[Plant Signaling & Behavior 4:5, 388-393; May 2009]; ©2009 Landes Bioscience

Review

Soluble sugars—Metabolism, sensing and abiotic stress

A complex network in the life of plants

Mariana Rosa,[1] Carolina Prado,[1] Griselda Podazza,[2] Roque Interdonato,[1] Juan A. González,[2] Mirna Hilal[1] and Fernando E. Prado[1,*]

[1]Cátedra de Fisiología Vegetal—Facultad de Ciencias Naturales e IML; Tucumán, Argentina; [2]Instituto de Ecología—Fundación Miguel Lillo; Tucumán, Argentina

Abbreviations: ABA, abscisic acid; AGPase, adenosine 5' diphosphate glucose pyrophosphorylase; ATB2 bZIP, Arabidopsis basic leucine zipper gene; G-6-P, glucose-6-phosphate; HXK, hexokinase; INV, invertase; INVcw, cell wall invertase; INVy, yeast invertase; PAR, photosynthetically active radiation; ROS, reactive oxygen species; SNF1-, sucrose-non-fermenting-1-; SPS, sucrose phosphate synthase; SuSy, sucrose synthase; UDPG, uridine 5' diphosphate glucose; UVBR, ultraviolet-B radiation

Key words: abiotic stress, gene expression, glucose, metabolism, sucrose, sugar sensing

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 adaptative 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

*Correspondence to: Fernando E. Prado; Cátedra de Fisiología Vegetal—Facultad de Ciencias Naturales e IML; Miguel Lillo 205; Tucumán CP 4000 Argentina; Email: fepra@csnat.unt.edu.ar

Submitted: 02/19/09; Accepted: 02/26/09

Previously published online as a *Plant Signaling & Behavior* E-publication: http://www.landesbioscience.com/journals/psb/article/8294

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 interconvertions 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.

Acknowledgements

We thank to Frantisek Baluska for his suggestion to write this article. This work was supported by a grant of Consejo de Investigaciones de la Universidad Nacional de Tucumán (CIUNT). F.E.P. is an investigator from CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas). We also apologize if some important references were not cited.

References

1. Lichtenthaler HK. Vegetation stress: an introduction to the stress concept in plants. J Plant Physiol 1996; 148:4-14.
2. Amtmann A, Bohnert HJ, Bressan RA. Abiotic stress and plant genome evolution. Search for new models. Plant Physiol 2005; 138:127-30.
3. Song J, Feng G, Tian C, Zhang F. Strategies for adaptation of *Suaeda physophora*, *Haloxylon ammodendron* and *Haloxylon persicum* to a saline environment during seed-germination stage. Ann Bot 2005; 96:309-405.
4. Mittler R. Abiotic stress, the field environment and stress combination. Trends Plant Sci 2006; 11:15-9.
5. Day TA, Neale PJ. Effects of UV-B radiation on terrestrial and aquatic primary producers. Annu Rev Ecol System 2002; 33:371-96.
6. Gratão P, Polle A, Lea PJ, Azevedo RA. Making the live of heavy metal-stressed plants a little easier. Funct Plant Biol 2005; 32:481-94.

7. Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ. Plant cellular and molecular responses to high salinity. Annu Rev Plant Physiol Mol Biol 2000; 51:463-99.
8. Munns R. Comparative physiology of salt and water stress. Plant Cell Environ 2002; 25:239-50.
9. Rosa M, Hilal M, González JA, Prado FE. Changes in soluble carbohydrates and related enzymes induced by low temperature during early developmental stages of quinoa (*Chenopodium quinoa*) seedlings. J Plant Physiol 2004; 161:683-9.
10. Bohnert HJ, Gong Q, Li P, Ma S. Unraveling abiotic stress tolerance mechanisms-getting genomics going. Curr Opin Plant Biol 2006; 9:180-8.
11. Hu YC, Schmidhalter U. Drought and salinity: a comparison of their effects on mineral nutrition of plants. J Plant Nutr Soil Sci 2005; 168:541-9.
12. Tester M, Davenport R. Na^+ tolerance and Na^+ transport in higher plants. Ann Bot 2003; 91:503-27.
13. Redondo-Gómez S, Mateos-Naranjo E, Davy AJ, Fernández-Muñoz F, Castellanos EM, Luque T, Figueroa ME. Growth and photosynthetic responses to salinity of the salt-marsh shrub *Atriplex portulacoides*. Ann Bot 2007; 100:555-63.
14. Browse J, Xin Z. Temperature sensing and cold acclimation. Curr Opin Plant Biol 2001; 4:241-6.
15. Rosa M. Efecto de las bajas temperaturas y la salinidad sobre la morfoanatomía y la fisiología en plántulas de quinoa (*Chenopodium quinoa* Willd.), con especial énfasis sobre el metabolismo de los carbohidratos y proteínas. PhD Thesis, Universidad Nacional de Tucumán, Argentina 2006.
16. Britt AB. Repair of DNA damage induced by solar UV. Photosynth Res 2004; 81:105-12.
17. Hilal M, Parrado MF, Rosa M, Gallardo M, Orce L, Massa ED, et al. Epidermal lignin deposition in quinoa cotyledons in response to UV-B radiation. Photochem Photobiol 2004; 79:205-10.
18. Ibañez S, Rosa M, Hilal M, González JA, Prado FE. Leaves of *Citrus aurantifolia* exhibit a different sensibility to solar UV-B radiation according to development stage in relation to photosynthetic pigments and UV-B absorbing compounds production. J Photochem Photobiol 2008; 90:163-9.
19. Hall JL. Cellular mechanisms for heavy metal detoxification and tolerance. J Exp Bot 2002; 53:1-11.
20. Shanker AK, Cervantes C, Loza-Tavera H, Avudainayagam S. Chromium toxicity in plants. Environ Intern 2005; 31:739-53.
21. Foyer C, Noctor G. Oxidant and antioxidant signalling in plants: a re-evaluation of the concept of oxidative stress in a physiological context. Plant Cell Environ 2005; 28:1056-71.
22. Apel K, Hirt H. Reactive oxygen species: Metabolism, oxidative stress and signal transduction. Annu Rev Plant Biol 2004; 55:373-99.
23. Rizhsky L, Liang H, Shuman J, Shulaev V, Davletova S, Mittler R. When defense pathways collide. The response of Arabidopsis to a combination of drought and heat stress. Plant Physiol 2004; 134:1683-96.
24. Chaves MM, Pereira JS, Maroco J, Rodrígues ML, Ricardo CPP, Osorio ML, et al. How plants cope with water stress in the field. Photosynthesis and growth. Ann Bot 2002; 89:907-16.
25. Welfare K, Yeo AR, Flowers TJ. Effects of salinity and ozone, individually and in combination, on the growth and ion contents of two chickpea (*Cicer arietinum* L.) varieties. Environ Pollut 2002; 120:397-403.
26. Mitra J. Genetics and genetic improvement of drought resistance in crop plants. Curr Sci 2001; 80:758-63.
27. Zhu JK. Salt and drought stress signal transduction in plants. Annu Rev Plant Biol 2002; 53:247-73.
28. Gupta AK, Kaur N. Sugar signalling and gene expression in relation to carbohydrate metabolism under abiotic stresses in plants. J Biosci 2005; 30:761-76.
29. Aarts MGM, Fier MWEJ. What drives plant stress genes?. Trends Plant Sci 2003; 8:99-102.
30. Yamaguchi-Shinozaki K, Shinozaki K. Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. Annu Rev Plant Biol 2006; 57:781-803.
31. Ho SL, Chao YC, Tong WF, Yu SM. Sugar coordinately and differentially regulates growth- and stress-related gene expression via a complex signal transduction network and multiple control mechanisms. Plant Physiol 2001; 125:877-90.
32. Chinnusamy V, Schumaker K, Zhu JK. Molecular genetic perspectives on cross-talk and specificity in abiotic stress signalling in plants. J Exp Bot 2004; 55:1-12.
33. Gill PK, Sharma AD, Singh P, Bhullar SS. Changes in germination, growth and soluble sugar contents of *Sorghum bicolor* (L.) Moench seeds under various abiotic tresses. Plant Growth Regul 2003; 40:157-62.
34. Meloni DA, Gulotta MR, Martínez CA. Salinity tolerance in *Schinopsis quebracho colorado*: Seed germination, growth, ion relations and metabolic responses. J Arid Environ 2008; 72:1785-92.
35. González JA, Gallardo M, Hilal M, Rosa M, Prado FE. Physiological responses of quinoa (*Chenopodium quinoa* Willd.) to drought and waterlogging stresses: dry matter partitioning. Bot Stud 2009; 50:35-42.
36. Jang JC, Sheen J. Sugar sensing in higher plants. Plant Cell 1997; 9:5-19.
37. Pego JV, Kortstee AJ, Huijser C, Smeekens SCM. Photosynthesis, sugars and the regulation of gene expression. J Exp Bot 2000; 51:407-16.
38. Loreti E, de Bellis L, Alpi A, Perata P. Why and how do plant cells sense sugars?. Ann Bot 2001; 88:803-12.
39. Tran LS, Nakashima K, Shinozaki K, Yamaguchi Shinozaki K. Plant gene networks in osmotic stress response: from genes to regulatory networks. Methods Enzymol 2007; 428:109-28.
40. Ho LC. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. Annu Rev Plant Physiol Plant Mol Biol 1988; 39:355-79.
41. Journet EP, Bligny R, Douce R. Biochemical changes during sucrose deprivation in higher plant cells. J Biol Chem 1986; 261:3193-9.
42. Yu SM. Cellular and genetic responses of plants to sugar starvation. Plant Physiol 1999; 121:687-93.
43. Prado FE, Boero C, Gallardo M, González JA. Effect of NaCl on germination, growth and soluble sugar content in *Chenopodium quinoa* Willd. seeds. Bot Bull Acad Sinica 2000; 41:27-34.
44. Santos HP, Buckeridge MS. The role of the storage carbon of cotyledons in the establishment of seedlings of *Hymenaea courbaril* under different light conditions. Ann Bot 2004; 94:819-30.
45. Prado FE, González JA, Gallardo M, Moris M, Boero C, Kortsarz A. Changes in soluble carbohydrates and invertase activity in *Chenopodium quinoa* ("quinoa") developed for saline stress during germination. Curr Top Phytochem 1995; 14:1-5.
46. Sigstad E, Prado FE. A microcalorimetric study of *Chenopodium quinoa* Willd. seed germination. Thermochim Acta 1999; 326:159-64.
47. Podazza G, González JA, Prado FE. Efectos de metales bivalentes en la germinación y desarrollo radicular de (*Chenopodium quinoa* Willd.). Lilloa 2005; 42:85-94.
48. Podazza G, Rosa M, González JA, Hilal M, Prado FE. Cadmium induces changes in sucrose partitioning, invertase activities and membrane functionality in roots of Rangpur lime (*Citrus limonia* L. Osbeck) Plant Biol 2006; 8:706-14.
49. Rosa M, Hilal M, González JA, Prado FE. Low-temperature effect on enzyme activities involved in sucrose-starch partitioning in salt-stressed and salt-acclimated cotyledons of quinoa (*Chenopodium quinoa* Willd.) seedlings. Plant Physiol Biochem 2009; 47:300-7.
50. Strand Å, Hurry V, Henkes S, Huner N, Gustafsson P, Gardeström P, Stitt M. Acclimation of Arabidopsis leaves developing at low temperatures. Increasing cytoplasmic volume accompanies increased activities of enzymes in the Calvin Cycle and in the sucrose-biosynthesis pathway. Plant Physiol 1999; 119:1387-97.
51. Dubey RS, Singh AK. Salinity induces accumulation of soluble sugars and alters the activity of sugar metabolising enzymes en rice plants. Biol Plant 1999; 42:233-9.
52. Gill PK, Sharma AD, Singh P, Bhullar SS. Effect of various abiotic stresses on the growth soluble sugars and water relations of sorghum seedlings grown in light and darkness. Bulg J Plant Physiol 2001; 27:72-84.
53. Castonguay Y, Nadeau P, Lechasseur P, Chouinard L. Differential accumulation of carbohydrates in alfalfa cultivars of contrasting winter hardiness. Crop Sci 1995; 35:509-16.
54. Morsy MR, Jouve L, Hausman JF, Hoffmann L, Stewart JM. Alteration of oxidative and carbohydrate metabolism under abiotic stress in two rice (*Oryza sativa* L.) genotypes contrasting in chilling tolerance. J Plant Physiol 2007; 164:157-67.
55. Almodares A, Hadi MR, Dosti B. The effects of salt stress on growth parameters and carbohydrates contents in sweet sorghum. Res J Environ Sci 2008; 2:298-304.
56. Roitsch T. Source-sink regulation by sugar and stress. Curr Opin Plant Biol 1999; 2:198-206.
57. Gibson SI. Control of plant development and gene expression by sugar signaling. Curr Opin Plant Biol 2005; 8:93-102.
58. Smeekens S, Rook F. Sugar sensing and sugar-mediated signal transduction in plants. Plant Physiol 1997; 115:7-13.
59. Koch K. Sucrose metabolism: regulatory mechanisms and pivotal roles in sugar sensing and plant development. Curr Opin Plant Biol 2004; 7:235-46.
60. Hilal M, Zenoff AM, Ponessa G, Moreno H, Massa EM. Saline stress alters the temporal patterns of xylem differentiation and alternative oxidase expression in developing soybean roots. Plant Physiol 1998; 117:695-701.
61. Juszczuk IM, Rychter AM. Alternative oxidase in higher plants. Acta Biochim Pol 2003; 50:1257-71.
62. Prado C. Efectos fisiológicos, anatómicos y morfológicos, y evaluación de la capacidad de absorción de Cr(VI) en medio acuático de helechos flotantes del género *Salvinia*. Thesis, Universidad Nacional de Tucumán, Argentina 2007.
63. Chiou TJ, Bush DR. Sucrose is a signal molecule in assimilate partitioning. Proc Natl Acad Sci USA 1998; 95:4784-8.
64. Krapp A, Stitt M. An evaluation of direct and indirect mechanisms for the "sink-regulation" of photosynthesis in spinach: changes in gas exchange, carbohydrates, metabolites, enzyme activities and steady state transcript levels after cold-girdling source leaves. Planta 1995; 195:313-23.
65. Rathinasabapathi B. Metabolic engineering for stress tolerance: installing osmoprotectant synthesis pathways. Ann Bot 2000; 86:709-16.
66. Flowers TJ. Improving crop salt tolerance. J Exp Bot 2004; 55:307-19.
67. Rolland F, Baena-Gonzalez E, Sheen J. Sugar sensing and signaling in plants: conserved and novel mechanisms. Annu Rev Plant Biol 2006; 57:675-709.
68. Chen JG. Sweet sensor, surprising partners. Sci STKE 2007; 373:7.

69. Stitt M, Krappe A. The interaction between elevated carbon dioxide and nitrogen nutrition. The physiological and molecular background. Plant Cell Environ 1999; 22:583-621.
70. Coruzzi GM, Bush DR. Nitrogen and carbon nutrient and metabolite signaling in plants. Plant Physiol 2001; 125:61-4.
71. Wingler A, Fritzius T, Wiemken A, Boller T, Aeschbacher RA. Trehalose induces the ADP-glucose-pyrophosphorylase gene, ApL3 and starch synthesis in Arabidopsis. Plant Physiol 2000; 124:105-14.
72. Koch KE, Nolte KD, Duke ER, McCarty DR, Avigne WT. Sugar levels modulate differential expression of maize sucrose synthase genes. Plant Cell 1992; 4:59-69.
73. Stitt M, Hurry V. A plant for all seasons: alterations in photosynthetic carbon metabolism during cold acclimation in Arabidopsis. Curr Opin Plant Sci 2002; 5:199-206.
74. Roitsch T, Bittner M, Godt DE. Induction of apoplastic invertase of *Chenopodium rubrum* by D-glucose and a glucose analog and tissue-specific expression suggest a role in sink-source regulation. Plant Physiol 1995; 108:285-94.
75. Jefferson R, Goldsbrough A, Bevan M. Transcriptional regulation of a *patatin-1* gene in potato. Plant Mol Biol 1990; 14:995-1006.
76. Hattori T, Fukumoto H, Nakagawa S, Nakamura K. Sucrose-induced expression of genes coding for tuberous root storage protein, sporamin, of sweet potato in leaves and petioles. Plant Cell Physiol 1991; 32:79-86.
77. Kim SR, Costa MA, An G. Sugar response element enhances wound response of potato proteinase inhibitor II in transgenic tobacco. Plant Mol Biol 1991; 17:973-83.
78. Yu SM, Lee YC, Fang SC, Chan MT, Hwa SF, Liu LF. Sugars act as signal molecules and osmotica to regulate the expression of α-amylase genes and metabolic activities in germinating cereals grains. Plant Mol Biol 1996; 30:1277-89.
79. James F, Brouquisse R, Suire C, Pradet A, Raymond P. Purification and biochemical characterization of a vacuolar serine endopeptidase induced by glucose starvation in maize roots. Biochem J 1996; 320:283-92.
80. Chevalier C, Bourgeois E, Just D, Raymond P. Metabolic regulation of asparagine synthetase gene expression in maize (*Zea mays* L.) root tips. Plant J 1996; 9:1-11.
81. Ismail I, de Bellis L, Alpi A, Smith SM. Expression of glyoxylate cycle genes in cucumber roots responds to sugar supply and can be activated by shading or defoliation of the shoot. Plant Mol Biol 1997; 35:633-40.
82. Lu CA, Lim EK, Yu SM. Sugar response sequence in the promoter of a rice α-amylase gene serves as a transcriptional enhancer. J Biol Chem 1998; 273:10120-31.
83. Sheu JJ, Yu TS, Tong WF, Yu SM. Carbohydrate starvation stimulates differential expression of rice α-amylase genes that is modulated through complicated transcriptional and posttranscriptional processes. J Biol Chem 1996; 271:26998-7004.
84. Rook F, Gerrits N, Kortstee A, van Kampen M, Borrias M, Weisbeek P, Smeekens S. Sucrose-specific signalling represses translation of the Arabidopsis *ATB2* bZIP transcription factor gene. Plant J 1998; 15:253-63.
85. Geiger M, Stitt M, Geigenberger P. Metabolism in slices from growing potato tubers responds differently to addition of sucrose and glucose. Planta 1998; 206:234-44.
86. Weber H, Heim U, Golombek S, Borisjuk L, Manteuffel R, Wobus U. Expression of a yeast-derived invertase in developing cotyledons of *Vicia narbonensis* alters the carbohydrate state and affects storage functions. Plant J 1998; 16:163-72.
87. Koch KE. Carbohydrate-modulated gene expression in plants. Annu Rev Plant Physiol Plant Mol Biol 1996; 47:509-40.
88. Xiao W, Sheen J, Jang JC. The role of hexokinase in plant sugar signal transduction and growth and development. Plant Mol Biol 2000; 44:451-61.
89. Smeekens S. Sugar induced signal transduction in plants. Annu Rev Plant Physiol Plant Mol Biol 2000; 52:49-81.
90. Brun T, Roche E, Kim KH, Prentik M. Glucose regulates acetyl CoA carboxylase gene expression in a pancreatic b-cell line (INS-1). J Biol Chem 1993; 268:18905-11.
91. Godt DE, Roitsch T. Differential regulation of a tomato invertase gene family suggests an important function of extracellular isoenzymes in establishing and maintaining sink metabolism. Plant Physiol 1997; 115:273-82.
92. Ehness R, Ecker M, Godt DE, Roitsch T. Glucose and stress independently regulate source and sink metabolism and defence mechanisms via signal transduction pathways. Plant Cell 1997; 9:1825-41.
93. Pego J, Smeekens SCM. Plant fructokinases: a sweet family get-together. Trends Plant Sci 2000; 5:531-6.
94. Gonzali S, Pistelli L, Alpi A, de Bellis L. Characterization of two *Arabidopsis thaliana* fructokinases. Plant Sci 2001; 160:1107-14.
95. Herbers K, Meuwly P, Frommer W, Métraux JP, Sonnewald U. Systemic acquired resistance mediated by the ectopic expression of invertase: possible hexose sensing in the secretory pathway. Plant Cell 1996; 8:793-803.
96. Halford NG, Purcell PC, Hardie DG. Is hexokinase really a sugar sensor in plants?. Trends Plant Sci 1999; 4:117-20.
97. Celenza JL, Carlson M. A yeast gene that is essential for release from glucose repression encodes a protein kinase. Science 1986; 233:1175-80.
98. Purcell PC, Smith AM, Halford NG. Antisense expression of a sucrose non-fermenting-1-related protein kinase sequence in potato results in decreased expression of sucrose synthase in tubers and loss of sucrose-inducibility of sucrose synthase transcripts in leaves. Plant J 1998; 14:195-202.
99. Zhou L, Jang JC, Jones TL, Sheen J. Glucose and ethylene signal transduction crosstalk revealed by an Arabidopsis glucose-insensitive mutant. Proc Natl Acad Sci USA 1998; 95:10294-9.
100. León P, Sheen J. Sugar and hormone connections. Trends Plant Sci 2003; 8:110-6.