

CARBOHYDRATE-MODULATED GENE EXPRESSION IN PLANTS

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ABSTRACT

Plant gene responses to changing carbohydrate status can vary markedly. Some genes are induced, some are repressed, and others are minimally affected. As in microorganisms, sugar-sensitive plant genes are part of an ancient system of cellular adjustment to critical nutrient availability. However, in multicellular plants, sugar-regulated expression also provides a mechanism for control of resource distribution among tissues and organs. Carbohydrate depletion upregulates genes for photosynthesis, remobilization, and export, while decreasing mRNAs for storage and utilization. Abundant sugar levels exert opposite effects through a combination of gene repression and induction. Long-term changes in metabolic activity, resource partitioning, and plant form result. Sensitivity of carbohydrate-responsive gene expression to environmental and developmental signals further enhances its potential to aid acclimation. The review addresses the above from molecular to whole-plant levels and considers emerging models for sensing and transducing carbohydrate signals to responsive genes.

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INTRODUCTION

In plants and microorganisms, sugars not only function as substrates for growth but affect sugar-sensing systems that initiate changes in gene expression. Both abundance and depletion of carbohydrates can enhance or repress expression of genes. Responses vary depending on the carbohydrate, though metabolic flux may be more important than actual levels of carbon resources. Many sugar-modulated genes have direct and indirect roles in sugar metabolism, which suggests that their altered expression may have adaptive value. Not only do collective, long-term changes in metabolism result, but patterns of carbohydrate allocation among plant parts can also be altered.

The existence and potential importance of sugar-regulated gene expression in plants has become apparent only in the past few years. Previous evidence indicated that sugar supplies could alter enzyme activities, metabolism, and development, but these data and their significance were generally not viewed in the context of gene expression. Initial work on photosynthetic genes and their metabolic effectors is reviewed by Sheen (161) and discussed by Stitt et al (175). Thomas & Rodriguez (187) summarize metabolite regulation in cereal seedlings and further appraise the germinating cereal seed as a model system (188). Koch & Nolte (84) relate advances in sugar-modulated gene expression to effects on transport paths. Classical aspects of altered carbohydrate availability on whole-plant and organ processes are appraised by Farrar & Williams (34) and Wardlaw (199), with updates by Geiger et al (43), Quick & Schaffer (139), and Pollock & Farrar (134). Information on sugar-responsive gene expression is also available for microbial (15, 40, 150, 158, 192) and animal systems (195).

CARBOHYDRATES AS SUBSTRATES AND SIGNALS

Biological Significance

In microbes, carbohydrate signals to sugar-responsive genes provide a way for these organisms to adjust to changes in availability of essential nutrients. This capacity is vital to their survival and/or effective competition. Classic examples include control of the lactose operon in *Escherichia coli* and the glucose responsive genes for sugar metabolism in *Saccharomyces cerevisiae* (15, 40, 150, 158, 192). Similar responses have more recently been identified in unicellular algae (9, 93, 155, 172).

In multicellular organisms, however, acclimation to altered carbohydrate availability occurs within a complex structure. Sugar-regulated genes provide a means not only for integrating cellular responses to transport sugars (carrying information on carbohydrate status of the whole) but also for coordinating

changes in resource utilization and allocation among parts. In addition, carbohydrate-responsive genes can effect changes in organismal development.

For plants in particular, carbohydrate-regulated genes represent an especially valuable mechanism for adjusting to environmental change. Plants are extremely sensitive and responsive to their surroundings because immobility leaves them few options for survival other than acclimation. Sugar concentrations vary over a wide range in plant tissues. This range typically exceeds that found in more homeostatic systems (such as the mammalian blood stream) and provides plants with both a broader range of signals and a greater challenge to adjustment. Sugar-mediated changes in gene expression are also unique in plants because changes in carbohydrate allocation can ultimately modulate form through processes affecting import/export balance (photosynthesis vs utilization).

Effects of carbohydrate availability on expression of specific genes may complement and amplify the influence of more immediate metabolic controls. Although gene-level responses are slower, they provide a magnitude and duration of change that cannot be accommodated by other means of regulation. The signals and regulatory mechanisms controlling the two processes appear to be quite different.

“FEAST AND FAMINE” RESPONSES AT THE GENE EXPRESSION LEVEL

“Feast and famine” is used here in a relative context and is not necessarily based on absolute levels of carbohydrate (see section on Carbohydrate-Sensing Systems). In the same way, “sugar-modulated,” “carbohydrate-responsive,” and “metabolite-regulated” gene expression are broadly inclusive. Transcriptional regulation is usually implied and is substantiated in many instances (77, 89, 160, 161), but message stability and turnover can also be involved (162). In any case, the ultimate effects of altered mRNA levels depend on the efficacy of translation, turnover and/or modification of protein products, and the metabolic context into which such changes are introduced.

The overall theme of Tables 1 and 2, together with discussion of salient features in this section, is that of carbohydrate-responsive gene expression as a mechanism for plant adjustment to altered availability of this essential resource. Known examples of sugar-responsive gene expression are organized by carbon-exporting and -importing tissues to help clarify the potential of their collective relevance to each. In general, carbohydrate depletion enhances expression of genes for photosynthesis, reserve mobilization, and export processes (Table 1), whereas abundant carbon resources favor genes for storage and utilization (Table 2). These effects, summarized schematically in Figure 1, reinforce the suggestion that sugar-responsive genes provide a means of adjusting whole-plant resource allocation and may ultimately contribute to adaptive changes in form.

Table 1 “Famine” genes: enhanced by sugar depletion

Genes/enzymes (function)	Evidence: plant, tissue	Effectors tested	Refs
<i>Photosynthesis</i>			
Rubisco S-subunit [rbcS]	<i>Zea</i> protoplast, trans expr tomato lvs <i>Chenopodium</i> cell cult + tobacco and potato plants tobacco leaf protoplasts	S, acet S, G G S, G + girdl G	160, 161 194 89 89 25
Rubisco L-subunit [rbcL]	<i>Chlorogonium</i> cell cult	acet	9, 172
chl a/b-binding protein (cab, Lhcb)	<i>Zea</i> protoplasts, trans expr <i>Chenopodium</i> cell cult tobacco leaf protoplasts rape cell cult <i>Chlamydomonas</i> cults	S, G, acet, oth G G, S G acet	160, 161 89 25 55 79
atp- δ thylakoid ATPase	<i>Chenopodium</i> cell cult	G	89
malic enzyme, C4 [Me1]	<i>Zea</i> protoplasts, trans expr	S, G, acet, oth	160, 161
PEP carboxylase, C4 [Pepc1]	<i>Zea</i> protoplasts, trans expr	S, G, acet, oth	160, 161
triose-phosphate translocator	tobacco lvs	S	82
pyruvate PPdikin [Ppdk1]	<i>Zea</i> protoplasts, trans expr	S, G, acet, oth	160, 161
C4-pyruvate phosphodikinase (C4 psynth)	<i>Zea</i> protoplasts, trans expr <i>Chenopodium</i> cell cult		160, 161 70 89
<i>Remobilization</i> (starch, lipid, and protein breakdown)			
Amy3D, Amy3E α -amylase	rice cell cults	S, G, F, Mal	61, 180
α -amylase	rice, cult embryo, and scutel barley aleurone	S, G, F, endo extract Na-butyrate	74, 187, 214 94
plastid starch phosphorylase	<i>Chenopodium</i> cells, lvs	G	91
phosphoglucose mutase	<i>Chenopodium</i> cells, lvs	G	91
isocitrate lyase [Icl] (glyox cycle)	cucumber cotyledons <i>Chlorogonium</i> cells	S, G, F, 2dG, M + acet	50, 51 155
malate synth (glyox cycle)	cucumber cotyledons	S, G, F, 2dG, M	50, 51
proteases	maize root tips	G	13
asparagine synthetase (N cycling)	<i>Arabidopsis</i> shoot tissues	S	95
<i>Sucrose and mannitol metabolism</i> (synthesis and breakdown)			
acid invertase	maize root tips [<i>Ivr1</i>]	G, S, F, oth	86, 209, 210
S synth	maize root tips [<i>Sh1</i>] maize protoplasts [<i>Sh1</i>] carrot, whole plant <i>Vicia</i> seeds, cotyledons	S, G, F, oth S pruning F, G	85 104 179 57
SPS	<i>Arabidopsis</i> [<i>ASus1</i>] sugar beet rts, lvs	sink manip S	106 60
Mtol dehydrogenase	celery cell cult	S, Mtol	133

Abbreviations: 2dG, 2-deoxy-glucose; acet, acetate; cult, culture; endo, endosperm; F, fructose; G, glucose; Lhcb, light-harvesting chlorophyll-binding protein (also cab); lvs, leaves; M, mannose; Mal, maltose; Mtol, mannitol; PEP, phosphoenolpyruvate; PPdikin, phosphodikinase (cytosolic); rts, roots; scutel, scutellum; *Sh1*, *Shrunken1*; S, sucrose; SPS, sucrose phosphate synthase; trans expr, transient expression; synth, synthase.

Carbohydrate Depletion and Sugar-Responsive Genes

Plant and microbial gene responses to carbohydrate depletion have important similarities but differ as well. In both plants and microbes, sugar and acetate effects favor uptake of preferred substrates requiring the least metabolic cost and promote heterotrophic growth over photosynthesis when possible. How-

Table 2 “Feast” genes: enhanced by sugar abundance

Genes/enzymes (function)	Evidence: plant, tissue	Effectors tested	Refs
<i>Polysaccharide biosynthesis</i> (starch and other)			
AGPase [<i>Sh2</i>] (starch)	<i>Chenopodium</i> cell cult + spinach, transgenic potato lvs potato/detached lvs in dark		91 92, 116 87
starch phosphorylase	potato tuber potato/detached lvs in dark	S S	171 87
starch synth [GBSS]	potato/detached lvs in dark	S, G, F	87
branching enzyme [BE]	potato/detached lvs in dark cassava stems and lvs	S, G, F S, G, F	87 152
<i>Storage proteins</i>			
sporamin, A & B types	sweet potato/cult plts/stems sweet potato/lvs and petiole	S S, G, F	56 65, 122
β-amylase (storage protein?)	sweet potatoes and lvs sweet potatoes and lvs	S, pgal a S, G, F	122 127
patatin class I	transgenic potato promoter potato tubers and lvs transgenic potato lvs and tuber potato tuber/transgenic tobacco potato leaf and stem explants potato leaf and stem explants transgenic potato tubers	S S S S, starch S S S, Gln, dk sol. sugs.	52 36, 143 78 99 202 202 131 117
proteinase inhibitor II [Pin2]	transgenic potato tubers potato lvs/transgenic tobacco detached potato lvs transgenic tobacco	sol. sugs. S, G, F, Mal ABA, MeJA S, G, F	117 70 131 78
lipoxygenase (storage protein)	soybean <i>Lox-NR</i> soybean <i>VspB</i> soybean <i>Vsps</i>	depodding S, Mal S, G, F, MeJA	53 149 107
<i>Pigments and defense</i>			
chalcone synth (pigment/path.)	petunia in <i>Arabidopsis</i> , alfalfa protoplasts, <i>Camelia sinensis</i>	S, G, F p-coumar sugars	193 101 183
RT locus (pigment synth)	petunia/petal, anther	G + light	14
dihydroflavonol-reductase	ivy lvs and stems	sugars	120
Mn-superoxide dismutase	rubber tree/all tissues	S	110
hrp (pathology)	<i>Xanthomonas campestris</i>	S + Met	157
chaperonin 60B (protein synth)	<i>Arabidopsis</i> lvs	S	215
<i>Respiration</i>			
PGAL-dehydrog. (<i>GapC</i>) cyto	<i>Arabidopsis</i> lvs	S	211
β-isopropylmalate dehydrog.	potato, tomato, <i>Arabidopsis</i>	S, AA	66
apocytochrome 6 (<i>co6</i>)	<i>Chlorogonium</i> cell cult		93
PP-F-6-P phosphotransferase	<i>Chenopodium</i> cell cult, tobacco, and spinach lvs	G G	92 92

Table 2 (Continued)

Genes/enzymes (function)	Evidence: plant, tissue	Effectors tested	Refs
<i>Sucrose metabolism</i>			
invertase	maize root tips [<i>Ivr2</i>] <i>Chenopodium rubrum</i> carrot, whole plant	S, G, F S, G, F, 6dG manip.	87, 209 144 179
S synth	maize [<i>Sus1</i>] rice embryos <i>Vicia faba</i> cotyledons potato tubers, lvs, stems potato plants, throughout <i>Chenopodium</i> cell cults	S, G, F S, G, F S S S S, G, F	86 74 57 151 37, 38 46
SPS	sugar beet petioles transgenic potato	G sol. sugcs.	60 117
<i>Other</i>			
nitrate reductase	<i>Arabidopsis</i> lvs light/dark <i>Arabidopsis</i> plants light/dark <i>Chenopodium</i> cells/spinach lvs	S, G, F G	196 18 91
SAM synth	<i>Lolium</i> lvs	S	208
ro/C gene of Ri plamid	transgenic tobacco/phloem	S	213
30-kD Rubisco-assoc. protein	soybean lvs	pod removal	171

Abbreviations: 6dG, 6-deoxy-glucose; AA, amino acids; cult plts, cultured plants; F, fructose; G, glucose; GapC, PGAL-dehydrogenase (cytoplasmic); Gln, glutamine; Glu, glutamate; lvs, leaves; Mal, maltose; MeJA, methyl jasmonate; Met, methionine; p-coumar, p-coumaric acid; PGAL, glyceraldehyde-3-phosphate dehydrogenase; pgal a., polygalacturonic acid; PP-F-6-P phosphotransferase, pyrophosphate:fructose-6-phosphate-phosphotransferase; S, sucrose; SPS, sucrose phosphate synthase

ever, in complex plant systems, carbohydrate-regulated genes also provide a means for optimizing investment of C, N, P, etc among different plant parts and processes. Localized expression of starvation-induced genes may also aid survival of key cells and tissues under stress (84, 85).

In carbon-exporting or other autotrophic cells, photosynthetic genes are typically upregulated by sugar depletion. These include genes for the primary CO₂ fixation enzymes of both C3 and C4 plants (18, 160, 161) and other genes critical to photosynthesis (113, 160). Both nuclear (Table 1; 89) and plastid genes (25, 89, 160, 161) are affected, though the latter may respond more slowly to altered carbohydrate levels (25, 163). Enhanced expression results largely from derepression of sugar and acetate controls on transcription (89), though longevity of mRNA can also contribute to sugar modulation in vivo (162). Photosynthetic genes are repressed most by acetate (160) and often more strongly by hexoses than sucrose (69, 160, 161). Acetate effects are observed in cotyledons and in unicellular algae (Table 1; 50, 51).

The physiological consequences of sugar-induced changes in gene expression are discussed further in the section on "Implications at the Cell and Organism Level." Coordinated but often contrasting responses to sugar depletion are also evident at the enzyme level (90, 153, 175, 194). Plastid proteins

and enzymes can differ in their responses depending on whether they are encoded by nuclear or plastid genes (10, 190, 194) and whether they are involved in photosynthesis or other processes (91).

Genes for remobilization of sugars and other small molecules from polymers and/or vacuoles are also induced in exporting cells by carbohydrate depletion. In photosynthetic leaves, those genes associated with starch breakdown can be upregulated by carbohydrate depletion and repressed by glucose (91). A similar response is observed in source tissues of germinating monocot seeds, where starch hydrolysis in endosperm provides the bulk of exported sugars (61, 74, 187, 214). In addition, carbohydrate depletion in cotyledons of germinating dicot seeds upregulates genes for remobilization of lipid reserves via the glyoxylate cycle (50, 51). β -amylase genes are not enhanced by carbohydrate depletion (125, 127); however, their *in vivo* function remains unclear.

The extent of protein remobilization (and associated gene expression) can vary markedly with the degree of carbohydrate depletion (33, 68, 173). Leaf storage proteins are broken down under these conditions (53, 170, 173), though typically nonphotosynthetic cells are involved (53). Starvation effects (see below) occur only if photosynthetic capacity is severely compromised.

In carbon-importing cells, transitions to net carbon export are favored by "famine-induced" changes in gene expression. This cellular altruism in higher plants is distinct from responses of microbes and unicellular algae. Genes related to carbohydrate, lipid, and protein remobilization (Table 2 and below), amino acid synthesis (95), and sucrose formation [sucrose phosphate synthase (SPS; 60, 81)] are upregulated. Responses of SPS genes to sugar availability may be complex. In sugarbeet, a taproot-specific form of this enzyme is upregulated and downregulated by glucose and sucrose, respectively (60), whereas a spinach gene is regulated in synchrony with the sink-to-source transition (81).

Starvation and carbon conservation responses at the level of gene expression initially affect genes related to reserve remobilization (see above) and respiration (see below) that preserve structural constituents of the cell (12, 13, 68). Prolonged stress may induce genes related to breakdown, shuttling, and scavenging of cellular resources (P Ramond, unpublished data). Detoxification of nitrogenous compounds may be facilitated by upregulation of asparagine synthase (68) and sucrose synthase (Table 1). These changes are accompanied by sugar-repressible increases in activity of endoglycosidases [implicated in glycoprotein breakdown (100)], endopeptidases (49), and unidentified starvation proteins (5, 200). Under extreme starvation, the activity of enzymes involved in β -oxidation (although not a fully operative glyoxylate cycle) increases and may be associated with metabolism of membrane lipids (12, 13, 31, 68). Specific subgroups of apparently immature mitochondria and their associated proteins also disappear from starved cells under these conditions (23, 73).

Starvation stress and transport sugars can also affect accumulation of osmoprotectants. Upregulation of a mannitol dehydrogenase gene by carbohydrate depletion allows use of this sugar alcohol as a carbohydrate source (133), whereas sugar repression favors accumulation and salt tolerance (133, 185, 186). A starvation-tolerant class of genes for sucrose synthase and for invertase is also induced (85, 86); these proteins are expressed in key tissues under stress (84, 85) and at specific stages in development (209; see below).

Carbohydrate Abundance and Sugar-Responsive Genes

A large but specific set of genes is positively regulated by sugars. The majority of identified genes that are induced by elevated sugar levels encode products that help set capacity for carbon storage, utilization, and import. Other important classes include defense genes, secondary product pathways, and storage proteins.

In carbon-exporting and/or autotrophic cells, the transitions to import and storage programs are typically initiated at elevated sugar levels. The decreased expression of photosynthetic genes described above allows reallocation of the C and N (otherwise utilized in photosynthetic proteins) to other processes more advantageous under the prevailing carbohydrate environment. In this context, the concurrent upregulation of genes for nitrate reductase and a putative SAM synthase in leaves (205; Table 2) could facilitate amino acid synthesis and turnover of other N sources. Such genes may also contribute to synthesis of leaf storage proteins (Table 2; 170) and other signals including polyamines that may enhance the positive effects of sugars (180). Other aspects of gene expression related to storage and carbon use also change in *Lolium* leaves as sugar levels rise (206).

Genes related to storage reserve synthesis can be upregulated by sugars. These genes are similarly affected in both photosynthetic and nonphotosynthetic organs (84, 122, 131, 188). These changes may be associated with conversion of chloroplasts to either amyloplasts (154) or chromoplasts as sugar levels rise (64).

Genes for sucrose metabolism can be upregulated in photosynthetic tissues following manipulations that cause sugars to accumulate (151). These changes often result in elevated starch levels (167, 168) especially in cells alongside major veins (124).

In carbon-importing cells, genes for starch biosynthesis have received the greatest attention. Those encoding ADPG-pyrophosphorylase (AGPase), a key step in starch biosynthesis, are markedly sugar responsive in potato (87, 89, 116). AGPase expression is also strongly enhanced by sugars in transgenic potato cell cultures (116) and in other species (175). Corresponding increases in activity of the AGPase enzyme are not necessarily observed but may occur

more slowly (175). Starch synthase and branching enzyme are also induced and/or expressed at elevated levels when sugars are plentiful (87, 152). Carbohydrate regulation of sucrose synthase genes is complex and not necessarily directly related to starch synthesis. The *Shrunken1* (*Sh1*) gene for sucrose synthase in maize can directly affect synthesis of starch and/or cell wall materials (20, 123, 124); however, a second gene, *Sus1*, responds more strongly to elevated sugars (85; see section on Contrasting Response Classes Among Genes for Sucrose Metabolism).

Genes encoding storage proteins were among the first sugar-responsive genes identified. A gene for sporamin storage protein in sweet potatoes (56) is upregulated in situ, and it is ectopically expressed in plantlets treated with high sugars. The patatin storage protein genes of potato also respond positively to high sugar levels (78, 99, 131, 202). An additional group of sugar-modulated genes includes vegetative storage proteins, which are expressed at elevated sugar levels in several species (29, 107, 149). Many of these proteins have enzyme activity in addition to a storage function. The *Vsp* gene groups A and B of tobacco encode proteins with phosphatase activity (149); a soybean vegetative storage protein has lipoxygenase activity (53); the patatins are lipid acyl hydrolases (52, 202); and the WIN and Pin-II storage protein genes of *Solanum* spp. are proteinase inhibitors (70). Studies of sugar responsiveness in these genes have revealed important interactions between carbohydrate supply and other signals (e.g. N, P, auxin, etc).

A number of pigment and defense genes are positively modulated by carbohydrates (77; Table 2). The products of these genes mediate plant interactions with other organisms, either as pathogens, pollinators, or fruit dispersal agents. Often these interactions involve enhanced carbon use by the plant; however, effects on biosynthesis of pigments, proteins, and chaperonins can be distinct.

Respiratory genes are affected to varying degrees by sugars (Table 2). Both nuclear- and plastid-encoded genes can show positive responses, with the latter upregulated through both mRNA abundance and gene copy number (93). Mitochondrial ubiquinone mRNA is also strongly affected (B Collins, P Raymond, R Brouquisse, CJ Pollock & JF Farrar, unpublished data), as are levels of cytochrome oxidase and activity of fumarase (91). As in yeast, however, carbohydrates do not globally upregulate respiratory genes. For example, mRNA levels may remain constant for glycolytic genes [often used as controls (89, 92)] even though other respiratory genes respond to elevated glucose levels (91, 92; see Table 2).

Genes for sucrose metabolism can be strongly affected by high sugar levels in importing as well as exporting cells. The complex carbohydrate regulation of the invertases and sucrose synthase genes that control the two known paths for sucrose breakdown is discussed in the following section.

Contrasting Response Classes Among Genes for Sucrose Metabolism

Genes for sucrose metabolism occupy a central position not only in carbon flow but also in the production of alternate potential effectors of the sugar-sensing system. This altered expression of genes in sucrose metabolism could affect whole-plant adjustment to changes in carbohydrate supplies at several levels. Shifts in resource allocation are often directly correlated with activity of the respective enzymes, and indirect effects on signaling systems could further amplify changes in expression of these genes as well as genes affecting developmental programs. Collectively, these changes could also lead to changes in plant form that fine-tune acclimation.

Sucrose metabolism is the first step in carbon use by the majority of importing cells in plants (21, 115, 181). Two recently appreciated features of sucrose metabolism are particularly interesting. First, the genes for invertase as well as sucrose synthase are sugar-modulated (84, 144, 179, 209). Second, isozyme forms of each enzyme show contrasting carbohydrate responses (84, 85, 209). (In each instance, one isozyme is upregulated while one or more others are repressed.) Sugar-modulation of genes for both known paths for sucrose metabolism provides a potential mechanism for coarse control of this process.

The presence of isozyme forms with contrasting carbohydrate responsiveness was an unexpected finding. Reciprocal expression was first observed for sucrose synthases (85) and subsequently for invertases (209, 210). Initial studies of sugar-modulated gene expression were perplexing because of contradictory results. Sucrose synthase was reportedly both repressed (83, 104, 169) and enhanced in the presence of abundant carbohydrate supplies (74, 151). The reciprocal sugar responsiveness of genes encoding distinct isozymes is likely to have been responsible (85). Differentially responsive genes could also explain the contrasting effects of light on expression of sucrose synthases of wheat (105).

The surprising similarity between differential sugar-modulation of different genes for invertases (209, 210) and sucrose synthases in maize indicates that there are two sugar-response classes among genes for sucrose metabolism. Both the *Sh1* gene for sucrose synthase and the *Ivr1* gene for invertase (210) are expressed maximally when supplies of metabolizable sugars are limited [e.g. ca 10 mM glucose (0.2% w/v)] (85, 209). Both types of mRNA persist during carbohydrate starvation stress in root tips, and they are enhanced at key sites and times during reproductive development (84, 85, 209, 210). In contrast, the *Sus1* gene for sucrose synthase and the *Ivr2* gene for invertase both respond positively to abundant carbohydrate supplies [e.g. ca 100 mM glucose (2.0% w/v)] and are expressed in a broad range of importing tissues (209, 210). A “feast”-responsive set of isozymes for both paths of sucrose breakdown could

aid adjustment of import and metabolism relative to photosynthate availability. The potential value of up- or downregulating sucrose utilization in balance with its supply is consistent with the broad distribution of this isozyme form among importing tissues. In contrast, the potential physiological significance is less clear for the isozyme genes expressed when carbohydrate supplies are limited. To date, little is known about differences between properties of the invertase isozymes, although the sucrose synthases appear to be enzymatically similar (32). It is possible that more recent work showing phosphorylation of this enzyme (63, 86, 159) may be related to differences in properties of the sucrose synthase isoforms (63).

Additional clues to the biological importance of sucrose synthase and invertase isozymes whose genes are upregulated under “famine” conditions may lie in the altered protein localization and reproductive timing of expression. Under starvation stress, sucrose synthase protein in maize root tips is localized to epidermis and vascular strands while being markedly depleted from the cortex (56a, 85). Cortical cells are often sacrificed during various stresses, including low oxygen, N, or P availability (56a, 84, 108), whereas vascular and epidermal tissues are preserved. Living epidermis appears to be essential for nutrient and water uptake in many species and is very often associated with a hypodermis (having endodermal-like functions) and a rhizosheath of soil particles bound to the root surface by polysaccharide secretions [also sugar modulated in their extent (114)] (132, 108). It is possible that import priority could be conferred on essential cells and tissues during periods of limited resources by localized upregulation of special isoforms of sucrose metabolizing enzymes (84, 85). This would be consistent with upregulation of the same starvation-tolerant isoforms in specific reproductive tissues and in their additional localization in apices of roots and shoots preserved at the expense of other tissues in a starving plant (6). Our current knowledge of the *Sh1* sucrose synthase and *Ivr1* invertases of maize is consistent with this hypothesis (86, 209).

IMPLICATIONS AT THE CELL AND ORGANISM LEVEL

Long-Term Metabolic Changes

The relatively slow kinetics of the carbohydrate-induced changes in gene expression (85, 175) and enzyme activity (84, 86) are consistent with the time frame often required for source/sink adjustments at the whole-plant level (41). The physiological changes parallel the altered expression patterns of individual genes. Photosynthesis and C-conservation are generally enhanced when sugar supplies are limited, and utilization usually predominates when sugars are abundant.

Changes in photosynthetic processes resulting from sugar-modulated gene expression generally occur over an extended time period (ca 3–7 days) (84,

86, 175) and may amplify shorter-term effects of direct metabolic control (35, 62). Altered transcript abundance can occur within a few hours or less in some systems (144, 161), although initial changes are often not evident until ca 12–24 h and progress slowly thereafter. Consistent with this time scale, early work by Geiger (41) showed that changes in photosynthetic capacity in response to altered source-sink balance takes 3–4 days. Also, as plants acclimate to elevated CO₂, photosynthetic rates decline over a period of days after an initial increase (27), possibly because of the repressive effects of accumulated sugars in leaves (194).

Invertase activity in leaves may indirectly affect repression of photosynthetic genes by accumulated sugars because hexoses may affect the sugar-sensing system more directly than sucrose (69, 160, 161; see section on Carbohydrate-Sensing Systems). Hexoses in particular have been implicated in long-term repression of photosynthetic genes (59, 175). Species with high levels of leaf invertase show a greater degree of photosynthetic inhibition in instances of reduced sucrose export (47). This effect is substantiated in transgenic invertase overexpressors (30, 58, 166, 168, 177, 198), where sucrose export from mature leaves is inhibited and hexose production enhanced. Pollock et al (136) also found that elevated leaf sucrose had little inhibitory effect on photosynthesis while fructans were being actively synthesized and stored in vacuoles (presumably removing hexoses from the cytosol). Long-term influences of hexoses on photosynthesis are likely to involve other factors as well (35, 42, 62, 176). Krapp et al (89) suggested that, as in yeast, hexose metabolism may be required for repressive effects of sugars on gene expression; they found an imperfect correlation between hexose levels and photosynthetic repression.

Leaf senescence may also be enhanced by long-term hexose effects on gene expression. In this context it is interesting that invertase activity is elevated during aging (135). Hexoses in particular may favor expression of genes involved in remobilization of photosynthetic machinery and altered pigment synthesis (Tables 1 and 2). Acetate effects are still more pronounced (160), which indicates that lipid breakdown and mobilization may accelerate senescence. The putative advantage of sugar repression of photosynthetic genes is that valuable resources need not be committed to this process if carbohydrate supplies are already sufficient.

Pigment changes and chloroplast-to-chromoplast conversions during fruit ripening and senescence may be affected by carbohydrate-sensitive genes (201). In ivy, sugar-sensitive gene expression has been directly related to induction of enzyme activity leading to pigment accumulation (119, 120). In citrus peel, sugars mediate interconversions between chloroplasts and chromoplasts (64). Regreening occurs in late-ripening oranges as peel sugar levels drop in spring. Rising sugar levels are consistently associated with the chloroplast-to-chromoplast conversion in autumn. Sugars can also stimulate these changes in

chlorophyll, carotenoid, and plastid characters *in vitro* (48). Chloroplast-to-chromoplast conversions are also enhanced by the induction of invertase at low temperature in citrus (138). Many of the nuclear-encoded plastid genes are also readily responsive to sugar levels (Tables 1 and 2), whereas chloroplast genes appear to be less so (194). As noted above, however, the responsiveness of chloroplast genes to acetate suggests that this metabolite could be important in plastid conversions.

Changes in storage processes are closely related to carbohydrate-responsive gene expression. Sugar effects on storage organ formation are discussed below (see section on Interaction with Developmental and Environmental Signals). In addition, most instances of enhanced gene expression cited in Table 2 are accompanied by respective increases in enzyme activity and storage of carbohydrate and/or proteins (e.g. 146, 197). Further, sugar effects on an α -amylase gene family and on sucrose synthase correlate with the balance between endosperm remobilization and the demands of the growing seedling (188).

Respiratory changes related to sugar-modulated gene expression are less clear. The hypothesis for “coarse control” described by Farrar & Williams (34) indicates that long-term respiratory responses follow extended changes in carbohydrate availability and probably require altered gene expression. Although evidence supports this view, the relationship between carbohydrates and gene expression is complex, and aspects of the story remain unresolved. Respiration typically rises in response to increasing levels of sugars (8, 34, 96, 109), and it decreases with starvation (12, 68, 140)—as do expression levels of many genes related to respiratory processes (Table 2). Concurrent increases in levels of key mRNAs and of associated respiratory activity have been observed as sugar content rises in maturing leaves of transgenic plants overexpressing invertase (175). Similar correlations have been made in several species (89, 93). Kroymann et al (93) suggested coordination through a signal related to cellular energy charge. The ATP/ADP ratio rises along with respiration and associated transcript levels (89). However, the evidence gathered thus far does not necessarily support adenylate charge as a direct signal for carbohydrate-responsive genes (175, 161; see section on Key Metabolites as Direct Signals). Other issues not yet fully resolved include the role of changes in organelle number (140) and genome copy number (93), the importance of the alternate oxidase (96), significance of Pi and adenylates to gene expression (161, 175), and the potential impact of acetate on the carbohydrate signaling.

Carbohydrate-Responsive Genes, Assimilate Partitioning, and Development

The ultimate significance of sugar-modulated gene expression may be induction of changes in whole-plant morphology. Taken together, the trends in gene expression, subsequent metabolic changes, and shifts in resource allocation

are consistent with this suggestion. Sugar modulation of developmental genes is implied by responses such as potato tuber induction (165); however, the specific genes involved have not been identified. The pronounced interactions between carbohydrate levels and plant growth regulators (especially auxin/sugar antagonisms) and other essential nutrients such as N or P suggest that sugars may affect development at the cell, organ, and whole-plant levels. The type of carbohydrate supplied to cells and callus cultures can also affect morphological change not attributable to osmotic effects.

Figure 1 summarizes the developmental trends implied by the gene expression changes known to occur in carbon-importing and -exporting tissues under feast and famine conditions (see Figure 1). A number of studies support the notion that C-availability can affect C-allocation through altered gene expression (see discussion on partition in section on Contrasting Response Classes Among Genes for Sucrose Metabolism). This in turn can affect partitioning between root and shoot structures (43, 134, 167, 179, 204). Other seemingly contradictory results obtained when different methods are used to manipulate sugar availability might also be interpreted within this simplified framework. Both root and shoot growth are inhibited in transgenic plants with excess invertase, presumably because translocation to the root system is disrupted (175) and high hexose levels simultaneously repress photosynthetic genes in leaves. In contrast, shoot growth may be indirectly enhanced when sugars are supplied to whole plants via the root system (56, 88), if increased root growth leads to increased capacity for cytokinin synthesis, which in turn may stimulate shoot growth and photosynthetic processes (112).

Carbohydrate-induced changes in vegetative morphology often involve an altered balance of growth regulators and mineral nutrients (130, 207). Sugars can repress auxin-mediated processes including apical dominance and upright stem growth (negative geotropism) resulting in more spreading, procumbent growth forms (203). Expression of genes now known to be sugar responsive may also have a role in gravitropism (75, 76). In addition, sugar induction of storage organs in potato and sweet potato can be distinguished from regulation of the genes associated with storage processes per se. Although some of the latter processes are coordinately regulated (197), the morphological program remains separately sugar responsive (117).

Cell differentiation and the cell cycle can also be strongly affected by sugar availability. Development of tracheid vs phloem cells can be controlled by sugar/auxin balance (39), and other effects of specific sugars on differentiation have been reevaluated in cultured cells (191). The cell cycle within a given tissue can be synchronized by withholding and resupplying sugars (200). In addition, cell divisions can be induced in nongrowing buds of sunflower by elevated sugar levels (2).

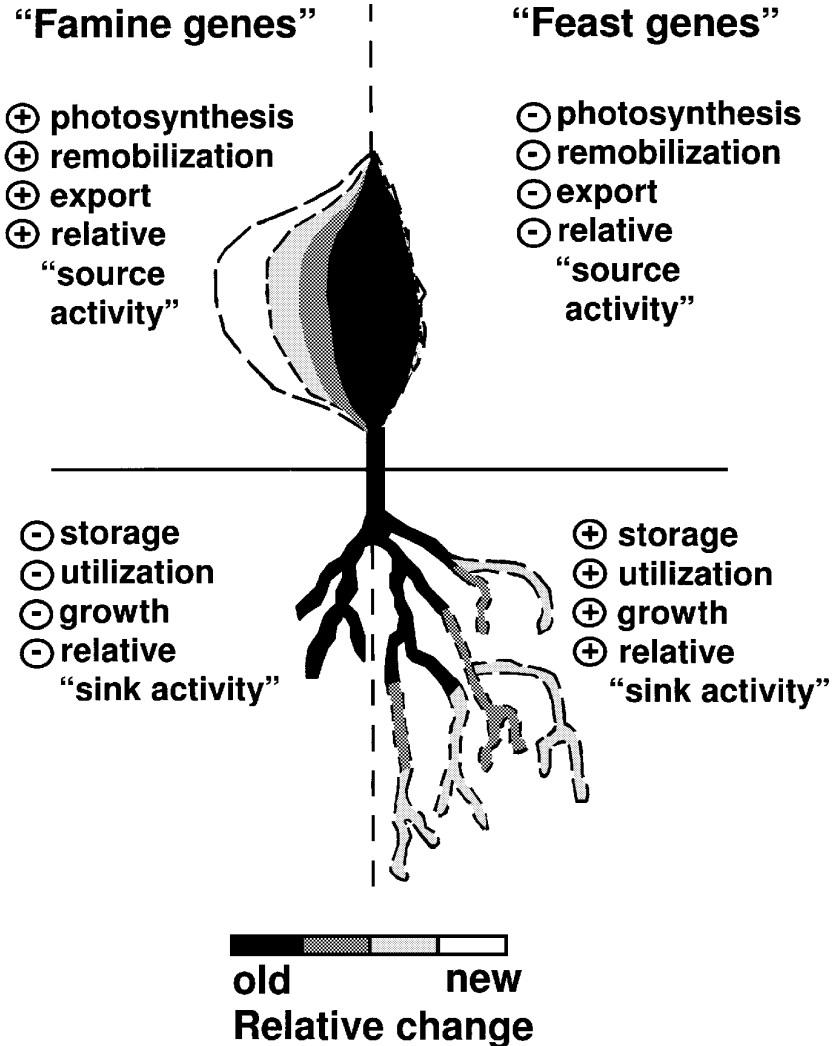


Figure 1 The impact of sugar-modulated gene expression on overall activity and resource allocation is diagrammed figuratively at the whole-plant level (changes do not necessarily represent actual morphological changes per se). “Feast” and “Famine” genes are those upregulated and downregulated under conditions of limited and abundant carbohydrate supplies, respectively, in either exporting (upper half) or importing tissues (lower half). Processes favored by these changes in gene expression are designated with a (+), and processes that are diminished are designated with a (-).

Sugar-induced changes to reproductive programs may be closely related to effects on the cell cycle. Sugar pulses to apical meristems can initiate synchronous cell divisions that precede other aspects of floral meristem differentiation (7, 97). High levels of apical sugars can also amplify photoperiod effects on floral evocation in *Lolium temulentum* and replace it fully in *Sinapis alba* (80, 137). In the latter case, concomitant with increased apical sugar levels, increases in invertase are observed in the apical meristem (137). Some invertase genes are sugar-regulated (84, 144, 210) and have the potential to enhance sugar perception by hexose sensing systems (see below). In addition, sugars supplied through roots can suppress phenotypes of early- and late-flowering mutants in dark-grown *Arabidopsis* plants (J Salinas, personal communication).

Interactions with Developmental and Environmental Signals

Effects of carbohydrate availability on fruit and seed set may mediate responses to certain environmental stresses. Studies of stress-induced kernel abortion in maize show that exogenous carbohydrate supply (11) and short-term reserves in young ovules (141) are crucial to kernel set in conditions of low water (216) or high temperature stress (17). Sugar-feeding studies have implicated the final phase of import and use of these substrates within the developing ovule as critical (11, 17; J Boyer, unpublished data). Effective sugar utilization in vivo is strongly dependent on the activity of sucrose metabolizing enzymes (21, 111, 115, 181) that are encoded by sugar-responsive genes (Tables 1 and 2; 85, 209). Soluble invertase occupies a conspicuous position during the earliest phases of fruit and seed set (181, 209), and that activity is selectively affected by abortion-inducing stresses such as low water potential (216). Although the evidence is thus far largely correlative, the sugar responsiveness of soluble invertase genes could provide a mechanism for integrating and transducing information on the C-resources available to the fertilized ovule.

Developmental signals mediated by growth regulators can have marked effects on carbohydrate-modulated genes. The nature of this interface is still poorly defined. However, work by Mullet and coworkers (29) indicates that one of two different sugar-responsive promoters they studied is sensitive to auxin/sugar antagonism. Similar response elements could explain the repression of sugar responses (179) by auxin analogs in cell cultures (178) and auxin modification of sugar effects on invertase expression at the whole-plant level (45, 148, 203). Gibberellin interaction with sugar signaling is apparent in germinating grain seeds (187, 188) and stolen starch metabolism (4). Cytokinin and sugar signals overlap in transcriptional regulation of nitrate reductase (18, 196), invertase (209), and other genes (26). They can also affect respiration

(121), the cell cycle (67, 98), auxin antagonism (112), kernel abortion (17, 71), and an array of morphological changes (112).

Interactions between environmental signals and sugar-responsive genes do not necessarily involve developmental programs. Elevated sugar supply, osmotic stress, and pathogen invasion all upregulate the *mtd* gene for mannitol metabolism and enhance synthesis of this osmotic protectant (133). Mannitol in turn imparts enhanced salt tolerance in transgenic plants (184, 185). Osmotic adjustment can also be affected by sugar-regulation of invertases (212), which could in turn sensitize cells to sugar supplies by the elevation of hexoses (161, 177). Similar to *mtd* and some other sugar-responsive genes (70), invertase is induced by wounding (178).

Recent progress has also been made in defining the interface between sugar-sensing systems and the transduction of various light signals (19). Sheen pointed out (161) that the carbohydrate-repression of photosynthetic genes supersedes many of the light effects. Chory (19) proposed that light signals are partly filtered through a sugar-regulated segment of the transduction pathway. Parks & Hangarter (128) also found that blue light effects can differ depending on tissue sugar status. The effects of sugars on photoperiodic responses were discussed above. In addition, high irradiance responses (HIR) such as anthocyanin biosynthesis in fruit skins overlap sugar effects.

Influence of essential mineral nutrients such as N (24) and P (186) on gene expression and morphology is often strongly linked to carbohydrate status (130). Several possible avenues for C/N interactions or P effects on C-signaling have thus far tested negative (175). Sadka et al (149), however, found that P availability altered sugar-regulated transcription of a carbohydrate-sensitive promoter element.

CARBOHYDRATE-SENSING SYSTEMS

Several lines of evidence indicate that sugar effects on gene expression involve specific signaling mechanisms and do not simply result from their nonspecific effects as substrates for plant growth. First, the effects of sugars on gene expression are highly selective; many genes are not affected. Second, sugars can repress as well as activate responsive genes. Third, in many cases, sugar-modulated gene expression can be mimicked by nonmetabolizable sugar analogs (69, 160, 161) and altered by selective metabolic perturbations (102, 161, 175, 182). Finally, sugars are well-known effectors of gene expression in microbes.

Microbial sugar-sensing mechanisms are an important resource for development of testable hypotheses in plants (50, 51, 69, 160). However, the emerging picture of sugar signaling in plants highlights important differences (40, 150, 192) and intriguing similarities with microbes.

Hexose Phosphorylation and Protein Kinase Cascades

An important hypothesis for sugar sensing stems from the evidence that phosphorylation of hexoses by hexokinase is a well-documented primary source of sugar signaling in yeast (161). The hexokinase itself is proposed to have a dual function as a protein kinase (40) sensitive to the flux of sugars entering metabolism. Because the rate of hexose phosphorylation is more important than the steady-state level of hexose-P produced in yeast, the concentration of hexokinase enzyme-product complex is proposed to be directly involved in signaling carbon flux through the pathway.

As in yeast, sugar concentrations per se are not necessarily correlated with changes in plant gene expression. Analysis of maize mutants with high-sugar kernels (44) and transgenic, sugar-storing potatoes (117) showed little or no change in expression of genes otherwise affected by sugars. Although compartmentalization of sugars was not addressed in these studies, the results may be interpreted as evidence that carbon flux rather than steady-state sugar level is the critical signal. The data that support a corresponding role for hexokinases in plants center largely on responses to sugars (2-deoxyglucose and mannose) that are rapidly phosphorylated by hexokinases but that do not readily undergo subsequent metabolism. Positive responses to these sugars have now been observed in several plants (50, 51, 69, 160, 161, 175). In at least one study, the effects of nonmetabolizable sugars were shown to be blocked by addition of mannoheptulose, an inhibitor of hexokinase (69). By analogy to yeast, these results are interpreted as favoring flux through the hexokinase reaction as the inductive signal (50, 51, 69, 160). Other associated perturbations have not been fully excluded, although changes in Pi levels appear to have little effect (175).

If the hexokinase hypothesis remains viable in plants, the wide variation in specificity of plant hexokinases for glucose as opposed to fructose (156) may add a fascinating layer of complexity to the regulatory scenario in plants. Recent data from yeast indicate that glucokinases do not have the same sugar-sensing impact as the hexokinases (145).

Extensive studies in yeast have also identified downstream components of a protein kinase cascade involved in transmitting signals to the nucleus (40). Putative homologs of the yeast *snf1* gene have been identified in rye (RKIN1) (1), tobacco (NPK5) (3, 118), and barley (a multigene family) (54). Nakamura and coworkers have shown that calcium levels (125) and a calcium-dependent protein kinase (CDPK) (126) may be involved in sugar induction of sporamin and β -amylase genes in transgenic tobacco. The latter finding suggests that sugar sensing in plants may be distinct from mechanisms in other systems because CDPKs appear to be lacking in other organisms (142). The localization of this CDPK on the plasmamembrane of plant cells suggest

a possible association with the sites of membrane transfer. Other recently isolated plant genes are similar to the glucose-regulated proteins (GRP) involved in secretion and ER function in mammals (28, 164). Putative sugar-sensing-related DNA binding proteins have been isolated from several plants (65, 78, 103), but as yet they have no clear relationship to components of signal transduction pathways in other organisms. The functions of these genes are under study.

Plasmamembrane Transfer

In microbes, transfer of sugars across the cell membrane is critical for sugar sensing and may be closely coupled to hexokinase action (150). In plants, the role of membrane transport has been tested using sugar analogs that are nonmetabolizable and nonphosphorylatable (as distinct from the analogs used to implicate hexokinases) but actively taken up by plant cells. Data from W Frommer (unpublished) and Roitsch et al (144) suggest that transfer across the plasmamembrane alone (or the configuration of the sugar analog per se) can initiate a signal. The studies of Jang & Sheen (69) indicate that transfer across the membrane was necessary but not sufficient to initiate a response. In plants, a direct involvement of membrane transport has the added implication that sugars entering the cell via plasmodesmata (symplastic transfer) might be perceived differently from sugars taken up from the apoplast (see Figure 2).

Depending on the tissue, sugars may enter a plant cell via any of three routes: (a) through plasmodesmata (symplastic transfer), (b) across the plasmamembrane as sucrose (from the apoplast), and/or (c) across the plasmamembrane as hexoses (again from the apoplast). As illustrated in Figure 2, each path has the potential to transmit different signals to a sugar-sensing mechanism. If plasmamembrane transfer is directly involved in signaling, then hexose uptake from the apoplast would potentially exert a greater effect per unit C than sucrose. Sucrose arriving via plasmodesmatal connections would not exert a similar membrane signal, although plasmodesmata might have an as yet undefined role in sugar sensing. Preliminary evidence indicates that altered photosynthate availability may affect size exclusion limits in plasmodesmata and promote pathway switching (i.e. extent of apoplastic vs symplastic transfer) (129, 147).

The alternative pathways by which sugars enter cellular metabolism may also impact sugar-sensing mechanisms (Figure 3). Hydrolysis of sucrose by invertase generates twice as much substrate for a hexokinase-based sensor as does sucrose synthase. Sucrose synthase, on the other hand, generates UDPG, which may feed into other signaling pathways. Vacuolar compartmentalization and hydrolysis by invertase may affect the timing of hexose-signaling events.

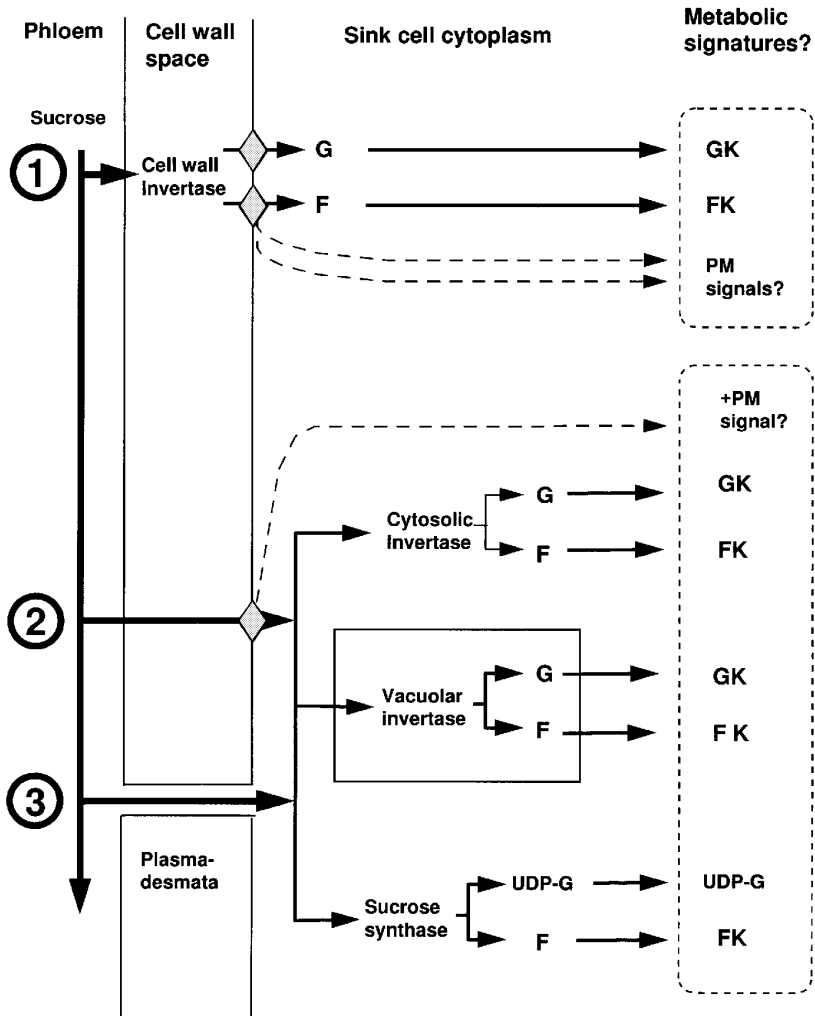
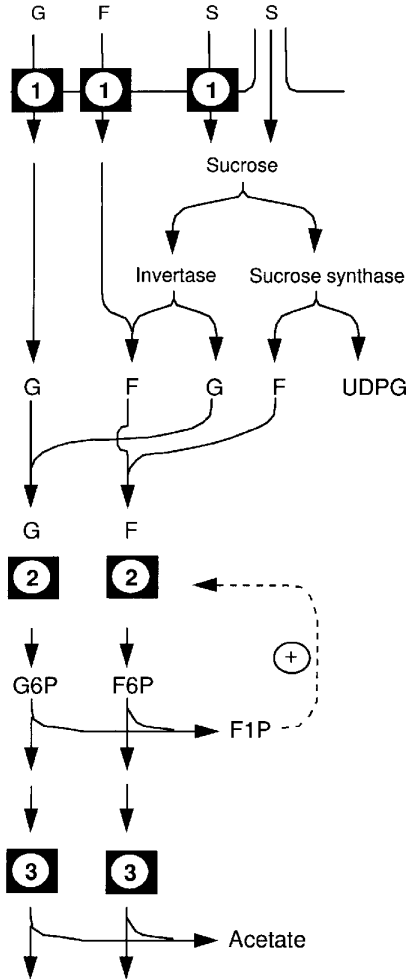


Figure 2 Potential differences in metabolic signatures of sugars entering plant cells and their relevance to the carbohydrate-sensing system. Three different physical paths of sucrose import are shown, with potential signals from plasmodesmata identified with diamonds and dashed lines. Within importing cells, potential input into the hexokinase aspect of the signaling system is designated by FK or GK. Differences in possible metabolic signatures depending on the entry path and initial sucrose cleavage reaction are shown in dashed boxes at the far right.

Carbon Flow:



*** Effectors of gene expression**

1 Plasmamembrane Signal?
(Plasmodesmata?)

2 Hexokinase Signal?
(UDPG?)

3 Acetate Signal?

Figure 3 Potential points of signal input into the carbohydrate-sensing system of plants. A simplified path of C-flow is shown at the left with corresponding sites of signal input at the right.

Key Metabolites as Direct Signals

A second source of hypotheses for sugar signaling has come from analogies to pathways for regulation of metabolism (175). The possibility that the same metabolites could mediate regulation of both metabolism and genes in these pathways would provide an attractive mechanism for coordinating rapid metabolic changes with longer-term adjustments in gene expression (34, 134, 175). However, key metabolites such as F-2,6-BP, sugar-P, adenylates, and the Pi/PPi ratio, which collectively regulate carbohydrate metabolism, appear to have little or no direct involvement in sugar regulation of gene expression in the systems studied thus far (161, 175). Levels of F-2,6-BP have been altered using inhibitors and in transgenic plants expressing an antisense gene for PPI-dependent phosphofructokinase without affecting carbohydrate-responsive genes (175; A Krapp and M Stitt, unpublished data). Likewise, various manipulations of Pi levels altered metabolism in predictable ways but did not change expression of sugar-modulated genes (175). Introduction of various phosphorylated sugars, adenylated sugars, and ATP into cells by electroporation failed to affect sugar-responsive genes (161).

Although sugar levels can vary widely in plants, maintenance of “energy homeostasis” is one proposed function of carbohydrate-regulated gene expression (69). The search for a link between respiratory metabolism and gene expression continues. One possible link to a mitochondrial function involves its role as a calcium reservoir sensitive to changes in respiratory substrates (72). Changes in redox potential are also a possibility, as observed for chloroplast mRNAs (28a). Adenylate balance may also be involved through an influence on a hexokinase-based sensing mechanism. In this respect, it seems not widely appreciated that the concentration of enzyme-product complex will be directly proportional to the net forward flux through the reaction only under initial velocity conditions, and these conditions are not likely to apply *in vivo*. Nearer to equilibrium, the intermediate enzyme complexes will be affected by concentrations of all substrates and products including hexose, hexose-P, ADP, and ATP. It might be more accurate to view yeast hexokinase as a sensor of some ratio of these metabolites rather than flux *per se*.

The profound effects of acetate on yeast and algal cultures are well known (9, 93, 172), yet the significance of this metabolite to higher plants has been explored only recently in leaf protoplasts (160) and intact cotyledons (50, 51). Acetate appears to be the strongest input into the carbohydrate-sensing system of maize leaf protoplasts (160). It is not clear whether there are points of overlap between this signal and sugar inputs. Signal initiation from these two metabolites appears to occur differently. In this context, it is also intriguing that lipid acyl hydrolases have been recruited as carbohydrate-responsive storage proteins in potato (52, 202).

CLOSING COMMENTS

In multicellular organisms, carbohydrate-responsive gene expression acquires a functional significance beyond that observed in microorganisms. As in yeast and bacteria, specific groups of genes show dramatically different responses to changes in the carbohydrate environment and include both up- and downregulation of gene expression. In multicellular structures, however, individual cells respond to changes in the internal carbohydrate environment of the organism, thus allowing coordinated long-term adjustments for the benefit of the whole.

Plants in particular appear to have successfully employed this mechanism for meeting the adaptive demands of their sessile existence. The sites, timing, and extent of sugar-modulated gene expression described here indicate that these processes may contribute to the dynamic allocation of carbon resources and the continuous adaptive adjustment of form so characteristic of multicellular plants. Sugars in vascular plants are thus long-distance messengers of whole-organism carbohydrate status as well as substrates for both cellular metabolism and local carbohydrate-sensing systems. Although the primary source of carbohydrate signals is currently unclear, hexokinase action and acetate levels remain a common theme shared by mammalian and microorganism sensing systems. The pathways for transduction of sugar signals overlap with other environmental and developmental signals affecting gene expression.

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