Chapter 22

Sugar Signaling Under Abiotic Stress in Plants

Giselle M.A. Martínez-Noël[1,2], Jorge A. Tognetti[3,4]

[1]*INBIOTEC and FIBA, Mar del Plata, Argentina;* [2]*Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina;*

[3]*Universidad Nacional de Mar del Plata (UNMdP), Mar del Plata, Argentina;* [4]*Comisión de Investigaciones Científicas (CIC), Provincia de Buenos Aires, Argentina*

1. INTRODUCTION

When plants encounter adverse (or potentially adverse) environments, primary metabolic processes, such as growth and/or photosynthesis, are, in general, rapidly affected, and the effect depends on the type and magnitude of stress (Arbona et al., 2017). For example, water deficit and low temperature directly inhibit growth, whereas low irradiance directly reduces the photosynthetic rate. The imbalance between carbon fixation and consumption leads to altered sugar levels in cells.

It is thus not surprising that plants have evolved mechanisms that enable them to get information from hazardous environments through the concentration of certain sugars. Not every sugar has been attributed a signaling role in plant stress, but there is compelling evidence that at least glucose (Glc), fructose (Fru), sucrose (Suc), and trehalose-6-P (T6P) may fulfill this role (Van den Ende and El-Esawe, 2014; Li and Sheen, 2016; Sami et al., 2016; Ceusters et al., 2017).

Sugar levels are perceived through sugar sensors that initiate a signaling cascade ultimately resulting in altered gene expression and protein modification. Upon these changes, plants may respond to a specific stressful condition and through this response may improve their chance of success. Many of the sugar-mediated responses do not occur in an independent manner, but rather are orchestrated with other endogenous or environmental stimuli. Two large signaling networks that essentially correspond to metabolically opposite situations have been identified. One of them corresponds to low carbon availability, this is, when C fixation is more affected than consumption or growth: the SnRK family-signaling network (Broeckx et al., 2016). The other corresponds to high C availability, when growth is more affected than photosynthesis: target of rapamycin (TOR) signaling network (Baena-González and Hanson, 2017).

Variation in sugar levels is associated not only with stressful environments, but also with normal functioning (i.e., day/night cycles). Accordingly, a large array of *Arabidopsis* genes (at least 10%) is sugar responsive (Cramer et al., 2011). Therefore, at first glance sugar signaling might appear as a rather unspecific way of responding to external stimuli. To solve this query, plants have evolved complex interplays with stress-related hormones, such as abscisic acid (ABA) and ethylene, as well as with direct environmental stimuli, such as light or mineral nutrients. Furthermore, not all abiotic stresses may be associated with C imbalance. Mechanical stress resulting in plant wounding may also elicit specific sugar-mediated plant responses to ameliorate plant status and to prevent pathogen infection.

In this chapter, we summarize the present status of knowledge about sugar roles in plant responses to abiotic stresses, indicating main research areas and gaps still existing in this knowledge. Furthermore, potential uses of the information gathered toward obtaining crops that may be more productive under unfavorable environmental conditions are briefly discussed.

2. VARIATION IN SUGAR LEVELS IN PLANTS UNDER ABIOTIC STRESS

It has been known for decades that sugar concentrations are severely altered in plants subjected to abiotic stress. Main examples of stresses under which sugars accumulate include water, salt, cold, and nutrient deficiency stresses. Accumulated sugars (which shortly after exposure to stressful condition often include especially Suc and also Glc and Fru) may serve as direct protective agents acting upon membranes or macromolecules (Sami et al., 2016 and references therein) besides initiating a signaling cascade.

In the case of water stress, a decline in turgor drastically impairs cell elongation, but photosynthesis may still proceed, since stomatal closure due to ABA signaling from roots (which limits CO_2 uptake), occurs usually later (Hsiao, 1973). This imbalance between sugar utilization and synthesis leads to sugar accumulation in different plant organs (Shinohara et al., 1995; Sami et al., 2016). Salt stress, which partially consists of a water stress, also commonly leads to an accumulation of sugars. In some cases, particularly high Suc concentrations can be found, as reported by Saito and Matsukura (2015) for tomato fruits from plants under salt stress.

A similar imbalance occurs in plants subjected to low temperature (Pollock, 1990). Again, growth may be much more affected by cold (mainly because of the kinetic effect on enzymes involved in cell cycle) than photosynthesis, and this phenomenon is especially remarkable in C_3 plants, such as grasses, which may accumulate sugars in very large amounts, in an inverse relationship with temperature (Lorenzo et al., 2015).

Mineral nutrient deficiency is another example of a stressful condition promoting sugar accumulation. Nitrogen deficiency impairs plant growth, whereas photosynthesis may still occur at a relatively high rate. For example, sugar accumulation was reported for barley leaves (Wang and Tillberg, 1996), barley seedlings (Comadira et al., 2015), and radish hypocotyls (Su et al., 2016) under N deficiency. Also phosphorus, potassium, and magnesium deficiencies were found to result in Suc accumulation in leaves, in parallel with a decrease of this sugar in phloem, which is indicative of growth impairment (Marschner et al., 1996). Sugars also accumulate under oxygen deprivation conditions. This has been explained as a consequence of either a decreased growth rate, or a reduction in respiratory rate that is greater than the reduction in C supply via phloem (de Sousa and Sodek, 2002).

On the other hand, environmental conditions that deplete Suc concentration are associated with those that directly limit photosynthesis (i.e., low irradiance or low concentration of carbon dioxide, although the latter may be observed only in enclosures such as greenhouses) or those that promote elongation growth under photosynthetic restriction, such as in the phenomenon called shade avoidance syndrome, which involves phytochromes, and occurs especially in the basal parts of dense canopies. Changes in sugar concentration due to variation in light intensity are generally less marked than those observed, for example, under contrasting temperatures. The reason may be attributed to the promotive effect of light on overall plant growth, which prevents sugars from accumulating. For example, Gent (1986) reported that in tomato plants grown at 370 μmol photons m^2/s, the total nonstructural carbohydrate concentration was just 41% greater than in plants at 110 μmol photons m^2/s. Besides, synthesis or mobilization of stored starch may buffer cell sugar concentration under changes in irradiance, such as those occurring in a day/night cycle.

In the case of phytochrome-mediated plant responses, a change in the relative amounts of different sugars can be usually found. For example, Lercari (1982) observed an increase in the proportion of monosaccharides (Glc and Fru) in both leaf blades and bulbs of onion, which depended on photoperiod. Similarly, Damayanthi Ranwala et al. (2002) reported an increase in the proportion of monosaccharides in the petioles of watermelon plants subjected to a far red treatment at the end of the day, which paralleled an increase in petiole length of these plants, compared with those treated with red light. From these results it is important to note that, although in most cases sugar accumulation in plants is associated with a photosynthetic surplus over C utilization, this is not always true, since in some cases (such as shade avoidance) the levels of specific sugars can increase even under photosynthetic C limitation, because of degradation of stored reserves, mainly starch.

3. SUGARS ACTING AS SIGNALS, AND THEIR SENSORS

Besides their evident role in metabolism, and in the protection of macromolecules, sugars may act as signaling molecules that regulate many important processes throughout the life of the plant (Ruan, 2014). The first described and best characterized sugar intracellular sensor is a hexokinase (HXK1), which is involved in Glc sensing (Jang and Sheen, 1994). It is important to notice that sugar signaling effects may differ among types of cells, tissues, and developmental stages (Tiessen and Padilla-Chacon, 2013).

3.1 Monosaccharides: Glucose and Fructose Sensing

Hexose sugars, Glc and Fru, have been recognized for long as signals that regulate gene expression to support plant growth and development in relation to internal and external cues. A direct Glc signaling pathway is mediated by HXK1, which may act independently of its enzymatic activity, forming a complex with two partners (VHA-B1 and RPT5B) (Cho et al., 2006). Thus a dual role should be assigned to hexokinases, one in Glc metabolism and the other in sugar signaling. Glucose sensing through HXK1 has been reported to affect photosynthesis, chlorophyll production, cotyledon expansion, and early seedling growth (Baena-Gonzalez and Sheen, 2008; Cho et al., 2010; Granot et al., 2013). HXK1 sensing under stress

generally involves interactions with hormones, as shown later. Besides, different Glc signaling pathways that are independent from HXK1 have also been described (Hausler et al., 2014 and references therein).

Fructose also induces a specific sugar signaling pathway. In this case, putative sensors are fructose 1,6 biphosphatase and fructokinase (FRK) (Cho and Yoo, 2011; Granot et al., 2013). Similarly, as with HXK1, the sensing role of FRK is independent from its enzymatic activity. The fact that HXK and FRK sensors have isozymes with enzymatic activity complicates the understanding of their involvement in sugar signaling (Tiessen and Padilla-Chacón, 2013).

3.2 Disaccharides: Sucrose and Trehalose Sensing

Sucrose is the main sugar transported in plants and sucrose-specific signaling was demonstrated with numerous evidences (Tognetti et al., 2013). For example, sucrose induces anthocyanin and fructan biosynthesis and these inductions have been broadly characterized. Regarding anthocyanin synthesis, high sucrose levels specifically activate the transcription factor MYB75 through the stabilization of DELLA proteins (Li et al., 2014). In the case of fructan metabolism, sucrose induces the transcription of fructan synthesis enzymes (FSS) in wheat and barley leaves (Martinez-Noël et al., 2001; Nagaraj et al., 2001). In addition to inducing FSS, sucrose has also been found to strongly inhibit 6-fructan exohydrolase, a main enzyme of fructan degradation, as shown by Lothier et al. (2014) in *Lolium perenne* and by Suárez-González et al. (2016) in *Agave tequilana*.

Another disaccharide that is essential for normal growth and development in plants, although it is often found in very low levels, is trehalose. This disaccharide is synthesized by a two-step pathway, T6P being the phosphorylated intermediate. T6P levels are directly related to sucrose levels and for that reason T6P was proposed as a signal of the C status. But it was not until recent years that T6P was recognized as a crucial signal in plants (Figueroa and Lunn, 2016; John et al., 2017). Yadav et al. (2014) have proposed a model in which T6P is a signal and also a negative feedback regulator of Suc levels, conforming Suc and T6P to a system similar to that of insulin and glucagon in animals. One of the best described effects of trehalose is the regulation of starch synthesis (Kolbe et al., 2005).

Regarding sucrose sensing, despite all the research carried out, a sucrose sensor has not yet been identified. However, H^+-sucrose cotransporters (SUT) have been proposed as specific sucrose sensors in sieve elements (Barker et al., 2000). Besides, sucrose synthases associated to membrane and calcium channels have been recognized as other putative sucrose sensors (Li and Sheen, 2016). Undoubtedly, more studies and new techniques are needed to clarify this issue.

3.3 Other Sugars

Substantial evidence indicates that, besides Glc, Suc, and trehalose/T6P, there are other sugar signals and sensors that may regulate plant metabolism and development (Li and Sheen, 2016 and references therein). One very important signaling role has been attributed to a specific type of oligosaccharides, the oligogalacturonides (OGs), which consist of α-1,4-linked galacturonosyl residues. OGs do not occur freely in the plant cells, but rather they are integral components of the cell wall, which may be released by hydrolytic enzymes under mechanical stress or wounding (Ferrari et al., 2013; Savatin et al., 2014). OGs induce plant responses that are similar to those elicited by pathogen infection. Because of their relevance regarding plant defense toward pathogens, they are mainly the subject of biotic stress studies, and will not be further discussed here.

4. SUGAR SIGNALING NETWORKS

After changes in sugar concentration are perceived by specific sensors, sugar signal transduction may directly result in altered gene expression, such as in many responses mediated by the HXK1 signaling pathway. However, sugar signaling may also involve networks that integrate changes in sugar concentration with other endogenous and environmental stimuli, to result in multiple developmental and/or metabolic plant responses. Two main signaling networks are known in plants, namely, the SnRK family and TOR kinases, which control metabolism and growth in a manner opposite to response to sugars (Li and Sheen, 2016). The precise manner in which sugar availability affects SnRK1 and TOR activity is, however, still largely unknown (Baena Gonzalez and Hanson, 2017).

4.1 Sucrose Nonfermenting Related Kinases

In plants, SnRKs are evolutionarily conserved proteins; sucrose nonfermenting 1 (SNF1) and AMP-activated protein kinase (AMPK) are their analogues in yeast and mammals, respectively. SnRKs are energy sensors that are activated under unfavorable conditions and regulate gene expression to cope with stress. These kinases activate catabolism and inhibit anabolism

to maintain energy homeostasis in response to energy deprivation (Rodrigues et al., 2013; Nukarinen et al., 2016). Through the analysis of in vivo phosphoproteome, proteome, and metabolome it was found that activation of SnRK1 is crucial for the repression of processes that demand high energy, such as protein synthesis (Nukarinen et al., 2016). Important enzymes of plant metabolism, such as sucrose phosphate synthase and nitrate reductase, and transcription factors are substrates of SnRK1 (Nietzsche et al., 2016). It has also been reported that sugars, such as Glc, G1P, G6P, and Suc, inhibit SnRK activity. Some studies, however, showed that Suc may, in some cases, activate SnRK1, and this discrepancy could be due to the complex regulation of SnRK1 depending on the tissue and the sucrose concentration (Crozet et al., 2014).

SnRK1 is directly involved in response to flooding. Cho et al. (2012) reported that in *Arabidopsis* and rice under hypoxic conditions, SnRK1 activity induced stress-responsive expression of genes coding for alcohol dehydrogenase and pyruvate decarboxylase, which are associated with tolerance to this type of stress. Furthermore, Rodrigues et al. (2013) found that two PP2C protein phosphatases, which are well-established repressors of the ABA hormonal pathway, interact with the SnRK1 catalytic subunit causing its dephosphorylation and inactivation, whereas conversely, PP2C inhibition by ABA resulted in the activation of SnRK1. This result, together with a large overlapping of transcriptional responses induced by SnRK1 and ABA, led the authors to conclude that these pathways are complementary and cooperate to result in a stronger response to stress (Rodrigues et al., 2013). Besides its role in plant stress responses, SnRK1 is involved in cell function and developmental processes (Crozet et al., 2014).

The SnRK family also includes SnRK2 and SnRK3, whose roles in plants under stress are being actively investigated. SnRK2 kinases (especially those belonging to group 3) are considered an important regulator of ABA signaling, promoting plant responses to water deficit (Kulik et al., 2011). These authors pointed out that SnRK2 takes part in phosphorylation of both anion and cation channels, which is necessary for the ABA-dependent stomatal closure in response to water deficit. Furthermore, McLoughlin et al. (2012) reported that two SnRK2 kinases are rapidly and transiently activated in roots exposed to salt stress (150 mM NaCl), and that under these conditions, knockout mutants had either a reduced primary root length (SnRK2.4) or a lower number of lateral roots (SnRK2.10). Regarding SnRK3, it has also been involved in plant responses to salt stress, as reviewed by Chandna et al. (2013).

4.2 Target of Rapamycin

TOR is a protein kinase highly conserved among eukaryotes that is considered as a central regulator of growth in relation to nutritional status (Verma and Chatterjee, 2009; Xiong and Sheen, 2013; Dobrenel et al., 2016). TOR, which forms two complexes (TORC1 and TORC2, but only the first was found in plants) with other proteins (Wullschleger et al., 2006; Cornu et al., 2013), is known to promote a huge number of biological processes, including mRNA translation and anabolic metabolism, while repressing nutrient remobilization and storage (Wullschleger et al., 2006). Most evidence comes from studies on mammals and yeasts, but work from recent years shows that it also plays a pivotal role in plant signaling in relation to energy availability (Xiong and Sheen, 2014). In plants, TOR inhibition results in slower growth of roots, leaves, and shoots, and in a delayed development, ultimately leading to low nutrient uptake and light energy utilization (Ren et al., 2012).

TOR also seems to be involved in plant sensitivity to salt and osmotic stresses (Mahfouz et al., 2006; Deprost et al., 2007; Robaglia et al., 2012). It has also been observed that inhibiting the TORC1 activity results in starch accumulation together with a decrease in biomass production (Dobrenel et al., 2013; Caldana et al., 2013). The accumulation of starch observed in TORC1-deficient *Arabidopsis* plants was found to be accompanied by a decrease in raffinose production. Since both starch and raffinose syntheses depend on the supply of G6P, it appears that TOR controls metabolic partitioning between these carbohydrates (Dobrenel et al., 2013). Moreover, raffinose usually accumulates in response to stress, but stressed *Arabidopsis* plants affected in the activity of the TORC1 complex failed to accumulate raffinose (Ren et al., 2012; Dobrenel et al., 2013).

Most evidence on sugar control of TOR activity in plants involves Glc signaling. Direct evidence for a Glc signaling role of TOR has been gathered by Sheen and coworkers on plant developmental control (Xiong et al., 2013; Xiong and Sheen, 2013). These authors showed that TOR transduces Glc signals by phosphorylating the N terminus of E2Fa, a transcription factor that controls transcription of S-phase genes to activate the root meristem, and thus promotes the proliferation of stem progenitor cells. Another plant developmental feature controlled by Glc-TOR signaling is root hair production (Xiong and Sheen, 2012). Because this Glc regulation was found to be unaffected in a hexokinase 1 Glc sensor mutant, the authors concluded that Glc-TOR signaling controls root hair production through a hexokinase 1–independent pathway.

Glucose-TOR signaling also controls many aspects of plant metabolism. A transcriptome analysis of *Arabidopsis* revealed that Glc-activated TOR signaling modulates genes encoding root growth factor peptides and glutathione synthesis, among other genes (Xiong et al., 2013; Xiong and Sheen, 2013). Since glutathione (GSH; γ-Glu-Cys-Gly) is well known as an essential small molecule maintaining cellular redox status via hydrogen peroxide detoxification, a link between TOR and reactive oxygen species (ROS) signaling has been envisaged (Yokawa and Baluska, 2016).

There is evidence indicating that Suc signaling may also control TOR activity. Zhang et al. (2016) showed that Suc signaling controls the accumulation of the brassinosteroid (BR) signaling transcription factor BZR1, which is essential for growth promotion in relation to hormonal and environmental signals. The authors showed that starvation due to darkness induces BZR1 protein degradation, but Suc together with TOR promotes the stabilization of BZR1 in the dark.

On the other hand, no direct evidence of a link between trehalose or T6P and TOR signaling has yet been described in plants (Figueroa and Lunn, 2016).

4.3 SnRK—Target of Rapamycin Interplay

Master switches SnRK and TOR appear not to operate independently, but rather in an interactive manner (Nietzsche et al., 2016). Through analysis of the in vivo phosphoproteome, proteome, and metabolome of *Arabidopsis* mutants with inhibited SnRK1 activity and subjecting to stress due to prolonged darkness, Nukarinen et al. (2016) found not only that the activation of SnRK1 is only essential for the repression of high-energy-demanding cell processes, such as protein synthesis, but also that these mutants had a constitutively high phosphorylation of ribosomal protein S6 (RPS6), which is in turn a major target of TOR signaling, and its phosphorylation correlates with translation. Further evidence for an antagonistic SnRK1 and TOR cross talk, comparable with that existing in animals, was demonstrated by the in vivo interaction of SnRK1α1 and RAPTOR1B (a member of the TOR complex) in the cytosol, and by phosphorylation of RAPTOR1B by SnRK1α1 in kinase assays (Nukarinen et al., 2016). To further complicate the relationship between SnRK and TOR signaling, it has been observed that, contrary to other processes, plant senescence is affected by TOR and SnRK1 in a similar manner, i.e., inactivating both SnRK and TOR kinase activities induce early senescence (Baena-Gonzalez and Hanson, 2017), although the precise mechanisms that explain this result are unknown. Clearly, much research is still needed to unveil the complexities of SnRK-TOR interplay.

5. INTERACTIONS BETWEEN SUGAR SIGNALS AND HORMONES OR OTHER STIMULI IN PLANTS UNDER STRESS

5.1 Abscisic Acid

ABA is the hormone that is most widely implicated in plant stress signaling. Abundant evidence has been gathered indicating an interaction between ABA and sugars regarding several plant responses to stress (Van den Ende and El-Esawe, 2014). The expression of genes involved in both ABA synthesis and signaling is positively modulated by Glc (Cheng et al., 2002; Arroyo et al., 2003). This is consistent with the fact that plant stresses that drastically impair growth and induce sugar accumulation, such as drought and cold, also result in an increased ABA concentration. Sucrose–ABA interactions are, however, very complex, and this is highlighted by the fact that diverse signal transduction pathways are involved, including HXK1 (Cho et al., 2010), SnRK1 (Rodrigues et al., 2013), SnRK2 (Kulik et al., 2011), and TOR (Dong et al., 2015).

Several studies on the interplay between sugars and ABA have been performed with grapevine plants. In this species, sugar and ABA signaling pathways appear to interact to control sugar transport into fruits. Stress-induced protein kinases that promote the expression of hexose transporters have been shown to be upregulated synergistically by ABA and sugars (Cramer et al., 2011). Also in grapevine, it has been shown that both trehalose and T6P induce stomatal closure, but this response ceases to occur under ABA-induced stomatal closure (Gamm et al., 2015). These authors reported that trehalose applied at low concentrations to grapevine epidermal peels induced a significant closure of stomata in a dose-dependent manner. However, the addition of trehalose to ABA-treated epidermis resulted in a significant reduction of the ABA-induced stomatal closure. In addition, T6P induced a more pronounced stomatal closure than trehalose, but it had a lesser effect on ABA-induced stomatal closure. To add complexity to the trehalose–ABA interplay, it has been found that the expression of several trehalose biosynthetic genes, which are particularly highly expressed in *Arabidopsis* guard cells, is upregulated by ABA (Figueroa and Lunn, 2016).

5.2 Ethylene

There are many reports of interactions between ethylene and sugar signals. Ethylene represses the expression of apoplastic invertase, an enzyme associated with C utilization in growth (Linden et al., 1996). Besides, ethylene inhibits anthocyanin accumulation induced by Suc (Jeong et al., 2010). These authors reported that the transcript level of sugar transporter gene SUC1 was enhanced in *Arabidopsis* ecotype Columbia treated with an ethylene-binding inhibitor as well as in ethylene-insensitive mutants. They proposed that SUC1 represents an integrator for signals provided by sugar, light, and ethylene, and that the suppression of SUC1 expression by ethylene inhibits Suc-induced anthocyanin accumulation.

There are also reports about interactions between ethylene, sugars, and ABA signaling pathways (Ramon et al., 2008). It has been known for many years now that ethylene may antagonize Glc–ABA signaling (Gazzarrini and McCourt, 2001). Glucose-mediated plant responses, such as the inhibition of cotyledon growth under high Glc concentration, may be prevented by exogenous application of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) (Ramon et al., 2008). The ethylene–ABA antagonism, however, may solely be observed under relatively high Glc concentrations (Cho et al., 2010). To further complicate this picture, ABA may even promote ethylene biosynthesis in ripening fruits (Zhang et al., 2009).

5.3 Auxin

Sugars directly promote auxin biosynthesis, and a tight relationship between sugar and auxin daily fluctuations has been reported (Sairanen et al., 2012). Genes that encode key auxin biosynthetic enzymes (i.e., YUCCA 8 and YUCCA9) are promoted by Glc or Suc, but differential effects between root and shoot have been reported (Ljung et al., 2015). It has been proposed that the growth-promoting effect of Suc on hypocotyl elongation may occur through the effect of the sugar on auxin, since it could be partially mimicked by directly adding auxin or blocked by adding polar auxin inhibitors (Lilley et al., 2012). Ljung et al. (2015) pointed out that this mechanism is reminiscent of the shade avoidance syndrome, in which shade detected primarily in cotyledons results in increased auxin biosynthesis. However, these relationships are unlikely to be extended to any growth-promoting effect of Suc, since in some cases both signaling molecules (Suc and auxin) may be antagonistic, such as in the case of lateral bud release (Assuero and Tognetti, 2010).

The sugar-mediated activation of auxin biosynthesis and promotion of cell expansion involve HXK1 (Li and Sheen, 2016). Nevertheless, SnRK1 and TOR signaling networks are also modulated by auxin, and TOR, in turn, regulates the expression of auxin signaling components (Baena Gonzalez and Hanson, 2017).

5.4 Cytokinin

This hormone promotes photosynthesis through an increased leaf chlorophyll content and nitrogen partitioning to leaves, and accordingly, its levels correlate with sugar availability in the plant. In transgenic rice, overexpressing a gene (IPT) that encodes a key cytokinin biosynthetic enzyme led to a higher Suc content together with an increased drought stress tolerance (Reguera et al., 2013). Sucrose in turn is known to promote lateral root development; this effect is modulated by light (Kircher and Schopfer, 2012), and root apices are the main source of cytokinins in the plant. The parallelism between sugar- and cytokinin-mediated responses was further investigated by Kushwah and Laxmi (2014) who analyzed gene expression of *Arabidopsis* under Glc and BAP (a cytokinin) exogenous supply, and found that of 941 BAP-regulated genes, 713 genes were affected by Glc treatment alone, and from these, 89% were agonistically regulated by either BAP or Glc. Interestingly, however, the rest of the genes (11%) that were antagonistically regulated by BAP or Glc were predominantly involved in stress responses. These authors also investigated the involvement of the HXK1-dependent and HXK1-independent pathways in Glc signaling in controlling hypocotyl growth, and concluded that at least regarding this response, cytokinin interacts with Glc via the HXK1-dependent pathway (Kushwah and Laxmi, 2014).

5.5 Gibberellins

Contrary to cytokinins, gibberellins are associated with low Suc concentration in plants, and this hormone is associated with remobilization of plant reserves. It has been shown that gibberellic acid inhibits the Suc-mediated induction of anthocyanin synthesis through repression of several genes of this biosynthetic pathway (such as CHS, encoding chalcone synthase) that are induced by Suc (Solfanelli et al., 2006; Loreti et al., 2008). It has been proposed that DELLA proteins, which act as important negative regulators in GA signaling, are also positive regulators in the Suc signaling pathway controlling anthocyanin biosynthesis (Li et al., 2014). These authors also reported an interaction between gibberellin signaling and Suc regarding the inhibiting effect of this sugar upon hypocotyl growth inhibition in the dark. Furthermore, other hormones, namely, jasmonates and BRs, may interact with Suc–gibberellin signaling (Ljung et al., 2015).

5.6 Brassinosteroids

Dark grown *Arabidopsis* hypocotyl elongation is promoted by sugars, likely by Glc, and this promotion is dependent on BRs. It has been shown that sugars positively regulate the transcription of *BZR1*, the gene that encodes a BR-activated

transcription factor (BRZ1), and also stabilizes the BZR1 protein (Zhang and He, 2015). These authors proposed that the function of HXK1 is dependent on the presence of BR, which may act downstream of HXK1 to positively regulate Glc-induced hypocotyl elongation in *Arabidopsis* in darkness. More recent evidence, however, points to a pivotal role of TOR in this response, whereas HXK1 has been suggested to play a minor role, since when TOR was inactivated, the hypocotyl elongation response to sugar and darkness was greatly diminished (by 61%) compared with TOR-uninhibited controls (Zhang et al., 2016). Glucose and BR have also been reported to interact on lateral root formation in *Arabidopsis* seedlings (Gupta et al., 2015; Singh et al., 2017).

5.7 Reactive Oxygen Species

ROS are harmful radicals that are generated especially under stress conditions, and they also have a systemic signaling role through the so-called ROS waves (Baxter et al., 2014). The possibility of an interaction between sugar and ROS signaling under stress has been put forward during recent years by Van den Ende et al., since several soluble sugars, including fructans, have ROS-scavenging properties (Van den Ende and El-Esawe, 2014). This novel perspective opens interesting possibilities to be investigated.

5.8 Environmental Stimuli

Several environmental factors have been shown to interact with sugar signaling, but the most deeply studied interaction is that involving light environment. As mentioned earlier, light and Suc interact on root development, and this interaction varies along plant ontogeny (Kircher and Schopfer, 2012). An important role in the sugar–light interplay is played by PIF (phytochrome-interacting factor). PIF is a family of transcription factors that were originally identified through their direct interaction with phytochromes but that are now known to integrate light and temperature cues to regulate photosynthetic genes through an antagonistic regulatory circuit with HY5 (LONG HYPOCOTYL 5) (Ljung et al., 2015). Glucose induction of auxin biosynthesis is enhanced in PIF mutants and repressed in plants overexpressing PIF. In contrast, the higher levels of auxin promoted by Suc supplementation are lost in PIF mutants, even when the auxin biosynthetic enzyme gene *YUCCA8* expression may be enhanced (Ljung et al., 2015).

Although knowledge about interactions between sugar and light signaling pathways is rapidly growing, a large effort is still needed to unveil interactions between sugars and most other environmental factors, such as mineral nutrient availability (Moore et al., 2003) or temperature (Tarkowski and Van den Ende, 2015), about which evidence is still scarce, and scattered.

6. CONCLUDING REMARKS AND FUTURE PROSPECTS

A large progress has been made since the first evidence of sugars playing a signaling role in plants was obtained. Many links between cell C status and molecular responses in plants under abiotic stresses have been established, including sugar roles in hormone synthesis, transport, and signaling. The manipulation of sugar signaling pathways is known to result in alterations in plant tolerance to abiotic stresses. However, a large effort is still needed to elucidate many steps of sugar signaling pathways, including targets for enzymes and transcription factors, which may help understanding how changes in sugar concentrations may affect plant responses at the cellular or whole-plant levels (Sami et al., 2016; Baena Gonzalez and Hanson, 2017).

There is an increasing interest in sugar signaling networks, which is accompanied by the development of new technologies, which in turn provide deeper insights of the mechanisms involved. Because of the multiplicative nature of signaling molecules on plant responses, it appears feasible to manipulate signaling pathways so that great effects on crop yield and resistance under stressful environments are obtained by modifying the concentration of some key molecules. An example of this is given by the chemical intervention strategy that directly modulates T6P levels *in planta*, recently reported by Griffiths et al. (2016). In their work, plant-permeable analogues of T6P were designed, which were exogenously supplied to wheat, which released T6P *in planta* upon sunlight illumination. This treatment led to improved recovery from drought, and to increased yield. This strategy, together with more conventional genetic modification, is an example of the many possibilities that knowledge of sugar signaling pathways offers for crop improvement toward increased production under unfavorable environmental conditions.

In sum, an in-depth knowledge of sugar-mediated plant signaling pathways is essential to identify major targets to be addressed for improving plant tolerance to stresses, such as drought, salt, and cold, that currently limit crop productivity and stability worldwide, in the context of a search for a more sustainable agriculture.

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