Source–sink regulation by sugar and stress
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The regulation of carbon partitioning between source and sink tissues in higher plants is not only important for plant growth and development, but insight into the underlying regulatory mechanism is also a prerequisite to modulating assimilate partitioning in transgenic plants. Hexoses, as well as sucrose, have been recognised as important signal molecules in source–sink regulation. Components of the underlying signal transduction pathways have been identified and parallels, as well as distinct differences, to known pathways in yeast and animals have become apparent. There is accumulating evidence for crosstalk, modulation and integration between signalling pathways responding to phytohormones, phosphate, light, sugars, and biotic and abiotic stress-related stimuli. These complex interactions at the signal transduction levels and co-ordinated regulation of gene expression seem to play a central role in source–sink regulation.

Introduction
Higher plants develop from an embryo which depends on heterotrophic metabolism of storage products. During the growth and differentiation of a plant, photosynthetically active source tissues (mature leaves) develop. They export carbohydrates to photosynthetically less active or inactive sink tissues such as roots, fruits or tubers, which are characterised by a net import of sugars; however, this physiological mosaic is not static. The plant life cycle is accompanied by source–sink transitions as well as changes with respect to the sink strength of individual organs and the number of sink organs competing for a common pool of carbohydrates. In addition, exogenous factors such as abiotic stress or pathogen infection may also influence carbohydrate partitioning. Thus, complex mechanisms have to be assumed which integrate the expression of enzymes involved in carbohydrate production in source tissues with utilisation in sink tissues. These regulatory mechanisms ultimately determine the pattern of carbon allocation between the different plant organs and regulate source–sink transitions. The regulation of carbohydrate partitioning has attracted a lot of attention in the past few years. Insight into these mechanisms is not only important for understanding plant growth and development, but it is also a prerequisite for the genetic manipulation of source–sink relations in transgenic plants to increase crop yield.

This review will focus on two aspects of source–sink regulation which are of particular importance: metabolic regulation by sugars, and the effect of stress-related exogenous stimuli. It has been recognised in the past ten years that sugars not only function as substrate to sustain the heterotrophic growth of sink tissues, but are also important signalling molecules that regulate both source and sink metabolism. In addition, both abiotic and biotic stress-related stimuli have profound effects on plant growth and development and are responsible for considerable loss of crop yield. An increasing number of studies are focused on the elucidation of the molecular mechanisms that link the effect of diverse stress stimuli to source–sink regulation.

Source–sink regulation by sugars
Feedback inhibition of photosynthesis as a result of decreased sink demand is a long known phenomenon. Different experimental approaches have shown that sugars play a key role in this regulatory mechanism by repressing the expression of photosynthetic genes [1]. The specific inhibitory effect of sugars on photosynthesis or on the expression of photosynthetic genes is further supported by recent studies which included some monocotyledonous species [2–4], whereas most previous studies concentrated on dicotyledonous plants. This feedback inhibition suggested that assimilates function as link between source and sink tissues. Indeed, sugars were shown to induce transcription of a number of sink specific enzymes involved in sucrose breakdown and metabolism and storage product synthesis [1,5–6,7]. The co-ordinated and inverse regulation of mRNA levels of a photosynthetic enzyme and a sink specific enzyme in the same experiment has been demonstrated in glucose treated photoautotrophic cultures of Chenopodium rubrum. The induction of the mRNA for the sink specific extracellular invertase by glucose showed the same time course and concentration dependence as the repression of the mRNA for the small subunit of the ribulosebisphosphate-carboxylase [8].

So far, most studies on source–sink regulation by sugars have concentrated on the effect of exogenously added sugars to protoplasts, suspension culture cells, and isolated tissues, or the analysis of transgenic plants with modulated carbohydrate metabolism. An alternative experimental approach was followed by Abdin et al. [9] who supplied exogenous sucrose into stems of soybean plants continuously for almost their entire life cycle using a modified pressurised injection technique. This sucrose supplementation suppressed photosynthesis and had positive effects on plant growth.

The elucidation of the underlying signal transduction pathways of source–sink-regulation is currently the major
focus of attention. A number of studies have shown that hexoses and sucrose can elicit sugar responses [1]. The studies involving sucrose, however, did not address the question as to whether sucrose itself or the readily produced hexoses were the actual inducer. Recent studies on the nature of sugar signal molecules have shown that, in addition to hexose signalling, sucrose-specific pathways may be differentiated. Chiou and Bush [10*] have shown that sucrose specifically reduces the steady state mRNA level of a proton–sucrose symporter thought to be involved in phloem loading. Sucrose-specific signalling pathways were also shown to be responsible for the repression of the Arabidopsis ATBZ bZIP transcription factor [11*] and for the modulation of phytochrome signalling [12*]. Studies on starch synthesis in slices of potato tubers [13] and on seed development in transgenic Vicia narbonensis [14*] support previous suggestions that sucrose specifically induces differentiation and storage product synthesis. Hexose sugars are thought to be important primarily to regulate growth and mitotic activity [15].

Several studies imply a possible role of hexokinase in sugar signalling and Jang et al. [16*] have even proposed that hexokinase functions as a sugar sensor in higher plants [16*]. However, there is still a matter of debate about the role of hexokinase in sugar sensing and signalling and it has been proposed that hexokinase dependent and independent pathways are present in higher plants [17–19]. Some of the conflicting suggestions stem from the differential effect of non-phosphorylatable glucose-analogues in the individual experiment system analysed. In some laboratories it has been found that 6-desoxyglucose or 3-O-methylglucose, that are not substrates for hexokinase, are able to trigger gene regulation, whereas in other laboratories these compounds are inactive and only the phosphorylatable glucose analogue 2-desoxyglucose is able to elicit the same effects as glucose [17,18,19]. The fact that the phosphorylatable glucose analogue is able to substitute glucose is interpreted as a direct interaction with hexokinase and a regulatory role of this enzyme in the system analysed. The observed differential effect of non-phosphorylatable glucose analogues on gene regulation, however, may be completely independent of a direct interaction of the different sugar compounds with hexokinase. This may rather reflect species specific differences in the specificity of an extracellular or membrane bound sugar binding protein. The function of such an extracellular sugar receptor would be in agreement with all experimental data and does not even exclude a role of a specific hexokinase isoenzyme in the corresponding intracellular signalling pathway, which is suggested both by transgenic approaches [16*] and inhibitor studies [20]. Although, so far, no direct experimental evidence exists for this hypothesis, extracellular sugar recognition in plants would be backed by the study of Herbers and Sonnewald and co-workers [21]. Possible paradigms for the extracellular sugar sensing molecules are extracellular sugar binding proteins in bacteria [22] and plasmamembrane bound sugar transporters in yeast [23].

Different screens have yielded a number of Arabidopsis mutants that are affected in sugar sensing and signalling and in feedback inhibition of photosynthesis [19,24*,25*,26]. So far, the corresponding target gene has been identified only from the highly pleiotropic mutant prl (pleiotropic regulatory locus-1) that causes sugar hypersensitivity [25*]. The prl protein was shown to be imported into the nucleus and to interact with a nuclear import receptor protein. Also the other mutants isolated to date are also characterised by pleiotropic phenotypes, and this indicates an interaction between different signalling pathways that will be discussed further below.

Transgenic plants overexpressing a heterologous invertase from yeast, or other enzymes to modulate carbohydrate metabolism, have greatly stimulated progress in understanding source–sink regulation [27]. Sugars accumulate to unphysiologically high levels in these plants, however, and the target genes are regulated by stress related stimuli and thus are also expected to be regulated by osmotic stress resulting from sugar accumulation (see discussion below). It may be difficult, therefore, to differentiate between sugar and stress responses. These problems, inherent to the use of constitutive promoters, have been circumvented by the use of an ethanol inducible promoter [28*].

Different components of sugar signal transduction pathways have been identified. There is increasing evidence that mitogen-activated protein (MAP) kinase pathways are important in plants to regulate the response to various exogenous and endogenous stimuli [29]. Work in our group has shown that MAP kinases are also involved in sugar signalling pathways [8*]. It has been demonstrated that in autotrophic suspension culture cells of Chlorella rubrum a myelin basic protein phosphorylating protein kinase is rapidly and transiently activated in response to the metabolic stimulus glucose. This finding indicates that different plant signalling pathways may have a common origin and the apparent parallels to pathogen activated pathways may also help to unravel the components of sugar related signalling pathways. The importance of protein phosphorylation in regulating sink specific metabolism is also demonstrated by the identification of a calcium-dependent protein kinase in maize which is active only in sink tissues [30*]. It has also been shown that a calcium-dependent protein kinase of tobacco that is associated with the plasma membrane is inducible by sucrose [31]. The latter two studies further suggest that calcium may be involved in source–sink regulation as a secondary messenger which has also been suggested on the basis of pharmacological studies (summarised in [18]). Parallels of plant sugar signalling pathways to the well characterised catabolite repression system in yeast are suggested by the identification and function of SNF-1-related protein kinases in plants [32,33]. Antisense repression of
SNF-1-related protein kinases was shown to result in loss of sugar inducibility of sucrose synthase [34•]. These studies indicate that proteins homologous to the SNF-1 kinase of yeast may have a function in sugar signalling of higher plants. However, future studies will be required to prove the speculations that plant SNF-1 related proteins are global regulators of carbon metabolism in plants [35] and that they even integrate cytokinin, light, glucose and brassinosteroid signalling [36].

By functional dissection of sugar regulated promoters it has been possible to identify cis-acting regulatory sequences required for sugar regulated gene expression [37,38,39•,40]. These results will be important to elucidate whether positively and negatively regulated promoters share the same regulatory sequences and thus are regulated by the same transcription factors. Furthermore, the identified regulatory sequences may be a valuable tool to isolate such regulatory proteins.

**Source–sink regulation by stress**

Stress related stimuli may be both of abiotic and biotic origin. Despite the dramatic effect of stress related stimuli on yield in agriculture, only few studies have focused on the regulation of enzyme activities and transcriptional regulation of genes in response to these stimuli. Therefore, it is difficult to compare the mostly unrelated studies on source-sink regulation by stress related stimuli and this section lists the recent advances sorted by the nature of the stimuli. Future work will require to focus on the effect of different stimuli on specific target proteins or genes to be able to better compare the results of different studies.

Water has long been recognised as a crucial abiotic determinant of carbon allocation [41] and drought is a major factor limiting plant distribution and productivity. Water stress induces large alterations in source–sink relations due to a modification of growth priorities and to a reduction of the performance of photosynthetic organs. With respect to the effect of water deficiency on whole plants, source limitations such as a reduced photosynthetic capacity, resulting in a decreased export of assimilates seem to be responsible for decreased crop load [42]. Variations in stomatal conductance resulting in decreased water loss due to transpiration were found to be important in stress tolerant cultivars [43,44]. A few studies have addressed the regulation of source and sink specific enzymes in response to drought. It has been shown that as water deficit is increased in discs of potato tubers, there is a progressive inhibition of starch synthesis [45]. This was also observed in peach seedlings where it appears to be caused by the inhibition of photosynthesis [46]. Different studies demonstrated an effect of water stress on soluble acid invertase that is thought to mobilise sucrose stored in the vacuole. It has been shown that induction of male sterility in wheat by meiotic stage water deficit is preceded by a decline in vacuolar invertase activity [47]. In contrast, mild water stress in maize leaves produced an early and large stimulation of vacuolar invertase activity which was tightly related to the mRNA concentration for a specific vacuolar invertase gene [48,49,50•].

Salinity is another important environmental factor resulting in suboptimal growth. Despite the far-reaching impact in agronomic terms, however, only limited information about the effect on plant metabolism and source–sink relations is available. It has been shown that salt stress not only alters photosynthesis and carbohydrate levels, at least transiently, but also alters the types of carbohydrates that are synthesised and exported by the source tissues [51•,52]. The proposal that alterations in the type of carbohydrate transported in response to salt stress may act as a (novel) sugar signalling system for acclimation responses in the sink tissues [51•] is an interesting extension of the concept of sugar signalling in plants but still lacks any experimental evidence.

An important biotic stress for plants is the infection by viruses. It has been shown that viral infection or expression of different viral movement proteins in transgenic plants influences photosynthesis, carbohydrate accumulation and assimilate partitioning (reviewed in [53]).

Infection by phytopathogenic fungi may be mimicked by the use of fungal elicitors which proved to be useful in numerous studies to analyse early, elicitor-induced defence responses of plant cells. The use of photoautotrophic cultures made it possible to analyse simultaneously the effect of elicitors on defence responses as well as source–sink relations [8•]. It has been shown that in photoautotrophic cultures of Chenopodium rubrum the regulation of mRNAs for representative enzymes of defence response and source and sink metabolism are coordinately regulated. Induction of the mRNAs for the sink-specific and defence-related enzymes, and the repression of the mRNA for the photosynthetic enzymes showed the same time course and concentration dependence to the fungal elicitor chitosan and two other stress stimuli.

Wounding is another severe environmental stress to which plants may be subjected and may come about through such diverse causes as mechanical injury and herbivore attack. Wounding of source leaves of Chenopodium rubrum plants
was shown to result in the same co-ordinated regulation of source–sink relations and defence responses as elicitor treatment of suspension culture cells. These studies involving both tissue culture cells as well as plants demonstrate that different stress related stimuli result in the same regulatory pattern of mRNAs for enzymes involved source and sink metabolism and defence reactions. This indicates that defence responses are tightly linked to the upregulation of sink metabolism to satisfy the energy requirements of the activation of the cascade of defence reaction.

Under natural conditions plants are simultaneously affected by a variety of both biotic and abiotic stress related stimuli and other environmental factors. The presence of one stress may change plant responses to other stresses, thus creating additive or synergistic interactions. This fact is neglected when usually only the effect of a single stress or other environmental factor is analysed. Three recent studies provide some preliminary results about such naturally occurring interactions or multistress situation on source–sink relations. By combining elevated levels of the air pollutant ozone and mild drought, the ozone-induced responses of all parameters, such as the disequilibrium of the carbon transfer between roots and shoots, were significantly amplified [54]. Elevated levels of CO₂ were shown to enhance the growth inhibitory effect of powdery mildew infection in barley [55] and to ameliorate ozone effects on biomass and leaf area in soybean [56•].

Fluorescence imaging has been suggested only recently as a diagnostic tool to analyse plant stress responses [57]. The relationship between laser-induced chlorophyll fluorescence and photosynthesis in drought and ozone stressed plants has been evaluated with respect to quantitative interpretation of the measurements and further practical applications of this method [58]. The available data indicate that this powerful noninvasive technique, which allows the measurement of both the photosynthetic activity as well as the sink status of the tissues analysed, could complement and extend molecular studies on the co-ordinated regulation of sink and source specific genes. In addition, this method may help to compare the effect of different types of stress related stimuli.
**Signalling pathways: crosstalk and integration**

Interaction between different phytohormones is well established and best exemplified by the effect of auxin/cytokinin ratio on plant morphogenesis [59]. There are several studies that demonstrate interactions between sugar and phytohormone signalling pathways which further support the significance of sugar signalling in plant growth and development. Modulation of sugar responses by phytohormones or vice versa, or cross talk between the underlying signalling pathways has been determined for gibberellins [60•], ethylene [24•], auxin [61] and cytokinin [25•]. Inorganic ions such as phosphate and nitrogen were also shown to modify sugar-mediated gene regulation in a gene specific manner [62,63]. Interactions between the environmental stimulus light and sugar has been reported by Dijkwel et al. [12•]. These studies demonstrate that sugar regulation in higher plants is linked to the effect of a number of other signals and that complex interactions exist between the underlying signal transduction pathways.

Based on the sugar inducibility of a number of defence related enzymes it has been proposed that regulation of defence related enzymes in response to pathogen infection is indirectly mediated via the initial induction of an extracellular invertase and the resulting increased sugar concentration [64]. The study of Ehness et al. [8•], however, shows that sugar and stress related stimuli independently activate different signalling pathways which are ultimately integrated to regulate source and sink metabolism and activate defence responses as depicted in Figure 1. Thus, sugars may function as an extracellular indicator for pathogen infection, as suggested before [64], but the corresponding genes are under dual control and directly regulated both by the metabolic stimulus glucose as well as in response to stress related stimuli. Based on the pleiotropic phenotype of the *pri1* mutation in *Arabidopsis* [25•], a connection between glucose and stress signalling has also been proposed [36].

**Invertase: a key enzyme in source–sink regulation**

Supplying carbohydrates to sink tissues via an apoplastic pathway involves the release of the transport sugar sucrose into the apoplast by a sucrose transporter (Suc TP), the disaccharide (Suc) is cleaved by an extracellular invertase and the hexose monomers (Fru and Glc) are taken up from the sink cell by monosaccharide transporters. Extracellular invertase is regulated by glucose, as well as by phytohormones and stress-related stimuli. Sugars are substrates for heterotrophic growth and function as signals for gene regulation.
Supplying carbohydrates to sink tissues
A number of studies demonstrate an essential function of extracellular invertase for phloem unloading, carbohydrate partitioning and growth of sink tissues (reviewed in [65,66•])

Regulation of source–sink transitions
The fast upregulation of extracellular invertase expression after the induction of metabolism in autotrophic cultures of tomato and Chenopodium rubrum [5•,67], and the induction of sink metabolism in source leaves of transgenic plants by overexpression of a yeast invertase [27] indicate a role of extracellular sucrose cleavage in regulating source–sink-transitions and establishing sink metabolism.

Amplification of signals that regulate source–sink relations
As unloading of sucrose from the phloem into the apoplast follows the concentration gradient, and hexose transport into the sink cells is mediated by high affinity monosaccharide transporters, extracellular invertase with a high \( K_{\text{m}} \)-value in the millimolar range is expected to be the limiting step for phloem unloading and thus a potential target for regulation. Indeed, extracellular invertases were shown to be specifically expressed under conditions that require a high carbohydrate supply and upregulated by a number of stimuli that affect source–sink relations (Figure 2). Extracellular invertase was shown to be specifically expressed in sink tissues. The corresponding gene was induced by growth stimulating phytohormones such as cytokinin and brassinosteroids ([68•], M Goetz and T Roitsch, unpublished observations), as well as elicitors, pathogen infection and wounding that lead to the requirement for additional energy to elicit defence responses [8•,69]. In contrast, ethylene, that is associated with fruit ripening and thus terminates fruit growth, represses the expression of extracellular invertase [70]. Extracellular invertases from different species were also shown to be transcriptionally induced by sugars [5•,67,71] and a higher extracellular invertase activity will increase the sugar concentration; therefore, any signal that upregulates extracellular invertase will be amplified and maintained by the positive sugar feedback circuit (Figures 1 and 2).

Integration of signals that regulate source–sink relations and defence responses
Since extracellular invertase is regulated by a number of different stimuli that influence source–sink relations, the corresponding signals are integrated via this enzyme. Elevated hexose levels brought about by an upregulated extracellular invertase expression have been suggested to be important in defence responses and systemic acquired resistance [21].

Conclusions and perspectives
Although there is accumulating evidence that stress related stimuli are important exogenous factors that regulate source–sink relations, it is still not known how these exogenous signals are sensed. Only scattered information is available about the intracellular transduction of these signals and about the molecular and cellular mechanisms that contribute to the physiological responses. To further elucidate the effect of plant stress on source–sink regulation, it will be important to consider naturally occurring multistress situations. That is, to say, it will be important to determine possible additive, synergistic and compensating effects between different stress related stimuli and other environmental factors.

Sugars have been identified as important signal molecules that regulate source–sink relations. There is accumulating evidence that several independent sugar signal transduction pathways, both specific for hexoses and sucrose, operate in parallel. The identified components of the underlying signal transduction pathways suggest homologies as well as distinct differences to well characterised signal transduction pathways in yeast and mammals. Interactions and crosstalk between sugar and hormones, phosphate and light signal transduction pathways are evident. There is experimental evidence that sugar and stress related signal transduction pathways are integrated to regulate defence reactions as well as source–sink relations.

To elucidate the mechanisms that regulate source–sink relations, complementing experimental approaches are required. Protoplasts and suspension culture cells are suitable experimental systems to study signal transduction, and photoautotrophic cultures have proven to be particularly suitable. Photosynthesis is usually repressed in heterotrophic cultures that also require a sugar depletion period which may cause artefacts. Studies involving whole plants will be required to assess source–sink relations, and controlled manipulation of pathways using regulated promoters seems to be very promising.

Parallels of plant signal transduction pathways to well characterised pathways in yeast will possibly allow cloning by complementation of yeast mutants, but the isolation and analysis of plant mutants will be necessary to identify components unique to plants. The analysis of signal transduction and response mutants was indispensable for the rapid and significant progress in the field of phytohormone signal transduction and the regulation of source–sink relations. To dissect the molecular basis for the apparent interaction and crosstalk between sugar and other signal transduction pathways it will be necessary to determine branch points, such as common second messengers or regulatory proteins, by identifying corresponding upstream and downstream mutants; such mutants would be expected to be characterised by either pleiotropic or more specific phenotypes, respectively.

An alternative approach to identify key genes controlling and co-ordinating acclimative reactions is the use of molecular marker technologies. Quantitative trait loci analysis has been applied to several key enzymes in carbohydrate metabolism [50•,72]. The QTL method is a powerful approach to dissect
and understand the complex regulation of processes taking place at the whole plant level and thus may be also a valuable tool to study the regulation of source–sink relations.

Understanding the complex interactions between different signals at the level of signal transduction pathways is likely to be the key for understanding source–sink regulation at the molecular level. Future studies should also consider possible interactions between carbohydrate, nitrogen and phosphate metabolism.

One driving force to study source–sink regulation was the projected practical application to manipulate assimilate partitioning in transgenic plants and to increase the partitioning of fixed carbon into harvestable sinks — however, the numerous approaches taken by many laboratories to modify carbon fluxes through modifying individual enzymatic steps have been largely unsuccessful [73]. This insight and the available literature on source–sink regulation indicate that plants may display an enormous and underestimated metabolic flexibility and crosstalk between different signal transduction pathways. The challenge remains, therefore, to unravel the underlying sophisticated network of highly flexible regulatory circuits to get insight into the fascinating biology of source–sink regulation. This will allow predictable genetic engineering of plants via manipulating signal transduction pathways rather than specific enzymatic reactions.

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:
* of special interest
** of outstanding interest


This study demonstrates that extracellular invertases of tomato are encoded by four differentially expressed and regulated genes. Specific isoenzymes are specifically expressed in sink tissue and/or induced in response to signals that require a high carbohydrate supply such as growth stimulating phyto-hormones, elicitors and wounding.


The effect of sugar and stress-related signals on photosynthesis, sink metabolism, and defense response was studied in photoautotrophic cultures of Chenopodium rubrum by analysing the regulation of mRNAs for representative enzymes. All stimuli resulted in the induction of the genes encoding the sink specific extracellular invertase and the defense responsive PAL, whereas the photosynthetic gene RbcS was repressed. The differential effect of the kinase inhibitor staurosporine demonstrated that glucose and stress independently activate different intracellular signalling pathways that are ultimately integrated to co-ordinately regulate source–sink relations and defense mechanisms. Both glucose and stress-related stimuli triggered the rapid and transient activation of protein kinases that specifically phosphorylate the MAP kinase substrate myelin basic protein.


The stem injection method has been optimised for soybean plants as an example of a non-cereal species. It was possible to administer concentrated sugar solutions into soybean plants continuously for almost their entire life cycle which was shown to suppress photosynthesis while positively affecting growth.


The authors demonstrate that the feeding of sucrose, but not of hexoses, decreased the activity of a proton–sucrose symporter in plasma membrane vesicles from leaves, which correlated with a repression of the corresponding gene expression. Inhibitor studies suggest that this novel sucrose-specific response pathway does not involve hexokinase. These results are in contrast to a study by Harme et al. [74] that demonstrated that the mRNA for a potato sucrose transporter is not regulated by sucrose.


The expression pattern of bZIP suggests a role in the control of processes associated with the transport of metabolites. The expression of a GUS-reporter gene construct was specifically repressed by sucrose, but not by hexose sugars, indicating regulation by a sucrose-specific pathway.


A plastocyanin promoter-luciferase reporter gene fusion was used to identify mesophyll reduced repression of luminescence by sucrose. The specific repression of phytochrome responses of seedlings suggested the interaction between a sucrose specific sugar signal transduction pathway and light regulation.


The expression pattern of bZIP suggests a role in the control of processes associated with the transport of metabolites. The expression of a GUS-reporter gene construct was specifically repressed by sucrose, but not by hexose sugars, indicating regulation by a sucrose-specific pathway.


The authors present evidence for a role of hexokinase in sugar signaling by modulating the in planta levels of hexokinase activity. Arabidopsis plants which overexpress hexokinase showed increased sugar sensitivity whereas anti-sense suppression of hexokinase resulted in a decreased sugar sensitivity.


novel carbohydrates. The authors provide the novel and interesting suggestion that alteration in the type of carbohydrate may act as a signalling system for the activation of acclimation responses in the sink tissue.


56. Miller JE, Heagle AS, Pursley WA: Influence of ozone stress on • soybean response to carbon dioxide enrichment: II. Biomass and Development. Crop Sci 1998, 38:122-128. The authors analyse the effect of the expected increase of the levels of both ozone and CO₂ in the environment on biomass and development. It has been shown that elevated CO₂ ameliorated ozone effects on main stem biomass, root biomass, and leaf area.


60. Perata P, Matsukura C, Vernieri P, Yamaguchi J: Sugar repression of • a gibberellin-dependent signaling pathway in barley embryos. Plant Cell 1997, 9:2197-2208. The results demonstrate that sugar and hormonal signalling specifically interact in the regulation of gibberelin acid-induced gene expression in barley grains in a highly tissue specific manner. Whereas the induction of α-amylase by gibberellic acid in the aleurone layer is unaffected by the presence of the sugar, carbohydrate repression is effective in the scutellar epithelium of the embryo.


66. Tang G-Q, Lüscher M, Sturm A: Antisense repression and vascular • cell wall invertase in transgenic carrot alters early plant development and sucrose partitioning. Plant Cell 1999, 11:1-14. Antisense repression of both invertase isoenzymes resulted in phenotypic alterations that appeared very early in development. This study further supports the hypothesis that not only extracellular and vacuolar invertases in plant growth and development. The data suggest that extracellular invertase plays an important role in early development, whereas both isoforms seem to have important functions in sucrose partitioning.


68. Ehness R, Roitsch T: Co-ordinated induction of mRNAs for • extracellular invertase and a glucose transporter in Chenopodium rubrum by cytokinins. Plant J 1997, 11:539-548. This study shows that extracellular invertase and hexose transporters are not only functionally linked but also coordinately regulated. It has been shown that upregulation of the two enzymes by cytokinin results in increased glucose and sucrose uptake (via hexose monomers). This regulatory mechanism was suggested to be one of the molecular mechanisms required for the stimulation of growth and cell division and the retardation of senescence.


