

Sucrose signaling in plants

A world yet to be explored

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Abbreviations: CAB, chlorophyll a/b-binding protein; LHCB1, light harvesting complex B1; PEP, phosphoenolpyruvate; PhyA, phytochrome A; Rubisco, ribulose-1,5-bisphosphate carboxylase; Snf-1, sucrose nonfermenting-1

The role of sucrose as a signaling molecule in plants was originally proposed several decades ago. However, recognition of sucrose as a true signal has been largely debated and only recently this role has been fully accepted. The best-studied cases of sucrose signaling involve metabolic processes, such as the induction of fructan or anthocyanin synthesis, but a large volume of scattered information suggests that sucrose signals may control a vast array of developmental processes along the whole life cycle of the plant. Also, wide gaps exist in our current understanding of the intracellular steps that mediate sucrose action. Sucrose concentration in plant tissues tends to be directly related to light intensity, and inversely related to temperature, and accordingly, exogenous sucrose supply often mimics the effect of high light and cold. However, many exceptions to this rule seem to occur due to interactions with other signaling pathways. In conclusion, the sucrose role as a signal molecule in plants is starting to be unveiled and much research is still needed to have a complete map of its significance in plant function.

The role of sucrose (Suc) as a signaling molecule in plants was put forward several decades ago by Pontis,¹ and more recently by Koch² and Wind et al.³ Yet, a long debate has taken place regarding whether Suc truly deserves such status. Unlike glucose (Glc), which has been recognized as a signaling molecule in plants for long, especially in relation to the widespread hexokinase (HK) signaling pathway, Suc role as such has been rather neglected. It has been argued that the reason for not giving Suc a signaling role is that the molecule is rapidly metabolized and thus it is uncertain whether plant responses are attributable to this molecule by itself or to the product of its degradation (i.e., Glc).⁴ However, Suc is relatively a stable molecule (it is transported between different plant organs and even stored for long periods)

when compared with monosaccharides, which are promptly metabolized and are seldom transported between cells or accumulated. A more likely reason for neglecting Suc a signaling role is the fact that in several physiological events regulated by Suc, the molecule is also the substrate for polysaccharide synthesis, so that it has proven to be extremely difficult to distinguish the signaling role from its contribution as mere building blocks for reserve and structural polysaccharide synthesis. The situation has nevertheless changed lately, since evidence accumulated indicating that many mRNAs and enzymes are synthesized de novo when the level of this disaccharide exceeds a certain threshold.⁵ The dual role of Suc has been most clearly evidenced in experiments with the direct addition of Suc to plants in which the responses could not be mimicked by the addition of hexoses. While both Suc and Glc are included in what is generally termed 'sugar sensing', both sugars play very different roles in plant function. Glc is associated with early organ growth, playing an important role in osmotic contribution to expansion of recently divided cells. Glc signaling is therefore prevalent during those stages.² Glc is also produced from the degradation of carbon reserves (such as starch), and it plays a signaling role in the induction of senescence processes,⁶ which commonly involve remobilization of reserves. Suc, on the other hand, is more associated with the maturity and full functionality of plant organs,² and its signaling roles are generally to be found among those processes as well.

While most well studied Suc driven processes affect general metabolism of plant and take place in different tissues and organs simultaneously, some others, which have been mostly neglected, appear to occur in meristems, giving raise to changes in developmental patterns. Developmental processes in which Suc has been widely recognized as a signaling molecule are still few, including phloem development⁷ and embryonic cell division in carrot and spruce.³ However, a compelling amount of scattered information clearly indicates that a wide array of plant developmental processes are controlled by Suc, and in this work we attempt to give a short but comprehensive review of these processes. Examples of both metabolic and developmental responses are illustrated in **Figure 1** and will be discussed separately.

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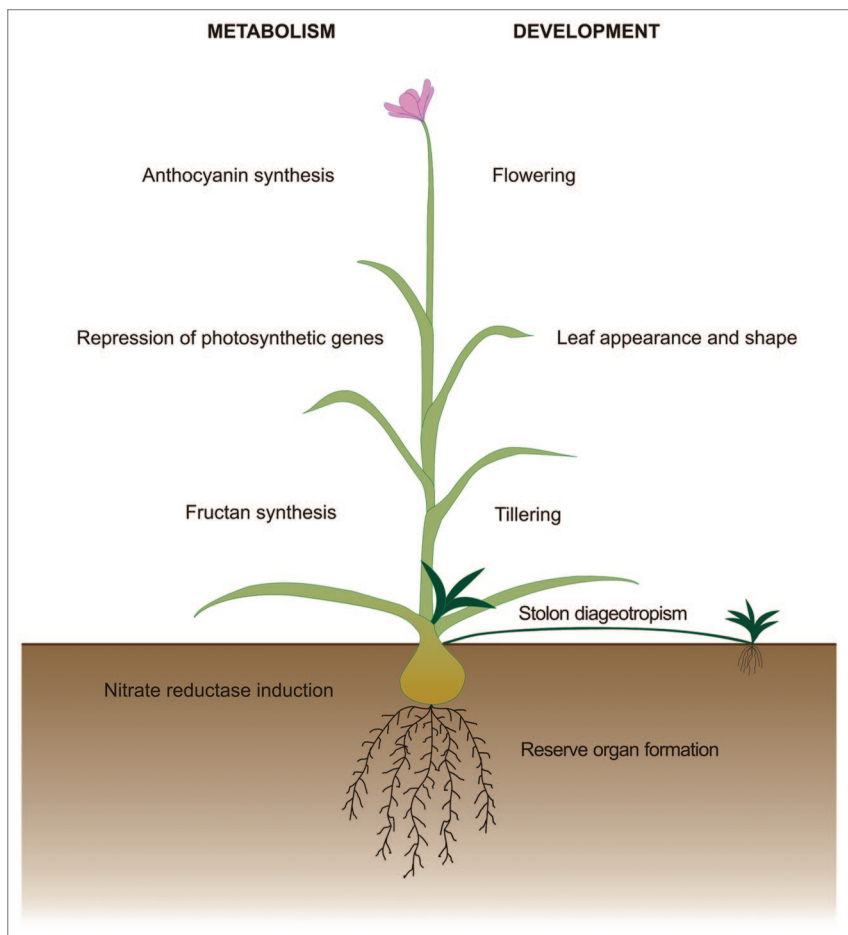


Figure 1. Examples of processes regulated by the endogenous Suc concentration, as schematized in a hypothetical plant. Metabolic and developmental processes are shown at the left and right of the scheme, respectively.

Sucrose Signaling in Plant Cell Metabolism

The effects of Suc on various aspects of plant metabolism have received more attention and are in general better known than those on plant development. Suc signaling has been involved in carbon and nitrogen assimilation and transport. Regarding carbon metabolism, one case that has been long studied is the induction of fructan (polymers of Fru) synthesis in grasses. Although in Nature fructan metabolism is mainly induced during periods of low temperature, the effect of cold is not direct but through its role in increasing cell Suc concentration due to lower carbon utilization.⁸ It has been shown that, at warm temperature, light induces fructan accumulation in detached leaves of different grass species, and that Suc mimics the light effect.⁹ Although Glc supply (and other sugars as well) can also induce fructan synthesis, the efficiency of these sugars is much lower than that of Suc. This fact, together with results from the application of various sugar analogs, led to the conclusion that in Nature, Suc is most likely the molecule which initiates the signaling cascade leading to the induction of fructan synthesizing enzymes.^{9,10}

Sucrose also appears to act as a signaling molecule that initiates/activates starch synthesis. Many reports have shown the

upregulation by Suc of diverse genes related to the starch biosynthetic pathway, such as those that encode specific subunits of ADP-Glc pyrophosphorylase (AGPase) in different species.¹¹⁻¹⁷ While in those reports it was not clear whether this induction was specific of Suc signaling or not, evidence that Suc is the only sugar capable of inducing the AGPase large subunits (*iAG-PLI-1* and *ApL3*) gene expression in sweet potato and *Arabidopsis thaliana* was provided by Harn et al.¹¹ and Nagata et al.¹² It has also been reported that both starch synthase (*GBSS1*) and β -amylase genes are induced by Suc in sweet potato,^{13,14} in the first case the induction was Suc-specific since Glc and Fru could not elicit the same response. Moreover, Suc activates, independently of its metabolism, the AGPase enzyme by post-translational redox modification in growing potato tubers.¹⁵ Although Glc could also produce the same effect, the signaling pathway elicited by Suc is different from that of the hexose, involving Snf1-related protein kinases (SnRK) and HK respectively.¹⁶ This redox regulation occurs also in leaves of pea, potato and *A. thaliana*.¹⁷ Increased levels of Suc have also been found to enhance expression of a Glc-6-phosphate/phosphate translocator¹⁸ which is related to carbohydrate uptake and starch synthesis in heterotrophic tissues.¹⁹

Regarding photosynthesis, the downregulation of CO₂ fixation by Suc is a widely known phenomenon. However, it is not always clear whether Suc plays a signaling function or if it exerts a feedback effect as an end product. In 1990, Sheen²⁰ reported that several photosynthetic genes, including PEP carboxylase, malic enzyme, CAB and Rubisco of maize protoplasts were repressed by Suc. Also, Van Oosten and Besford²¹ found that Suc decreased Rubisco content in tomato leaves. However, in both works, Glc exerted similar or even stronger effects, which cast doubt whether Suc is the true signaling molecule in vivo regarding these effects. The action of Suc on photosynthetic genes seems to be very complex since environmental conditions which lead to Suc accumulation may be associated with either downregulation (i.e CO₂ enrichment) or upregulation (high light and cold) of Rubisco content.²²⁻²⁴ Besides, Nielsen et al.,²⁵ working with tobacco and *Chenopodium* cell cultures demonstrated that Rubisco repression by Suc occurs solely under nitrogen and phosphate limiting conditions. Suc repression of *CAB* and *LHCBI* transcript accumulation in *Brassica napus* and *A. thaliana*, respectively were reported by Harter et al.²⁶ and Cottage et al.²⁷ However, a rather intriguing increase in *CAB* transcripts with Suc supply has recently been reported for *A. thaliana* plants grown in vitro.²⁸

Sucrose may control its own synthesis, at least indirectly. An *A. thaliana* *ugp* gene that encodes the UDP-Glc pyrophosphorylase (UGPase) which is substrate for the action of Suc-phosphate

synthase (SPS), was found to be upregulated by Suc in excised leaves.²⁹ The Suc effect on gene expression and activity of UGPase was apparently specific and was mimicked by cold and by exposure of dark-adapted leaves to light.²⁹ Besides, *ugp* regulation was shown to be independent of Glc signaling by HK.²⁹

Not only carbohydrate synthesis but also its partitioning is regulated by Suc. It was reported that the mRNA levels and activity of Suc symporters from sugar beet source leaves drastically decreased by Suc treatment.³⁰ Hexoses did not elicit the same response, while mannoheptulose, a HK inhibitor, did not block the Suc effect.³⁰ The authors proposed that this was a Suc-specific response pathway, and thus that Suc can control assimilate partitioning at the level of phloem translocation.^{30,31} On the other hand, the nonfunctional Suc symporter from potato source leaves StSUT2, which is specifically enhanced by Suc, has been suggested to act as a Suc sensor.³²

Sucrose appears to control chlorophyll and non-photosynthetic pigment synthesis. It was reported long ago that supplying Suc to the in vitro media prevented chlorophyll accumulation in carrot callus culture.³³ Suc was later proposed to affect synthesis of the chlorophyll precursor 5-aminolevulinic acid.³⁴ It must be taken into account that decreased chlorophyll synthesis not necessarily leads to less green plants, since Kumar et al.³⁵ reported an increased chloroplast number in explants of carrot roots treated with Suc. On the other hand, a well-known case of Suc regulation is the induction of the anthocyanin biosynthesis. While this effect was described many decades ago,³⁶ the strong specificity of the Suc signal was demonstrated by Solfanelli et al.³⁷ in experiments with *A. thaliana* seedlings supplied with different sugar analogs and hexoses. These authors showed that most of the genes coding for enzymes involved in anthocyanin and flavonoid biosynthesis are induced by this sugar. They also suggested that the effect of Suc is performed through the specific induction of the transcription factor PAP1. Besides, there is evidence suggesting that Suc influences carotenoid levels, as shown by Legha et al.³⁸ on callus cultures of *Calendula officinalis*. In general, it appears that Suc plays a role inducing responses associated with free radical scavenging. Among these responses, which in general appear to be Suc-specific since Glc does not elicit similar effects, are included increased ascorbate levels, mitigation of anoxia and photo-oxidative stress related to the herbicide atrazine.³⁹⁻⁴³

The role of Suc on nitrogen metabolism signaling is also very important, since this sugar appears to control not only nitrogen assimilation and transport but also carbon:nitrogen balance. It has long been reported that Suc elicits an increase of nitrate reductase (NR) mRNA accumulation in dark-adapted green *A. thaliana* plants⁴⁴ and other dicotyledons.^{45,46} Suc increases not only NR gene expression, but also activity⁴⁶ and post-translational activation of the enzyme.^{45,46} The effect of Suc on NR expression is so determinant that it may override the well-known upregulation of nitrate on NR expression.⁴⁷ Furthermore, Suc stimulates the amino acid biosynthetic pathways.^{46,48} Suc stimulates the flow of carbon from glycolysis into organic acids, since a decrease of 3-phosphoglycerate and PEP and a large increase of α -oxoglutarate were found in tobacco plants fed with Suc.⁴⁶ Accordingly, the in vivo net rate of ammonium assimilation doubled after feeding

detached tobacco leaves with Suc.⁴⁶ The authors suggested that it is Suc rather than Glc the signal that regulates nitrogen and respiratory metabolism after feeding tobacco with different sugars. Suc promotion of *ASPARAGINES SYNTHETASE1* and *PROLINE DEHYDROGENASE2* gene expression was shown to occur through regulation of the transcription factor bZIP11.⁴⁸ It was suggested that bZIP11 is a direct regulatory link between Suc-mediated signaling and amino acid metabolism.⁴⁸ In contrast, an inverse correlation appears to exist between amino acid biosynthesis and Suc content in potato tubers,⁴⁹ which suggests differences between Suc signaling pathways between source and sink tissues. While free amino acid content is reduced by Suc in potato tubers,⁴⁹ the reserve proteins sporamin and patatin are induced by the sugar.^{14,50} Nitrogen transport also appears to be regulated by Suc. A case in which the ammonium transporter gene, *CitAMT1*, is specifically induced by Suc has been reported for citrus plants.⁵¹ Besides, it has been shown that the *A. thaliana* nitrate and ammonium transporter genes (*NRT* and *AMT*, respectively) are induced after the addition of Suc; however, it is uncertain whether Suc is acting as a signal molecule in this response since hexoses are effective as well.⁵²

A particularly important protein in carbon and nitrogen metabolisms is PII, which coordinates the regulation of nitrogen assimilation in response to nitrogen, carbon and energy availability.⁵³ The expression of the gene (*GLB1*) that encodes PII protein is induced by light and Suc in dark-adapted *A. thaliana* plants.⁵⁴ This effect is not triggered by mannitol or non-metabolizable carbon source.

Regarding other mineral nutrients, the expression of genes encoding for ion transporters for phosphate, sulfate and potassium may be upregulated by Suc.^{55,56} Suc appears to modify the expression of a number of genes related to P starvation which lead to an altered root physiology.⁵⁷ Suc also plays an important role in control of copper homeostasis through sugar-responsive miRNAs in *A. thaliana*.⁵⁸

Sucrose Signaling in Plant Development

The fact that the developmental pattern of a plant may be affected by Suc concentration in tissues was demonstrated several decades ago in the pioneering works by Lawrence and Barker⁵⁹ and Montaldi.⁶⁰ Although not always recognized, enough evidence has been gathered to support the role of Suc as a signal molecule acting on a wide array of plant developmental processes that take place throughout the whole life cycle of the plant. Suc appears to affect both plant growth and differentiation, giving rise to profound changes in plant shape.

A notorious effect of Suc on plant growth is the increase in plant size after exogenous supply of this sugar, which has been found for a large variety of species.⁶¹ Growth promotion by Suc must be at least in part the consequence of increased cell number, and this sugar has been reported to promote cell division in apical meristems as demonstrated long ago in studies with *Pisum* root meristems.⁶² In cell cultures of *A. thaliana*, removal of Suc from the growth medium leads to the cessation of cell cycle, while Suc readdition has been used to generate partially synchronous

cultures.⁶³ Further studies with *A. thaliana* have showed that Suc enhances the expression of cyclins B and D,⁶⁴ and promotes ribosome synthesis.⁶⁵

Besides influencing plant size, Suc may also modify whole plant morphology by controlling the activation of different types of meristems, in both aerial and subterranean parts. The involvement of Suc as a signal molecule acting in the coordination of cell division within the shoot apical meristem (SAM) has been suggested by Francis and Halford.⁶⁶ The SAM increases in size through cell division, and then forms a bulge on its side which becomes the next leaf primordium,⁶⁶ and several evidences suggest that Suc may induce shortening the time interval between the appearance of two successive leaves, this is, the phyllochron. Evidences include shortening of the phyllochron in plants subjected to conditions that favor Suc synthesis or accumulation such as high light and low temperature⁶⁷ (in the latter case, in thermal time units). In accordance with this, wheat plants that accumulate photoassimilates after treatment with an inhibitor of gibberellin synthesis exhibit shorter phyllochrons.⁶⁸ Leaf shape also appears to be controlled by Suc. In monocots, leaf extension was found to be reduced by Suc while the opposite was observed under sugar restriction^{60,69} and the latter effect was similar to what was found by shading.⁷⁰ In dicots, Hanson et al.⁷¹ reported an inhibition of lateral expansion of *A. thaliana* leaf epidermal cells in sugar-treated seedlings, which is mediated by the transcription factor ATHB₁₃.

Regarding stems, the possibility that Suc promotes branching through the release of dormant axillary buds in grasses (i.e., tillering) has been proposed for long time and is known as the nutrition hypothesis of apical dominance, which states that the development of those buds is directly related to assimilate availability.⁷² Although experiments with direct injection of Suc have not given convincing results⁷³ evidence of a correlation between tiller bud outgrowth and photoassimilate availability has been provided.⁷⁴ Again, Suc response seems to mimic the effects of high light and low temperature on tillering. Other known example of the effects of Suc on stem meristems is the control of the gravitropic response.⁶⁰ Willemoës et al.⁷⁵ found that diageotropic (this is, horizontal) growth of stolons in *Cynodon* and other grass species was stimulated by Suc, while Glc and fructose (Fru) did not give similar results. This effect of Suc on plastic growth favors plant propagation, since it allows plants to explore adjacent territories, and is analogous to what is observed under high light intensity.⁷⁰ Furthermore, Digby and Firn⁷⁶ reported a photosynthetic effect on the *Tradescantia* gravitropism, which the authors related to either a direct effect of Suc or an indirect one, through the Suc regulation of *PhyA* gene expression. In any case, these effects of Suc are coherent with an environmental situation in which photoassimilates are abundant and plant invests them in colonization of new spaces.

Sucrose has been long related to the promotion of root growth.⁷⁷⁻⁷⁹ However, the addition of Suc to whole plants in several species has caused no increase in the root to shoot ratio.⁶¹ Thus, Suc might not cause a differential root vs shoot growth promotion. Lateral root formation has also been shown to be promoted by Suc in *A. thaliana*⁸⁰ but this might not be a true Suc

signaling case, but rather an effect linked to Suc metabolism. A further putative role of Suc in root meristems concerns cambium activity. The involvement of Suc in phloem differentiation in in vitro grown plants was showed many decades ago⁸¹ and accordingly, it has been found that conditions that favor Suc accumulation also induce the development of phloem parenchyma (which is the most important sink for assimilates) in carrot roots.⁸² In agreement with the role of promoting reserve structures formation, Suc has been found to induce the development of storage organs in different species. The most well-known case is that of potato tuber induction. In potato, Lawrence and Barker⁵⁹ showed that the level of sugars in the medium, notably Suc, affected tuberization in vitro. It has been found that Suc regulates tuber formation by influencing the levels of gibberellic acid (GA), which is a potent inhibitor of tuber formation.⁸³ This agrees with the findings of Park,⁸⁴ who reported that Suc induced the expression of tuber-specific genes and that the sensitivity toward Suc was modulated by GA. Contrary to the effect of Suc on tuberization, Mares et al.⁸⁵ detected an increased level of reducing sugars with the application of GA. More recently, it has been suggested⁸⁶ that GA inhibits tuberization downstream of the inductive effects of Suc and other positive factors in spontaneous tuberizing potato mutants. Besides tuberization, the formation of other underground storage organs may also be promoted by Suc. This is the case of bulb formation in onion and leek⁸⁷ and rhizome formation in *Bambusa bambos*.⁸⁸

Many other developmental processes, including flowering, regulation of the circadian clock and senescence also appear to depend on Suc signaling. After the early finding by Friend et al.⁸⁹ that flowering of *Brassica campestris* grown in vitro occurred earlier when Suc was added to the medium, the participation of Suc in flower evocation was shown in many other dicotyledons, such as *Sinapis alba*,⁹⁰ *A. thaliana*^{91,92} and *Vitis vinifera*.⁹³ These effects of Suc are in agreement with the well-known promoting effect of irradiance on flowering. Nevertheless, the participation of Suc in the differentiation at the apical meristem is very complex, and the steps that are regulated by this sugar are just recently being unveiled. For example, Roldán et al.⁹⁴ have reported that Suc addition to the medium promotes flower development in the dark in late-flowering *A. thaliana* ecotypes, but Suc is not always effective promoting flowering.⁹⁵ The use of mutants for different genes involved in flower development has led to the suggestion that Suc-mediated signals are incorporated into the photoperiod flowering pathway, probably downstream of *CONSTANS* but upstream of *FLOWERING LOCUS T* genes.⁹⁶ It is also likely that similar roles of Suc in flower differentiation may take place in monocots such as maize.⁹⁷ Recent reports show that Suc regulates the circadian clock in *A. thaliana*,⁹⁸ particularly in the dark. The authors demonstrated that the circadian oscillator *GIGANTEA* is required for the Suc response, being part of the Suc signaling pathway. Regarding senescence, a clear separation between the effects of hexoses and Suc can be observed, since leaf senescence is induced by Glc and Fru but not by Suc.⁹⁹ In the rose cultivar Super Star, Suc retarded while abscisic acid (ABA) promoted senescence in cut flowers.¹⁰⁰ The authors proposed that ABA accelerates senescence of cut roses by promoting petal growth and

respiration, thus decreasing the carbohydrate level in the petals and triggering the chain of metabolic processes leading to aging. A delayed leaf senescence in transgenic poplar with elevated SPS activity, and therefore enhanced Suc content toward the end of the vegetative cycle, was shown by Park et al.¹⁰¹

Finally, several aspects of seed development are also controlled by Suc. In developing seeds of *Vicia faba* high Suc levels have been associated with end of embryo cell division and increasing cell differentiation, expansion and reserve accumulation.¹⁰² Also, radicle growth of carrot seeds was found to be inhibited by this sugar in a similar fashion than it occurs under natural dormancy.¹⁰³ These authors also demonstrated that hexoses did not mimic the effect of Suc; and furthermore, HK signaling was ruled out.

Intracellular Sucrose Signaling

The nature of the Suc receptor that may initiate the signaling pathway is largely unknown. It has been suggested that symporter SUT2 may act as Suc sensor in tomato and in *A. thaliana*.³² This possibility was mainly based on the close structural similarity with the yeast Glc sensors SNF3 and RGT2.³² However, arguments against this putative role have also been raised.¹⁰⁴ Besides, it was recently reported that the vacuolar low-affinity Suc transporter of *A. thaliana* (SUT4) is involved in signaling pathway of the Suc-induced inhibition of seed germination.¹⁰⁵ The authors proposed that SUT4 interacts with 5 members of cytochrome *b5* family (Cyb5-2) to directly sense Suc or acts as a downstream component of a Suc sensing system.¹⁰⁵ Despite scarcity of information regarding the primary Suc sensor molecule, the components that are involved in the transduction pathway were more extensively studied. It appears that calcium as a second messenger, protein kinases (PKs)^{13,106-108} and protein phosphatases (PPs)^{13,109-111} are generally involved in intracellular Suc signaling processes.

One of the clearest processes regulated by Suc is the induction of fructan synthesis in wheat and other grasses. It has been described several years ago that in leaves and roots of a variety of plants fructans accumulate after Suc levels increase beyond a concentration threshold.⁵ Thereafter, it was suggested that Suc plays a double role in fructan metabolism, it is the essential substrate used in fructan synthesis and it also starts the signal transduction pathway that induces the fructosyl-sucrose synthesizing activities (FSS = 1-SST + 6-SFT; 1-SST: 1-Suc:Suc fructosyltransferase, 6-SFT: 6-Suc:fructan fructosyltransferase).¹¹² The induction of fructan synthesis has been used as a model system to study Suc signaling by incubating detached wheat leaves in the darkness and supplemented with Suc. The advantage of this system is that fructan synthesis is strongly induced 6 h after the addition of Suc and virtually no fructans are produced in control leaves.¹⁰ Using different inhibitors and channel blockers it was demonstrated that calcium, CDPKs and PP2A activities are involved in the Suc signaling cascade which leads to the activation of fructan biosynthesis.¹¹³⁻¹¹⁶ In barley, the participation of small GTPases in Suc signaling has also been suggested.¹¹⁷

It has been proposed that Suc enters rapidly from the apoplast through a symporter (SUT)¹¹⁸ and after reaching a concentration

threshold it induces the signaling pathway that regulates expression of genes, including those related to fructan synthesis. The presence of high levels of Suc triggers an increase in the concentration of cytoplasmic calcium that in turn may activate CDPKs downstream in the signaling cascade.^{113,114} On the other hand, PP activity may be necessary for the expression of *SUT* gene and also probably to maintain the symporter in an active (unphosphorylated) form.^{115,119} In a later phase, Suc may inhibit PP2A enzyme activity, which could in turn lead to the inhibition of *SUT* gene expression and/or the inhibition of SUT activity. According to the proposed model, this negative feedback would lead to a decreasing rate of Suc uptake and ultimately stop the Suc-mediated FSS induction.¹¹⁵

Sucrose also appears to modulate central regulators of metabolism and development, mainly SnRK1 but possibly also the 'target of rapamycin'.¹²⁰ SnRK1 is a central integrator of stress and energy signaling in plants, causing extensive reprogramming of gene transcription and controlling plant growth.¹²¹ It has been described that Suc activates SnRK1, and that this kinase is required for the Suc signal transduction leading to starch synthesis and sucrose synthase induction in potato.^{16,122} However, Baena Gonzalez et al.¹²³ showed that KIN10/KIN11 (members of SnRK1 subfamily that are the closest relatives of SNF1 and AMPK of yeast and mammals, respectively) activities are repressed by Suc in maize protoplasts. This signal transduction seems to be HK independent, although the response was also obtained with Glc.¹²³ The reason for this apparent discrepancy is unknown, but it has been suggested that Suc effect on SnRK1 may be different in autotrophic and heterotrophic tissues and also depends on the physiological status of the cells.¹²⁴ It is unclear whether SnRK regulation by Suc occurs in all Suc signaling events or not, and it is even uncertain whether SnRK1 regulation depends on the overall energy status of cells rather on Suc by itself.^{121,125,126} Additionally, intracellular signaling by Suc has proven to be very complex and additional components seem to be necessary in certain processes. For example, Suc increases trehalose-6P levels, and this compound in turn is regarded as a signal molecule which controls carbon metabolism and growth.¹²⁷

Many genes, which have been proven to be Suc-regulated, have conserved *cis* elements in their promoters. Different Suc-responsive elements have been described, including SURE-box, A and B-boxes, TGGACGG element and SP8 motif.^{128,129} Cognate binding factors of SURE-box and SP8, which participate in Suc-signaling, have been identified as SUSIBA2 and SPF1 respectively. Both DNA-binding proteins belong to WRKY transcription factors family but they have opposite effects: while SUSIBA2 is induced by Suc,¹³⁰ SPF1 is a Suc-repressed negative regulator.¹³¹ Suc affects gene expression through the regulation of other transcription factors, such as bZIP11, MYB75/PAP1 and WRKY. The *A. thaliana* *ATB2* bZIP genes encode transcription factors that are important regulators of metabolism, and it has been reported that Suc specifically represses the translation of S-group of bZIP family.¹³² This repressive effect is not mediated by Glc or Fru, used separately or in combination, nor by the Suc-to-hexose ratio.¹³³ Suc effect occurs through an upstream open reading frame (uORF) present in the 5' leader of the bZIP

transcripts.^{134,135} Even though bZIP translation is repressed by Suc, transcription can be induced by Suc.¹³⁶ On the other hand, Suc induces the *MYB75/PAP1* transcription factor gene expression that leads to anthocyanin accumulation.¹³⁷ Suc also strongly induces the expression of *AtWRKY20*, a transcription factor that induces *ApL3* transcription in *A. thaliana*. Other sugars and osmotic controls are either less effective or ineffective.¹²

As it can be envisaged from this revision, most of our knowledge about the intracellular signaling cascade initiated by Suc is mainly related to metabolic processes. Despite the importance of developmental changes for the plant life cycle, intracellular Suc signaling in meristematic cells is largely unknown. The difficulty of such a study is apparent from the fact that differentiation processes in only one or a small group of cells within the meristem may ultimately decide the fate of the whole plant.

Sucrose Cross-Talks with Environmental Signaling Pathways

In plant tissues, Suc is constitutively present; therefore it is necessary that its concentration exceeds a certain threshold to exert a signaling role.⁵ In general, Suc accumulates in vivo when carbohydrate utilization is more restricted than its synthesis, such as when plants are exposed to cool temperatures under relatively high irradiances.⁸ In agreement with this, it has been found that Suc mimics the effect of both cold and high light intensity in many of the metabolic and developmental examples of Suc signaling cited in the present work, such as induction of fructan biosynthesis,¹³⁸ anthocyanin synthesis,³⁷ nitrate reductase regulation,⁴⁴ and tuber induction.¹³⁹ Moreover, Suc might be involved as a signal molecule in plant responses to elevated CO₂ levels, as proposed by Coupe et al.¹⁴⁰ These authors found that the nature of the signal which is transported from CO₂-fed source leaves to the SAM where stomata development is inhibited was fully compatible with Suc. The responses of plants to increased CO₂ levels, which have been the subject of thorough research during the last two decades mainly due to the prospects of climatic change, often resemble those described for high Suc levels. For example, elevated CO₂ (700 ppm) resulted in a large (189%) increase in the fructan concentration in perennial ryegrass leaf blades, in parallel with increased Suc concentration in these organs.¹⁴¹ Also, CO₂ enrichment often results in down-regulation of photosynthetic genes,¹⁴² in a similar manner than that elicited by high Suc. While in these cases Suc appears to be the signal molecule that integrates cold, high irradiance and probably high CO₂ levels, in other cases a more complex picture arises from cross-talks with environmental signaling pathways. It should be recalled that cold and high irradiance are sensed independently of Suc and present their own signaling network. In the case of low temperatures, changes in the level of two plant hormones (increase in ABA and decrease in GA) are commonly observed, that in turn elicit proper responses.¹⁴³ In the case of the light environment, both phytochromes and cryptochromes are the most important sensors.¹⁴⁴ Cross-talks between Suc and

these signaling pathways seem to be frequent. For example, the phytochrome-interacting factor PIF5, which integrates the response to light and time of day, was found to be upregulated by Suc, and overexpression of PIF5 led to growth dynamics similar to plants exposed to Suc.¹⁴⁵ Regarding ABA, this hormone was found to present a synergic role with Suc on anthocyanin synthesis, while Suc-induction of this pathway was repressed by addition of GA.¹⁴⁶ Cross-talks between Suc and another endogenous or environmental signals seem to be complex and much work is needed to shed light on this kind of interactions. For example, up to day no studies about possible interactions between cryptochrome signaling and Suc have been reported. Nevertheless, based on information available and revised in the present work, a schematic picture of the Suc signaling pathway may be drawn (Fig. 2).

Conclusion and Perspectives

After many years of debate, the role of Suc as a signaling molecule in plants has gained wide consensus. It is generally accepted now that Suc plays an essential role in the regulation of important metabolic processes including carbon and nitrogen assimilation and transport, and responses to oxidative damage, and that its role cannot be replaced by that of other sugars such as Glc. Moreover, there is also ample evidence suggesting that Suc takes part as a signaling molecule in a large array of developmental processes, which we have attempted to review in the present work. Taken together, it appears that Suc role as a signal molecule is of uttermost importance to plant life. However, very important gaps in knowledge remain unsolved. First, the precise nature of the Suc sensor is still unknown. Second, it is uncertain how the Suc concentration threshold required for eliciting responses is monitored. Third, even though several intracellular components of the Suc signaling pathway are already known for several metabolic processes, little is known about control of developmental processes within meristems. Fourth, cross-talks between intracellular pathways elicited by Suc and those related to other environmental or endogenous signals appear to be very complex. In conclusion, Suc signaling in plants comprises a vast territory whose exploration has started not long ago and extensive research is still required to have an accurate map of its participation in the plant signaling network.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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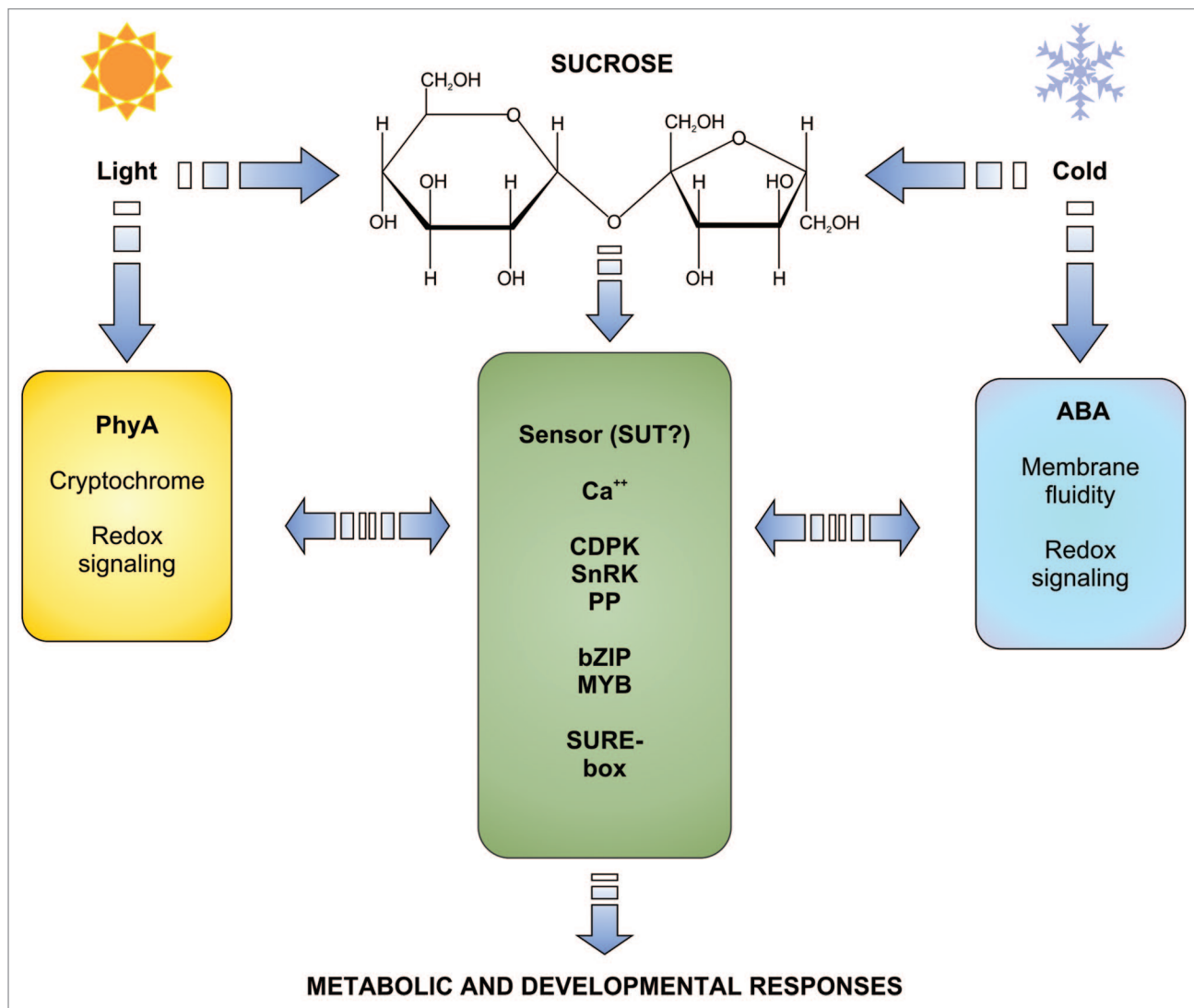


Figure 2. A schematic diagram of the Suc signaling pathway and its interaction with signaling by light and cold. Components of the intracellular Suc signaling pathway include the still unknown sensor, cytosolic intermediates, transcription factors that are target of Suc and the SURE response element found in many promoters exhibiting Suc regulation. Suc mimics the effect of high light and cold on a number of metabolic and developmental responses. Horizontal arrows indicate well-known (PhyA and ABA) and putative components of light and low temperature signaling pathways which may cross-talk with Suc.

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