolites has not been fully demonstrated. Jossier et al. (2009) point out that phosphorylation of SnRK1 in response to glucose leads to its activation. Here the role of evolutionary conserved 14-3-3 proteins has been documented. The 14-3-3 proteins have been reported to bind specifically to phosphorylated substrates and thus controlling the enzyme activities, subcellular location, and protein–protein interactions required for such signal transduction pathways (Finnie et al. 1999; Sehnke et al. 2002). It has also been proposed that the loss of 14-3-3 protection and the resulting proteolysis bring about the major metabolic shift to reduce nitrate assimilation and sugar synthesis upon sugar starvation (Cotelle et al. 2000). Moorhead et al. (1999) also reported the interaction of plant trehalose-6-phosphate synthase with 14-3-3 proteins, thereby supporting a role for trehalose-6-phosphate in the starvation response, while Paul et al. (2001) suggested that loss of 14-3-3 binding releases trehalose-6-phosphate from the trehalose synthesis complex under conditions of low carbon supply. Recently, the transcription factor bZIP11 has been identified as an important component of the T6P/SnRK1 regulatory pathway (ÓHara et al. 2013). In *Arabidopsis* seedlings, an interaction between bZIP11 and SnRK1 has been found in response to trehalose feeding, and a subtle mechanism including a regulatory loop that regulates growth in response to sucrose through an increase in T6P and inhibition of SnRK1 and therefore of bZIP11-dependent gene expression has been proposed. It has been suggested that too much T6P in the absence of a sufficient sucrose supply can result in carbon deficit because of over-activation of biosynthetic pathways and reduced carbon salvage through catabolic pathways, whereas too little T6P inhibits growth because of the downregulation of biosynthetic pathways required for growth (Delatte et al. 2011).

5.2.4 Glycan Signaling

Apart from sugars like glucose, fructose, sucrose, or trehalose, glycans or oligosaccharins have been reported to act as signaling molecules in plants. The first indication of glycans or oligosaccharins as signaling molecules came from the studies on plant defense responses where it has been shown that plant or pathogen cell wall-released glycans elicit the defense response. It has been reported that specific free glycans in picomolar to micromolar concentrations have signaling capabilities for the initiation of a number of biological processes, particularly in the defense response of plants and the initiation of the nitrogen-fixing *Rhizobium*–legume symbiosis. Glycan signaling systems have been suggested to involve various glycoconjugates as has been demonstrated by the changes in cytoskeleton, gene transcription, and enzyme activation on the addition of O-GlcNAc to cytoplasmic and nuclear proteins. Specific receptors on the plasma membrane have been found to recognize the glycans. Experimental studies with plant cell cultures and isolated plasma membranes have demonstrated the existence of specific cell-surface or membrane-binding sites with binding

specificities similar to those required for biological behavior. The recently identified protein CEBiP (a 75-kDa plasma membrane protein from cultured rice cells), as a candidate for such receptors, is a chitin oligosaccharide elicitor binding protein that binds chitin elicitors. This protein has been recently purified and the corresponding gene cloned. The protein was found to be a membrane protein without any appreciable portion on the cytoplasmic side of the membrane, suggesting that it might be part of an elicitor–receptor complex. Further studies have shown that reduced expression of the corresponding gene resulted in suppression of the defense response. Similarly, the role of glycosaminoglycans (GAGs) as signaling molecules is also evident from the fact that they interact with receptor tyrosine kinases and/or their ligands and facilitate changes in cell behavior, e.g., hyaluronan oligosaccharides have been found to bind to specific membrane proteins (such as CD44) resulting in clustering of CD44 and activation of several kinases (such as c-Src and focal adhesion kinase [FAK]) to bring out phosphorylation resulting in the alteration in the interaction of the cytoplasmic tail of CD44 with regulatory and adaptor molecules that modulate cytoskeletal assembly/disassembly and cell survival and proliferation. Such a signaling by hyaluronan oligosaccharides has been reported to depend on the degree of polymerization of the glycans, with low-molecular-weight chains more active than high-molecular-weight chains. Likewise, glycosphingolipids are also known to form lipid rafts, which act as a platform for sequestering signaling receptors, or can associate with receptor tyrosine kinases to modulate their activity (Etzler and Esko 2009).

5.3 Sugar Signaling and Gene Regulation

Sugars are known to activate various pattern recognition genes (Johnson and Ryan 1990; Herbers et al. 1996a, b; Rolland et al. 2002). A wide variety of genes have been found to be regulated by sugars at the transcriptional level, e.g., genes involved in photosynthesis, carbon/nitrogen metabolism, stress responses, and secondary metabolism. The initial candidate-gene approaches have demonstrated that variations in sugar levels could significantly modify the expression of genes related to abiotic stress. For example, the expression of chalcone synthase, which allows the synthesis of photoprotective anthocyanins and superoxide dismutase, has been reported to be induced by glucose (Koch 1996). Similarly, sucrose synthase gene (*Sus1*) encoding sucrose synthase protein (SuSy) has been found to be regulated by glucose and mannose. Based on the effects of hexokinase inhibitor, *N*-acetyl glucosamine, and using the mutational approach (plants with impaired *HXK1* expression), it has been shown that both the sugars (glucose and maltose) employ different regulatory mechanisms, suggesting that the regulation of *Sus1* involves multiple transduction pathways. At low concentration of sugars, hexokinase is thought to be involved, while at higher concentrations, the involvement of osmoticum pathway has been suggested (Ciereszko and Kleczkowski 2002). Moreover, the role of phosphoprotein in mediating the signal transduction has also been confirmed but the signaling pathway it affects has not been clearly demonstrated for *Sus1* regulation (Ciereszko et al. 2001). It has been further reported that the effect of sucrose on *Sus1* gene is not a direct effect of sucrose; instead, it is due to the effect of glucose (a cleavage product of sucrose) through hexokinase-dependent pathway. Using mutant analysis approach in *Arabidopsis*, a positive correlation between glucose feeding and aliphatic glucosinolate biosynthesis has been reported. Aliphatic glucosinolates have been demonstrated to play an important role in plant–herbivore interactions and nonhost resistance in the *Arabidopsis–Pseudomonas* pathosystem. Glucosinolate biosynthesis genes *CYP79F1* and *CYP79F2* have been found to be upregulated by glucose. However, the upregulated expression of these genes in double mutant *myb28/myb29* has not been reported, suggesting that the glucose-mediated aliphatic glucosinolate biosynthesis genes are regulated via MYB28/MYB29 transcription factors. Moreover, the total aliphatic glucosinolate content and the expression level of *MYB28* and *MYB29* have been found to be

substantially reduced in the glucose-insensitive (*gin2-1)* mutant, the ABA-insensitive 5 (*abi5-7*) mutant, and sugar-insensitive RGS1 (regulator of G protein signaling 1) mutant (*rgs1-2)* which suggests the hexokinase and/or G protein involvement in mediating glucose signaling for glucosinolate biosynthesis. The evidence for glucose-specific induction of glucosinolate biosynthesis/accumulation is also evident from the fact that fructose or mannose has been found to be ineffective in mimicking the induction of glucosinolate genes (Miao et al. 2013). In cyanobacterium *Synechocystis*, Ryu et al. (2004) have shown that glucose induces expression of carotenoid synthesis genes in the dark. In this way, it mimics the effects of high light on carotenoid synthesis genes and thereby opens the possibility that glucose plays a role in the regulation of carotenoid synthesis in response to high light. The reports by Price et al. (2004) in *Arabidopsis* seedlings have also confirmed the glucose induction of several stress response genes including oxidative-stress-related genes, such as chalcone synthase, glucose-6-phosphate dehydrogenase, glutathione-S-transferases, and glutathione conjugate transporters. Similarly, a fine example of sugar regulation of genes at translational level is the sucrose repression of basic leucine zipper gene (*ATB2*) in *Arabidopsis*. For this repression, glucose and fructose individually or together have been found to be ineffective. The *ATB2* mRNA has been found to carry a complex leader containing small open reading frames and its deletion from the transcript has been reported to abolish the sucrose-mediated repression (Rook et al. 1998). These results indicate that a sucrose-specific signal controls translation repression of mRNA levels (Fig. 5.2).

A sugar-signaling cascade involves sugar sensors to feed information (sugar signaling) into signal transduction cascades to result in various types of plant responses. The signal transduction cascade has been found to involve various components like mitogen-activated protein kinases (MAPKs), calcium-dependent protein kinase (CDPK), protein phosphatases (PPs), Ca^{2+}, calmodulin, SnF1-related protein kinase (AtSR2), and transcription factors (Ishiguro and Nakamura 1994; Takeda et al. 1994; Ohto and Nakamura 1995; Ehness et al. 1997; Rook et al. 1998; Gupta and Kaur 2005). Sugar regulation of gene expression can be mediated at the transcriptional and post-transcriptional levels. Most progress has been made through the functional dissection of sugar-induced gene promoters. Whether it be the characterization of sucrose-responsive elements in the patatin class I promoter, SP8 motifs in the promoters of sweet potato sporamin and α-amylase genes, or sucrose-responsive sequences in some sucrose-inducible sucrose synthase genes (Liu et al. 1990; Ishiguro and Nakamura 1992, 1994; Grierson et al. 1994; Kim et al. 1994; Fu et al. 1995). Both positive and negative *cis*-elements have been found. Ishiguro and Nakamura (1994) have identified and cloned a gene *SPF1*, which encodes a DNA-binding protein that can recognize the SP8 motif in the sporamin and α-amylase gene promoters. It has also been reported that the gene encodes a negative regulator which is transcriptionally repressible by sucrose. *SPF1* homologs have been identified and isolated from cucumber and *Arabidopsis* that were found to encode a WRKY domain transcription factor. W-box and G-box elements have been identified as essential motifs for these transcription factors (Kim et al. 1997). Likewise, glucose repression of rice α-amylase gene promoters has revealed multiple *cis*-elements important for sugar-related gene expression. In the promoter of a rice α-amylase gene *αAmy3*, major sugar response sequence (SRS) has been found to be located between 186 and 82 base pairs upstream of transcriptional site. Three essential motifs, i.e., the GC-box, G-box, and TATCCA element, within the SRS have been identified (Lu et al. 1998). A more complicated interaction has been shown in the regulation of photosynthetic genes, particularly the interactions between sugar and oxidative cues. In the absence of abiotic stress, sugars such as glucose or sucrose have been shown to repress photosynthesis-related genes (e.g., *psbA* or D1 protein accumulation) in plants and in cyanobacterial cells. In the cyanobacterium *Synechocystis*, glucose feeding has been found to derepress the steady-state mRNA levels of PSII genes and induces the destabilization of *psbA* transcripts. However, the enhancement of psbA gene expression (in dark) has been reported

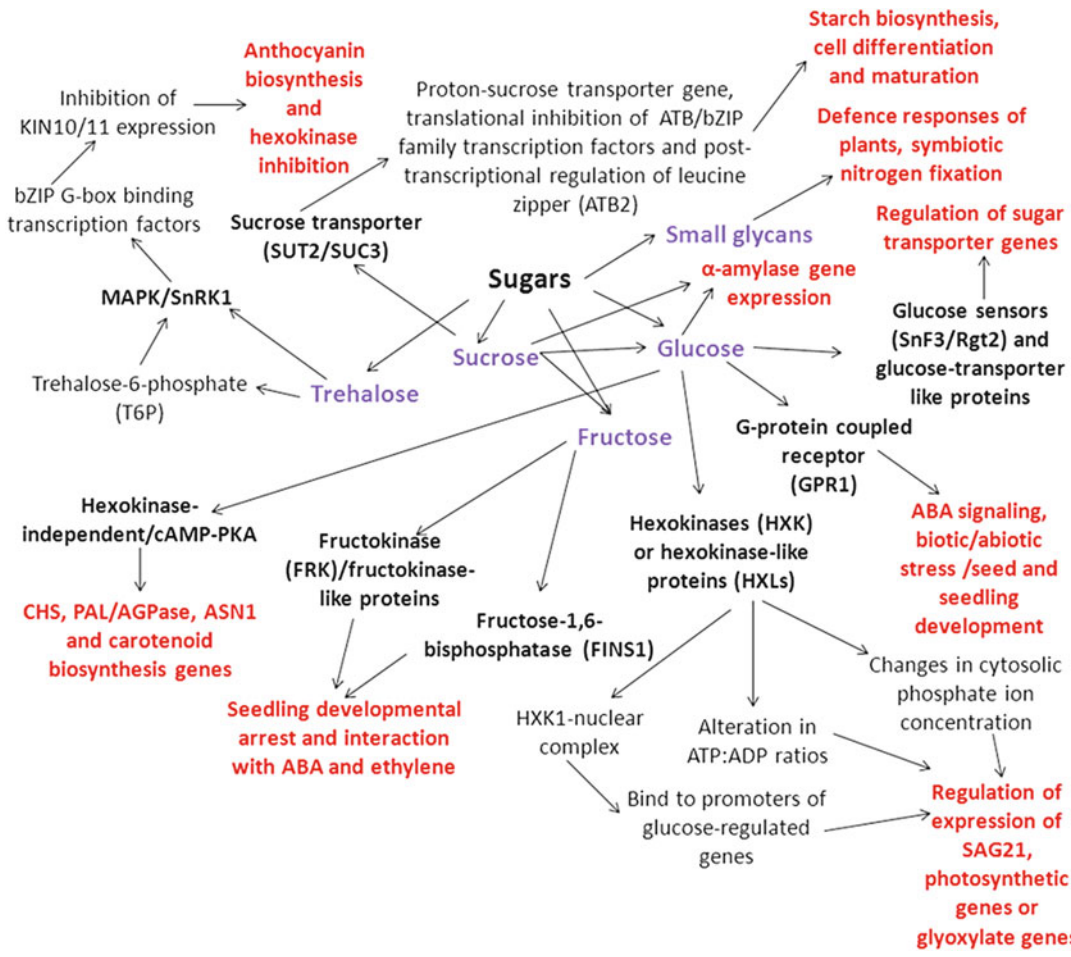

Fig. 5.2 Sugars: sensing and signaling capabilities

to occur in response to reactive oxygen species, hydrogen peroxide, or changes in the glutathione redox state (Couée et al. 2006). Another classical example of sugar-induced repression of photosynthesis-related genes is provided by the *Arabidopsis* seedlings where the increased accumulation of *psbA* mRNA and D1protein in the presence of atrazine has been reported (Sulmon et al. 2004). Atrazine treatment itself has negative effects on D1 protein levels; therefore, the derepression in the presence of sugar and atrazine might result from interactions between sugar and oxidative signaling cues. Thus, on the one hand, the effects of soluble sugars on gene expression are mediated through sugar-specific signaling pathways, and, on the other hand, these effects are linked to regulations by redox, ROS, light, stress, and photosynthesis electron transfer signals. These interactions have been found to be mediated through common target genes particularly photosynthesis genes (*psbA*), ROS defense genes (chalcone synthase, glutathione synthase, ascorbate synthesis gene, carotenoid synthesis gene), and stress defense gene (HSP). However, the interactions in their signal transduction pathways remain to be fully elucidated. Sugars have also been found to activate the genes encoding nitrate transporters, nitrate reductase, asparagine synthase (*ASN2*), and glutamine synthase (*GS*) which support the existence of relationship

between sugars and nitrogen metabolism (Sheen et al. 1999). However, a distinct asparagine synthase (*ASN1*) gene has been found to be repressed by sugars. Moreover, the glucose regulation of *ASN1* and *GS2* genes in transgenic *Arabidopsis* has been found to involve hexokinase-independent pathway. The importance of sugar and nitrogen balance in plant life has also been demonstrated in maize where high nitrate signals enhance the expression of photosynthesis genes for sugar production (Sakakibara et al. 1998; Sheen 1999). Similarly, in senescing *Arabidopsis* leaves, exogenously supplied sugars have been found to induce expression of the senescence-associated gene *SAG21* (in an HXK-dependent manner), while another well-characterized senescence marker, *SAG12*, has been found to be repressed by sugars (Noh and Amasino 1999; Xiao et al. 2000). It has been postulated that the regulation of different *SAGs* might be controlled differentially by other factors besides sugars, such as developmental state and hormones (He et al. 2001). Moreover, little is known about the actual transcriptional machinery underlying these responses and they have been suggested to involve diverse transcription factors (Sheen 1990, 1999).

5.3.1 Involvement of Protein Kinases

The involvement of protein kinases (PKs) and protein phosphatases (PPs) as important components in sugar signaling has been implied (Smeekens 1998). The discovery and development of specific protein kinase and phosphatase activators/inhibitors in the past decade have provided valuable tools to examine the involvement of protein phosphorylation/dephosphorylation in diverse signal transduction pathways (MacKintosh and MacKintosh 1994). It has been shown that PP1 and PP2A inhibitors mimic glucose repression of photosynthesis genes in maize leaf cells and in photoautotrophic cultures of *Chenopodium rubrum*, besides activating glucose/stress-inducible invertase and phenylalanine ammonia lyase genes (Ehness et al. 1997; Sheen 1999). Moreover, the transcriptional repression of large number of genes involved in metabolic processes (respiration, gluconeogenesis, or the alternative-carbon source metabolism and uptake) has been found to involve the "main glucose repression pathway" wherein the glucose sensor hexokinase (HXK2) has been reported to interact with Glc7-Reg1 protein phosphatse1 (PP1) complex to bring out dephosphorylation and inactivation of SnRK1 (Moreno et al. 2005). However, the differential effect of protein kinase inhibitor staurosporine on such signals suggests the involvement of different protein kinases in different transduction pathways. One such plant protein kinase is the SnF1-related protein kinase (SnRK1) with potential involvement in carbon metabolism and sugar signaling (Halford and Hardie 1998; Hardie et al. 1998). Four plant SnRKs from rye, tobacco (NPK5), and Arabidopsis (AtKIN10 and AtKIN11) have been identified and found to complement the glucose repression in yeast snf1 mutant (Sheen et al. 1999). The SnF1 protein kinase, an ortholog of mammalian AMP-activated protein kinase (AMPK), has been reported to be involved in derepression of gene expression under low glucose and starvation conditions probably through phosphorylation of Mig1 (a zinc-finger DNA-binding transcription factor). The phosphorylation of Mig1 results in the dissociation of Mig1 from the repressor complex and subsequent export to nucleus where it interacts with HXK2 to form a stable complex to recruit corepressor proteins (Moreno et al. 2005). In *Arabidopsis*, the activity of KIN10 and KIN11 has been shown to be of central importance in linking stress, sugar, and developmental signals to regulate metabolism, energy balance, growth, and survival under stress, which in turn are regulated by several factors, including cell wall-derived factors (Baena-Gonzalez et al. 2007; Li et al. 2007; Polge and Thomas 2007). Recently, a novel protein kinase, MsK4 (glycogen synthase kinase 3-like kinase), from *Medicago sativa* has been reported to be involved in stress signaling and carbon metabolism. It has been found to be a plastid-localized protein kinase, associated with starch granules, whose activity is induced by high-salt stress.

Moreover, plants overexpressing MsK4 have been found to accumulate more starch and carbohydrate content than those of wild-type plants, suggesting that MsK4 acts as an important regulator of carbohydrate metabolism to environmental stress (Kempa et al. 2007). The role of protein kinases in plant defense responses, induced by cell wall-derived oligogalacturonides, has also been documented (Ridley et al. 2001; Denoux et al. 2008). Also, some plant defense genes have been found to be upregulated in response to fungal invasion. Cell wall-derived oligogalacturonides, released from the plant cell walls, have been suggested to act as elicitors of the plant immune system and that the actual receptors for these signaling molecules probably involve wall-associated kinases (WAK1 and WAK2) that can transfer the signal across the plasma membrane (Brutus et al. 2010). Moreover, the link between WAKs and transcriptional/enzyme regulation has been found to be established by mitogen-activated protein kinases (MAPKs) like MPK3 and MPK6 (Kohorn et al. 2012).

5.3.2 Involvement of Calcium

The use of chemicals that inhibit calmodulin or Ca^{2+} ion channels has pointed out the involvement of Ca^{2+} ions in sugar signaling (Ohto et al. 1995). One such sugar-induced calcium-dependent protein kinase (associated with plasma membrane) has been identified in tobacco (Ohto and Nakamura 1995) which has been proposed to control the activity of sugar transporters located in the membrane. Calcium is also reported to be an essential component of the sucrose signaling pathway that leads to the induction of fructan synthesis (Martinez-Noel et al. 2006). Pharmacological studies with Ca^{2+} channel blockers (LaCl3), EGTA, and calmodulin inhibitors also provided additional evidence for the involvement of Ca^{2+} signaling particularly in the sugar induction of sporamin and α-amylase gene expression in sweet potato and of anthocyanin biosynthesis in cell suspension cultures of *Vitis vinifera* (Ohto and Nakamura 1995; Vitrac et al. 2000). In transgenic tobacco leaf discs expressing apoaequorin, sucrose has been found to induce increase in cytosolic levels of free Ca^{2+}. It has been suggested that increases in free cytosolic Ca^{2+} concentrations might be due to membrane depolarization caused by sugar–proton symport (Rolland et al. 2002). Further studies at cellular and molecular level are required to elucidate the precise role of Ca^{2+} in sugar signaling.

5.4 Sugar Signaling and Plant-Hormone Interactions

Recent genetic and molecular studies of sugar-signaling mutants in *Arabidopsis* have revealed multiple interactions between sugar and plant-hormone signaling which is evident from the fact that these mutants display phenotypes as are found in mutants deficient in hormone biosynthesis and signaling (ABA or ethylene), in addition to altered sugar responses; e.g., glucose-insensitive (*gin1*) mutant in *Arabidopsis* has been found to display phenotypes as displayed by constitutive triple response (*ctr1*) mutant. The ethylene receptor mutant (*etr1*) and ethylene-insensitive mutants (*ein2* and *ein3*) have been found to be hypersensitive to glucose, while constitutive triple response 1 (*ctr1*) mutant to be glucose insensitive. Also ethylene-insensitive mutant (*ein2-1*) of *Arabidopsis* has been reported to have increased anthocyanin accumulation in response to sucrose treatment, indicating a negative role of ethylene in the sucrose and fructose signaling pathways (Kwon et al. 2011). Moreover, the application of an ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) to wild-type plants, in the presence of excess exogenous glucose, has demonstrated that the glucose-dependent developmental arrest could be overcome by ethylene (Zhou et al. 1998) thereby paving ways for the growth-promoting role of ethylene in Arabidopsis. Interestingly, the transcription factor ethylene insensitive 3 (EIN3), a key regulator in ethylene signaling has also been shown to be differentially regulated by protein stability by glucose in a hexokinase (HXK1)-dependent manner (Yanagisawa et al. 2003) (Fig. 5.3).

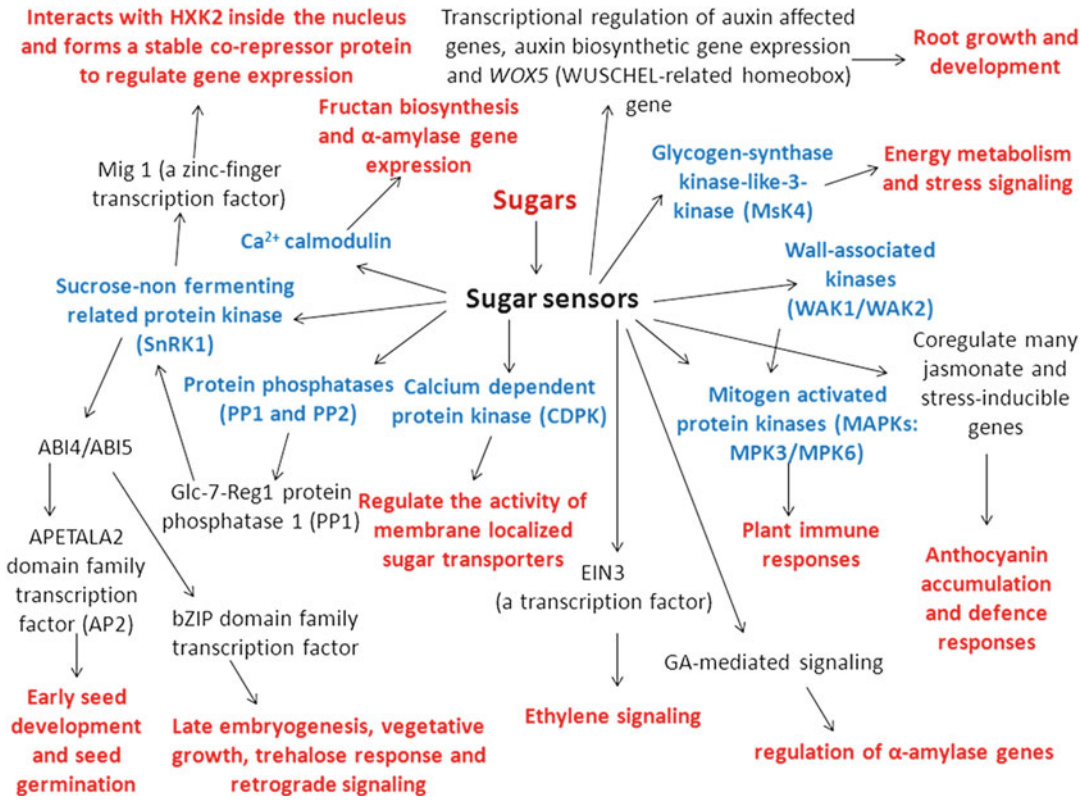

Fig. 5.3 Sugar signaling components and regulation of plant growth and development

Similar cross talk between sugar and abscisic acid (ABA) signaling has been demonstrated through the study of various glucose-insensitive mutants (*gin1* and *gin5*) in *Arabidopsis*. It has been found that the sugar-insensitive *gin1* and *gin5* mutants show reduced seed dormancy and wilty phenotypes as displayed by ABA-deficient (*aba*) mutants and that the ABA-deficient mutants (*aba1*, *aba2*, *aba3, abi4,* and *abi5*) also displayed a *gin* phenotype. Further studies on sugar-signaling mutants (*gin1*, *gin5*, *isi4,* and *sis4*) have also revealed that these mutants contain lower endogenous ABA levels than wild-type plants and that the addition of exogenous ABA (at physiological concentrations) reverts back the sugar sensitivity in these mutants (Leon and Sheen 2003). The characterization of the *gin6* mutant in *Arabidopsis* has resulted in the identification of *ABI4* as a candidate for the transduction of the glucose-specific signal (Arenas-Huertero et al. 2000). Although, overexpression of *ABI5* has also been found to confer hypersensitive response to sugars, the *gin* phenotypes displayed by *abi5* alleles have not been found to be as strong as that of the *abi4* alleles (Huijser et al. 2000). *ABI4* locus has been found to encode a transcription factor of the APETALA2 (AP2) domain family that plays a major role during seed development and germination together with two other loci, *ABI3* and *ABI5* (Finkelstein 1994; Finkelstein et al. 1998), while the *ABI5* locus encodes a transcription factor that belongs to a large basic leucine zipper (bZIP) domain family which plays its role during late embryogenesis, in postgermination developmental arrest, and in specific tissues during vegetative growth. It has also been observed that important *cis*-acting sequences required for the regulation of *ABI4* gene lie at least 2-kb upstream of the start codon and the predicted amino acid sequence of ABI4 contains

a serine/threonine-rich domain, which is the possible target for protein kinases such as those of SnRK family. More importantly, ABI4 protein has been shown to mediate trehalose responses, to act as an essential element in the retrograde signaling (from plastids to the nucleus), and to regulate its own sugar-dependent expression (Koussevitzky et al. 2007; Ramon et al. 2007; Bossi et al. 2009). Moreover, both *ABI4* and *ABI5* are activated by glucose in an ABA-dependent fashion (Cheng et al. 2002). Extensive cross talk between sugar and ABA signaling pathways has been described for various aspects of plant growth and metabolism. On the one hand, sugars and ABA tend to act synergistically during embryo growth and storage reserve accumulation which is evident from the co-induction of sucrose induction of starch biosynthetic genes by ABA, while on the other hand, ABA and glucose has been found to act antagonistically during seed germination or early seedling growth, where exogenous glucose enables Arabidopsis seeds to germinate on otherwise inhibitory ABA concentrations (Eveland and Jackson 2012). α-Amylase transcript has also been reported to be induced by ABA (Ohto et al. 1992). Cho and Yoo (2011) have also reported a positive interaction between ABA and fructose signaling through hormone biosynthesis. Another link between the ABA and sugar-signaling pathway is supported by the observation that expression of GSQ5/DOG1 requires the ABA-mediated sugar-signaling pathway, whose alleles have been found to promote sugar induction of *ABI4* (Teng et al. 2008). Recently, a splicing factor SR45 has been identified as a negative regulator of sugar-signaling pathway and reported to be involved in the repression of glucose-induced ABA accumulation and downregulation of genes for ABA biosynthesis and signaling (Carvalho et al. 2010). The detailed analyses of sugar-insensitive mutants have suggested that ethylene and ABA act antagonistically in bringing the glucose response. The cross-linking interaction between these two hormones with respect to glucose has been further clarified by the analysis of double mutants *gin1 etr1* and *gin1 ein2*, which display the glucose-insensitive phenotype of the *gin1/aba2* mutant that clearly depicted that ethylene sensing and signaling pathways are tightly interconnected with those for sugar and ABA (Gazzarrini and McCourt 2001; Leon and Sheen 2003). Similarly, *gin1* mutant seedlings in *Arabidopsis*, overexpressing the *AtHXK1*, have been found to display glucose insensitivity, suggesting that *AtHXK1* acts upstream of ABA synthesis (Zhou et al. 1998) and FINS1 (fructose-1,6-bisphosphatse)-dependent fructose signaling has been found to act downstream of the abscisic acid pathway and interact positively with ABA signaling (Cho and Yoo 2011). FINS1 has been found to act downstream of *GIN1*, involved in ABA synthesis. These findings suggest that both fructose and glucose interact with ABA signaling with FINS1 and HXK1 function downstream and upstream of the ABA pathway, respectively. Further studies by Cheng et al. (2002) and Leon and Sheen (2003) have demonstrated that *GIN1/ABA2* encodes a short-chain dehydrogenase/reductase in ABA synthesis and that *CTR1/GIN4* encodes a putative mitogen-activated protein kinase kinase kinase which functions as a negative regulator of ethylene signaling, thereby suggesting that fructose signaling interacts positively with ABA signaling via hormone biosynthesis and interacts antagonistically with ethylene signaling via MAPKKK.

Cytokinins are another class of plant hormones found to regulate various processes including plant immunity (Barna et al. 2008). As far as their role in sugar sensing and signaling is concerned, they have been found to induce cell wall invertase (CWI) and hexose transporter expression in *Chenopodium rubrum* (Ehneb and Roitsch 1997). Cytokinins are known to delay senescence in plants and it has been speculated that they cannot delay leaf senescence in the absence of CWI activity (Balibrea-Lara et al. 2004). Invertases have been found to play an important role in sugar signaling by regulating the sucrose levels, sink strength, and sucrose: hexose ratio. Here the role of different invertases, including vacuolar, cell wall, and neutral/alkaline invertases, has been recognized (Xiang et al. 2011). De Coninck et al. (2005) have reported the existence of two forms of vacuolar invertase in

Arabidopsis (AtVI1 and AtVI2), both of which have been found to produce a rare sugar "1-kestose" in significant amounts under high sucrose concentration. A strong correlation between sucrose and cytokinin has been found to exist in the induction of the anthocyanin biosynthesis genes (Shan et al. 2009). Moreover, the effect of nitrate in the activation of maize photosynthesis gene expression has been proposed to be mediated through the elevation of cytokinins (Sakakibara et al. 1998).

Auxin is an important plant hormone that is a general regulator of growth and is also implicated in pattern formation, lateral organ development, and cell expansion (Kieffer et al. 2010). Various aspects of plant growth and development have been reported to be linked by sugar and auxin signals. The analyses of mutants like *hxk1/gin2* in *Arabidopsis* have revealed that these mutants on one hand are resistant to exogenous auxin and on the other hand are insensitive to high glucose (Moore et al. 2003). In *Arabidopsis* roots, the expression of a WUSCHEL (WUS)-related homeobox gene (*WOX5*), reported to maintain localized auxin in the root apical meristem, has been found to be induced by auxin and a non-metabolizable sugar analog "turanose" (Gonzali et al. 2005). A substantial overlap of glucose and auxin response pathways has been reported by Mishra et al. (2009) in *Arabidopsis* seedlings in the control of root growth and development where about 62 % genes affected by auxin are transcriptionally regulated by glucose either antagonistically or synergistically. And more recently, in developing maize kernels, an auxin biosynthetic gene (*ZmYUCCA*) has been reported to be modulated by sugars thereby representing a link between sugar status and auxin signals (Le Clere et al. 2010). The conserved F-box and leucine-rich repeats between the glucose-regulated GRR1 in yeast and the auxin signaling component TIR1 in *Arabidopsis* also suggest another possible connection between glucose and auxin signaling (Ruegger et al. 1998). Interestingly, ethylene has also been suggested to play a role in root meristem maintenance through a mechanism that possibly involves auxin as has been evidenced by attenuation of ethylene effects in roots of certain auxin mutants (Ortega-Martinez et al. 2007) and ethylene-induced expression of auxin biosynthetic genes in the root meristem (Stepanova et al. 2008). However, it is not clearly determined whether sugar signals contribute to such signals or not, hence needs further elucidation.

Defense reactions of plants have also demonstrated an extensive cross talk between sugar and hormone signaling pathways (Leon and Sheen 2003). It has been suggested that plants react to pathogen invasion by production of some phytohormones which might function as signaling molecules for stimulation of plant innate immunity to activate defense responses (Pieterse et al. 2009). For that purpose, a fine-tuned cross talk among abscisic acid, jasmonate, salicylic acid, and PAMP-triggered signals has been shown to result in stomatal closure and then affects the defense responses together with other signaling pathways (Melotto et al. 2008; Ton et al. 2009; Cutler et al. 2010). In addition, many jasmonate and stress-inducible genes have been found to be coregulated by sugars (Reinbothe et al. 1994; Sadka et al. 1994). Jasmonic acid and a number of transcription factors have been recognized as potential regulators of the anthocyanin pathway in *Arabidopsis* (Gao et al. 2011; Qi et al. 2011), and it has also been shown that the cross talk among gibberellins, jasmonates, abscisic acid, and sucrose in a complex signaling network can modulate anthocyanin accumulation where sucrose signaling is regarded as a primary and essential component (Loreti et al. 2008). Similarly, the TATCCA element is also an important component of gibberellin response complex of the α-amylase gene in germinating cereal grains, suggesting the regulation of α-amylase gene expression by sugar and hormonal signal may share common regulatory mechanisms (Lu et al. 1998). In *Arabidopsis*, D-allose has also been reported to interfere with gibberellic acid (GA)-mediated signaling in a hexokinase-dependent way (Fukumoto et al. 2011). This underlines the central role of sugar-derived signals in plant growth, physiology, and development. However, many aspects of sugar-signaling pathways remain to be discovered and further studies will be required to reveal the genetic and molecular basis of sensing and signaling pathways connecting sugar and hormonal regulation in plants.

5.5 Conclusion

During the last decade, a significant progress has been made in elucidating the role of sugars or their analogs in diverse signal transduction pathways in plants and other organisms. It is the result of tireless efforts by the researchers that led to identification of sugars as signaling molecules, earlier thought to be only simple metabolites and energy sources. Sugar sensing has been implicated in a wide range of metabolic activities related to plant growth and development ranging from seed germination to seedling development and root/leaf differentiation or flower formation to senescence and in regulating responses to light, stress, and pathogens, through a complicated network of signaling cascades involving diverse signaling components. The research progress made in the past few years has also made it clear that different sugars (glucose, fructose, sucrose, mannose, etc.) act as distinct signals suggesting the involvement of multiple sugar sensors/receptors in mediating parallel signaling pathways. Different sugar sensors have been identified and found to coordinate various developmental processes involving at least three distinct pathways: hexokinase-dependent/metabolism-dependent, hexokinase-dependent/metabolism-independent, and hexokinase-independent pathways. These signal transduction pathways involve their respective sensors and the downstream components involving hexokinases, fructokinases, sucrose transporters, G proteins, protein kinases, protein phosphatases, cyclic nucleotides (cAMP), Ca^{2+}/calmodulin, and a range of transcription factors to regulate gene expression. Although a detailed study of hexokinase-dependent pathway has been made, the hexokinase-independent pathway has not been fully characterized, and here the combination of molecular, biochemical, and genetic approaches promises to unravel more detailed mechanisms underlying it. The role of trehalose in defense responses of plants has also been demonstrated but the exact signaling nature and the transduction pathway of trehalose is not clear as yet. The analyses of sugar-signaling mutants in *Arabidopsis* have also demonstrated an extensive and complicated cross talk between sugar and hormone signaling pathways particularly between glucose and abscisic acid signaling. Similar crosstalk between sugars and other hormones is also emerging but needs further elucidation at the molecular or biochemical level.

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