Review

Soluble sugars—Metabolism, sensing and abiotic stress

A complex network in the life of plants

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Plants are autotrophic and photosynthetic organisms that both produce and consume sugars. Soluble sugars are highly sensitive to environmental stresses, which act on the supply of carbohydrates from source organs to sink ones. Sucrose and hexoses both play dual functions in gene regulation as exemplified by the upregulation of growth-related genes and downregulation of stress-related genes. Although coordinately regulated by sugars, these growth- and stress-related genes are upregulated or downregulated through HXK-dependent and/or HXK-independent pathways. Sucrose-non-fermenting-1- (SNF1-) related protein pathway, analogue to the protein kinase (SNF-) yeast-signalling pathway, seems also involved in sugar sensing and transduction in plants. However, even if plants share with yeast some elements involved in sugar sensing, several aspects of sugar perception are likely to be peculiar to higher plants. In this paper, we have reviewed recent evidences how plants sense and respond to environmental factors through sugar-sensing mechanisms. However, we think that forward and reverse genetic analysis in combination with expression profiling must be continued to uncover many signalling components, and a full biochemical characterization of the signalling complexes will be required to determine specificity and cross-talk in abiotic stress signalling pathways.

Introduction

Environmental factors affect the distribution of plants and exercise a selective effect toward those that have a better adaptation.[1,2] Maximum selectivity corresponds to reproduction capacity; that is to say, plants that are unable to reproduce will not be able to prosper into a community. Among environmental factors that have evolved with plants, drought, salinity and extreme temperatures are the most important; however, others such as ultraviolet-B radiation (UVBR), heavy metals, flooding and atmospheric pollutants acquired a relevant interest in last years.[3-6] To survive in the nature, plants developed a broad range of adaptive strategies to avoid environmental stresses. Responses to a specific stress can vary with the genotype, but some general reactions occur in all genotypes. Abiotic stresses affect different cellular processes such as growth, photosynthesis, carbon partitioning, carbohydrate and lipid metabolism, osmotic homeostasis, protein synthesis and gene expression.[7-9] However, plant metabolism can be affected of both general and specific manner. For example, drought limits plant growth due to photosynthesis decrease, constraint of metabolic processes and interference with nutrient availability.[10,11] Salinity interferes with plant growth as result of both physiological drought and ion toxicity.[12,13] Chilling (temperatures below optimal but above freezing) and freezing temperatures affect metabolic activities and can cause osmotic stress.[14-16] UVBR produces DNA damage, photosynthesis decrease and secondary metabolites (phenolic compounds) synthesis.[17,18] Heavy metals induce oxidative damage and alteration in mitochondrial respiration.[19,20] However, oxidative stress and reactive oxygen species (ROS) production appear as the more common consequences of exposure to abiotic stresses.[21,22]

Although, stress conditions individually have been subjected to intense researches.[2,4,10] In the field, however, plants are routinely subjected to a combination of different abiotic stresses,[6,23] so responses of plants to combined stresses are unique and the responses to each stress cannot be applied individually. In addition, stresses can be synergistically or antagonistically modified.[24] Therefore, responses of plants to stresses are very complex phenomena, for example, drought responses can occur at leaf level, while the stimuli can be perceived in the leaf itself or in another

part of plant such as roots.[12] Plant strategies to cope with stresses normally involve a mixture of stress avoidance and tolerance mechanisms. For example, during drought avoidance plants develop a deep-rooted system, while drought-tolerance involves metabolic adjustments, mediated by alteration in gene expression, to help improve the plant functionality. However, not all plants exhibit the same responses to different stress combinations and there are significant variations between genotypes.[25] Although, tolerance to combinations of different abiotic stresses e.g., drought and salinity is a well-known breeding target in some crops,[26] the molecular and metabolic mechanisms underlying the responses of plants to combinations of different stresses are scarcely known.

Perception of environmental stress signal relays a specific signalling cascade and evolves adaptive responses; therefore, differences in stress tolerance between genotypes or different developmental stages of a single genotype may arise from differences in signal perception and transduction mechanisms.[27-29] In plant stress responses the regulation of gene expression also involves both universal and unique changes at transcription level for certain genes,[30,31] so it is logical to expect that plants with multiple stress perception and signalling pathways, can have crossing at various steps in signal transduction pathways. Thus, different signalling pathways might share one or more components or have some common outputs (cross-talk).[32] When different abiotic stresses affect plant functionality, alterations in photosynthesis and carbon partitioning are common features that take place at organ level as well as in whole plant.[33-35] Soluble sugars do not only function as metabolic resources and structural constituents of cells, they also act as signals regulating various processes associated with plant growth and development.[36-38] Sugar signalling pathways interact with stress pathways into a complex network to modulate metabolic plant responses.[31,39] Soluble sugars may either act directly as negative signals or as modulators of plant sensitivity and thus, they can also play important roles in cell responses to stress-induced remote signals. In the context of this review, we analyse diverse sugar responses to abiotic stresses and summarize biochemical and genetic evidences for different sugar-sensing mechanisms.

Soluble Sugar Metabolism under Stress

Plants are autotrophic and photosynthetic organisms that both produce and consume sugar; however, they can act as carbon heterotrophs during some part of their life cycle or in some of their non-green organs like roots, stems and flowers that are not involved in photosynthesis.[40] Furthermore, sugar depletion normally occurs during ontogeny of plants. For instance, variations in environmental factors, such as light, water or temperature and attacks by pathogens or herbivores may lead to a significant decrease in the efficiency of photosynthesis in source tissues and thus, reduce the supply of soluble sugars to sink tissues. Under conditions of sugar deprivation, substantial physiological and biochemical changes occur to sustain respiration and other metabolic processes.[41,42] In the life cycle of plants, seed germination and early seedling growth are depending upon storage substances mainly carbohydrates, which are mobilized in the form of soluble sugars (sucrose, glucose and fructose) from storage seed tissues to various organs like stem and radicle, where they are required for growth and maintenance of the osmotic homeostasis of cells.[43,44] Thus, germinated seeds and growing seedlings appear as the most vulnerable stages to soluble sugar fluctuations, and constitute an excellent material to study the effect of different environmental stresses.

There are, however, few studies on sugar status in germinated seeds and seedlings growing under stress conditions, therefore, changes in sugar content during early development stages of seedlings are poorly understood and thus, the information on physiological events involved in seedling growth under abiotic stresses is scarce. For fifteen years, our laboratory is working on the effect of abiotic stresses on growth and carbohydrate metabolism of germinated seeds and growing seedlings of different glycophytic and halophytic species.[9,15,17,18,43,45-49] Our data and others available in the literature, demonstrated that sugar concentrations and source-sink partitioning are not affected according to unique pattern in different organs as well as under different stresses.[9,33,43,49] Drought, salinity, low temperature and flooding, in general, increased soluble sugar concentrations, whereas high light irradiance (PAR, UVBR), heavy metals, nutrient shortage and ozone decreased sugar concentrations.[50-52] Nevertheless, sugar changes do not follow a static model and vary with the genotype and the stress factor.[53,54] In addition, have also been reported that not all soluble sugars play similar roles in events associated to metabolism of stressed plant.[52,55] Sucrose and glucose either act as substrates for cellular respiration or as osmolytes to maintain cell homeostasis,[28] while fructose is not related to osmoprotection and seems related to secondary metabolites synthesis, like it was demonstrated in our laboratory. Hilal et al.[17] demonstrated that fructose might be related to synthesis of erythrose-4-P, which acts as substrate into lignin and phenolic compounds synthesis. Hence, this picture shows that under stress conditions the metabolism of soluble sugars is a dynamic process simultaneously involving degrading and synthetic reactions. Soluble sugar fluctuations under abiotic stresses also involve changes in CO_2 assimilation, in source-sink carbon partitioning and in activity of related enzymes as well as in the expression of specific genes.[28,45,49,56,57] According to stress factors these changes either can be related with disruption of chloroplast structure and blocking of chloroplast electronic transport as in high UVBR irradiance, ozone and heavy metals stresses;[5,6,17,37] with posttranslational activation and increased expression of sucrose synthesis enzymes, and inhibition of enzymes of the Calvin cycle as in low temperature and salinity stresses;[28,57-59] with inhibition and delayed activity of enzymes involved in sucrose-starch partitioning as in drought, salinity and low temperature stresses;[49] with activation of antioxidant enzymes and lipid oxidation as in heavy metals and ozone stresses;[21,22] or with oxidase alternative expression as in salinity, drought and heavy metals stresses,[60-62] among others.

As much as 80% of the CO_2 assimilated during photosynthesis is channelled into synthesis of sucrose.[59] It is the major transport form of organic carbon exported from the photosynthetic source to sink organs, and thus this process is crucial for survival and productivity of plants.[23,59,63] Therefore, changes in its functionality induced by environmental stresses are very important and

afflict the farmers worldwide, because they cause extensive losses to agricultural production.[4,10,26] The effects of abiotic stresses on CO_2 assimilation and source-sink transitions have been extensively studied and a lot of papers have been published.[23,28,37,40,52,56,58,63] Descriptive ecological and agronomic studies have uncovered a strong correlation between soluble sugar concentrations and stress tolerance. However, because energy and resources are required for plants to cope with abiotic stress conditions, the source-sink partitioning between different organs is a key component within mechanisms of stress tolerance.[40,64] Recent studies for increasing tolerance to environmental stresses, through metabolic engineering of compatible solutes, have shown that increases in soluble sugars and/or other osmolytes provide optimism to increase plant tolerance to abiotic stresses such as drought, salinity and cold.[65] However, in some cases engineering increased levels of compatible solutes have unpredicted negative effects on growth and development of plants.[66] It is also interesting to notice that increasing the level of compatible solutes through genetic engineering does not provide a straightforward solution, probably as a reflection of highly integrated nature of sugar metabolic pathways. Therefore, we believe that source-sink relationships at the whole-plant level must be considered in attempts to enhance stresses tolerance through conventional breeding programmes, interspecific hybridization, in vitro selection, and/or transgenic manipulation.

Sugar Sensing and Gene Regulation

Soluble sugars principally function as metabolic resources and structural constituents of cells, so it is reasonable to ask which and how soluble sugars can be sensed to transduce specific signalling pathways. Does sensing of soluble sugars depend upon their metabolism? It is not easy to answer these questions since soluble sugars are rapidly interconverted: sucrose is broken down into glucose and fructose, while these hexoses lead to sucrose synthesis.[56] Moreover, these interconversions are strongly affected by environmental stresses.[9,48,49] Soluble sugars, like hormones, can act as primary messengers and regulate signals that control the expression of different genes involved in plant growth and metabolism.[67,68] They regulate the growth and metabolism by modulation of gene expression and enzymes activities in both sugar exporting (source) and importing (sink) tissues. This ensures optimal synthesis and use of carbon and energy resources.[69,70] In general, a low sugar status enhances photosynthesis, reserve mobilization and export, whereas high sugar concentrations promote growth and carbohydrate storage.[58,59,63,68] Accumulation of soluble sugars in source tissues downregulates photosynthesis thus maintaining homeostasis. Differential source-sink effects on metabolism induced by unfavourable environmental factors lead to a differential expression of several proteins related to carbohydrate metabolism e.g., enzymes related to starch biosynthesis (AGPase, ADP-Glc pyrophosphorylase) and sucrose metabolism (SuSy, sucrose synthase; SPS, sucrose phosphate synthase; and INV, invertase).[71-74]

However, genes whose products are involved in another metabolic pathways and cellular functions are also positively regulated by soluble sugars, examples include genes that encode storage proteins such as patatin in potato and sporamin in sweet potato,[75,76] and genes that encode defence proteins such as proteinase inhibitor II in potato.[77] In contrast, many genes are negatively regulated by sugars; for example, sugars repress expression of α-amylase genes in suspension cells and germinating embryos of rice;[78] endopeptidase, sucrose synthase and asparagine synthase genes in maize root tips;[72,79,80] and malate synthase and isocitrate lyase genes in cucumber cotyledon and suspension cells.[81] However, nothing is known about whether a common mechanism is responsible of the differential sugar regulation. Although mechanisms involved in sugar signal transduction and sugar gene regulation in higher plants are entirely no clarified yet, important progresses have been made to obtain their understanding, principally, about signals that trigger these processes and how the regulation of photosynthetic carbon metabolism interacts with other processes during stress conditions.[27,28,38,39] Many studies about sugar activation and repression mechanisms have shown that regulation take place to transcription level.[30,82] However, sugar repression of α-amylase gene expression involves controls at both transcription and mRNA stability levels.[83] Sucrose and hexoses (mainly glucose and fructose) are recognized as main sensing-molecules and elicit sugar responses in both source and sink organs.[31,36,38,59,67] Studies involving sucrose did not address the question if the sucrose itself or the readily produced hexoses were the true inducer, but Chiou and Bush[63] showed that sucrose specifically reduces the steady state mRNA level corresponding to a proton-sucrose symporter involved in phloem loading. Sucrose-specific signalling pathways showed also to be responsible for repression of the Arabidopsis ATB2 bZIP transcription factor.[84] In addition, studies on starch synthesis in slices of potato tubers and on seed development in transgenic *Vicia narbonensis* support previous suggestions that sucrose specifically induces differentiation and synthesis of storage product.[85,86] Nevertheless, Loreti et al.[38] communicated that both glucose and sucrose independently modulate expression of α-amylase gene in barley embryos. Fructose moiety appears to be an essential component in sensing disaccharides analogues to sucrose such as palatinose and turanose.[38] However, trehalose a disaccharide not containing fructose is also able to induce gene expression.[71] This fact probably signifies that distinct sensors sense trehalose and sucrose analogues.

Despite these findings, cells have independent sensors for sucrose and hexoses. They sense changes in the ratio between sucrose and hexoses induced by stresses and feed this information into markedly different signal transduction pathways. Environmental stresses through sugar-sensing pathways also affect enzymes involved in both synthesis and cleavage of sucrose.[72-74] Sucrose is degraded by either INV or SuSy making a difference in the number of phosphorylable hexoses produced. Invertase hydrolysis produces glucose and fructose (two phosphorylable hexoses) whereas SuSy cleavages produces uridine 5' diphosphate glucose (UDPG) and fructose (one phosphorylable hexose), thus INV action only amplifies the metabolic signal.[87] According to these considerations plants should be able to sense changes in soluble sugar concentrations within cells to modulate their metabolic status through sugar-sensing pathways. In this context, high sugar concentrations suggest a good regulated metabolic status whereas low sugar levels

indicate a possible metabolic deregulation. Sensing intracellular soluble sugar pathways, however, provides incomplete information about the metabolic status of plant cells, since they ignore the concentration of soluble sugars in the apoplast and, perhaps more importantly, the apoplast-cytosol and the vacuole-cytosol fluxes of sugars. Consequently, a complex signalling network underlying to sugar-sensing pathways is present.

Transgenic plants have revealed that the well-characterized intracellular sensing model present in yeasts, where hexokinase (HXK) acts as sugar sensor, plays the same role in plants.[28,38,88] Two systems for glucose sensing in plants have been suggested: one is HXK-dependent, and the other is HXK-independent system. HXK-dependent system requires the phosphorylation of glucose while the independent one senses the hexose without phosphorylation.[89] Evidences in favour of the HXK-dependent signalling came from observations that those glucose-analogue sugars such as 2-deoxy glucose, mannose (a glucose epimer) and 2-deoxy mannose can be phosphorylated by HXK and are able to trigger repression of photosynthetic genes. Whereas the possibility of glucose being converted to other derivatives that could trigger repression without undergoing phosphorylation was ruled out.[36] It appears, therefore, that the sugar phosphorylation step rather than the phosphorylated sugar represents a signal for the plant. Glucose-6-phosphate (G-6-P) was also shown to act as repression signal,[90] however, based on the intracellular concentration of G-6-P, which did not increase upon treatment with glucose, it was suggested that glucose is the direct signal. In contrast, the evidence for the HXK-independent signalling pathways came from observations that glucose analogues: 6-deoxy glucose and 3-O-methyl glucose, which can be transported across the plasma membrane but cannot be phosphorylated by HXK, activated the expression of genes encoding for cell wall invertase (INVcw), SuSy and phenylalanine ammonia lyase the first one, whereas the second for patatin class-1 promoter.[56,77,91,92] Since a complex set of enzymes with different affinities and specificities is able to phosphorylate not only glucose (glucokinases), but also fructose (fructokinases) or both glucose and fructose (HXK), determines that HXK system operating in plants is very different from that operating in yeasts.

Arabidopsis plants show that sugar-phosphorylating activity is higher toward fructose than glucose, and indeed, fructokinase is particularly active, whereas HXK showing a reduced affinity for fructose, is present at relatively low levels.[38] Interestingly, a mig Arabidopsis mutant (mig: mannose-insensitive germination) turned out to be a fructokinase mutant, suggesting that this enzyme, and not just HXK could be involved in sugar sensing.[93] However, fructokinase is normally unable to phosphorylate mannose, so the link between mutation and phenotype is intriguing.[94] On the other hand, the assumption that HXK acting exclusively as cytosolic sugar sensor, is not compatible with results showing that transgenic tobacco plants expressing a yeast invertase (INVy) in the apoplast or in the vacuole are able to sense high hexose levels due to increased sucrose breakdown, while hexoses are not sensed if generated in the cytosol by a INVy targeted to the cytosol.[95] To explain this response, it has been suggested that sensing may occur in the endomembrane system, where HXK is unlikely to be localized.[96] On the other hand, in Arabidopsis HXK transgenic plants (AtHXK) have been suggested three distinct glucose signal transduction pathways. These are AtHXK1-dependent pathway in which gene expression was correlated with the AtHXK1-mediated signaling function. Second was a glycolysis-dependent pathway that was influenced by the catalytic activity of both AtHXK1 and the heterologous yeast HXK2. Third was an AtHXK1-independent pathway in which gene expression was independent of AtHXK1.[88] Hence, the role of HXK in sensing the sugar status is still under discussion.[97]

Plants also contain a sucrose-non-fermenting-1- (SNF1-) related protein, analogue of the protein kinase (SNF-) yeast-signalling pathway.[38] The role of SNF1-related protein in sugar sensing has been tested by using potato plants expressing an antisense SNF1-related protein kinase. Results indicated that SNF1-related protein plays a role in transducing the sugar signal, triggering the induction of sucrose synthase in potato leaves.[98] However, even if plants share with yeast some elements involved in sugar sensing, several aspects of sugar perception are likely to be peculiar to higher plants. Furthermore, abiotic stresses may elicit the production of stress-related hormones such as ABA and ethylene, which appear to be involved in sugar-sensing mechanisms.[99,100] The level of complexity depicted suggests that despite the successful description of some sugar-sensing mechanisms in recent years, additional efforts are needed to obtain a complete picture of sugar sensing in plants and thus, increase our knowledge of the mechanisms for plant abiotic stress tolerance and adaptation.

In conclusion, soluble sugars have dual role in plants. They are involved in various metabolic events and act as molecule signals regulating different genes, especially those involved in photosynthesis, sucrose metabolism and osmolyte synthesis. However, at the present day the more overwhelming conclusion is that it is virtually impossible to generalize the results between all plants, because almost all data were obtained using only a few species, principally Arabidopsis, cereals (maize, wheat, rice and barley), soybean, potato, carrot, sugar beet, tobacco and some others.

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