Source–Sink Relationships

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The term source–sink relationship refers to the integration of suger and amino acid production in photosynthesis with sugar and amino acid utlisation in growth, storage, maintenance and production.

Introduction

Plants, in contrast to animals, consist of autotrophic organs that produce sugars and amino acids from photosynthesis, and heterotrophic organs that consume these products in growth, storage and reproduction. These metabolically contrasting parts of the plant are often referred to as source and sink tissues, respectively. Source tissues are net exporters of assimilate. These are principally mature green leaves, green stems and green seed pods, but also nonphotosynthetic tissues such as germinating seeds, tubers, tap roots, etc. (**Figure 1**). Photosynthesis, either directly or indirectly, provides the building blocks for all biomass production as well as sink development and growth. Sink tissues are net importers of assimilate and consist of organs that are rapidly growing such as meristems and immature leaves and vegetative storage tissues such as tubers, seeds or roots. Source and sink metabolism are tightly coupled because information on assimilate availability in each organ is perceived and used to orchestrate gene expression. This coordination is necessary to avoid large fluctuations and imbalances between supply and demand, which would lead to a 'feast and famine' scenario. The metabolic and molecular mechanisms that facilitate this coordination are key determinants of plant productivity, dominating plant responses to environmental change and the efficiency with which resources, such as fertilizers, are used.

All biomass production depends on photosynthesis. Crop yield is hence related to net whole plant photosynthesis over the growing season. Producers of glasshouse crops have long used carbon dioxide enrichment to stimulate photosynthesis and improve yield. However, single time-point measurements of photosynthesis reveal little concerning biomass production and breeding programmes using selection for high photosynthetic rates have generally failed to achieve yield increases. This is because yield is not only determined by the availability of assimilate, but also by the way it is partitioned throughout the plant. Put most simply, plant dry matter production is determined by the balance between photosynthesis and respiration. Although light and carbon dioxide availability are key limiting factors the growth of sinks is also crucial in determining plant growth. Low sink demand can lead to assimilate accumulation in source leaves. This causes decreased expression of genes coding for photosynthetic components and results in a lowering of photosynthetic capacity. Hence, the capacity of the sink can regulate the activity of the source.

The Transition from Sink to Source

Plant hormones and other signals such as the availability of sugars, integrate growth responses among roots, stems and leaves. The development of these organs is highly dependent on environmental cues that act via sensory systems to regulate metabolic reactions controlling the growth of individual cells. The quantity and quality of light and the availability of water are particularly important influences on leaf development and expansion. Leaves expand to intercept light and carbon dioxide for photosynthesis and to transpire water for cooling and circulation of nutrients. Leaf expansion is required for cell division and development of the meristematic tissues. It is an integrating behaviour that ultimately determines canopy development and function. The transition from sink to source that accompanies this development determines whole plant partitioning of assimilates, which influences the relative shoot : root ratio and controls the onset of reproduction.

The transition from a sink to a source leaf requires the acquisition of functional photosynthetic machinery, changes in the enzymes of carbohydrate metabolism and associated changes in import/export behaviour. As leaves emerge, exposure to light induces expression of genes coding for components of the photosynthetic apparatus.

Figure 1 Sources and sinks: (a) wheat grains; (b) sunflower seeds; (c) sugar beet plant with storage root; (d) potato plant with tubers.

The expression of these genes is generally repressed by high sugar concentrations but young leaves, apart from the first emerging leaves, are not strong sinks. Sugar import into developing leaves starts to decline early in development, generally falling to zero long before maximal photosynthetic capacity is attained. Maximal photosynthetic capacity occurs either before or at the time of full leaf expansion.

The developing green leaf undergoes massive metabolic reorientation in order to switch from import to sucrose export. As in other sink tissues, young leaves depend on imported sucrose to provide energy to drive metabolism and carbon skeletons for metabolic interconversions and biosynthetic processes. Sucrose import from the phloem is driven by a gradient of sucrose, controlled by sucrose utilization. Imported sucrose is cleaved to hexoses by the action of either invertase or sucrose synthase (SS), depending on species (**Figure 2**). During the transition to source activity these enzymes decline while the pathway of sucrose synthesis increases. The activity of the penultimate enzyme of sucrose synthesis, sucrose phosphate synthetase

(SPS), increases proportionally with photosynthesis, while the capacity and rate of sucrose export is correlated with SPS activity. Large changes in the relative activities of invertase, SS and SPS are early events in the transition from net sucrose import to sucrose export. Indeed, the ratio of SS to SPS can often be used as an indicator of the sink to source transition.

Unlike animals, which use glucose as a transport sugar, plants transport sucrose. We can only speculate as to the reason for this difference in preference. Oligosaccharides and sugar alcohols, such as stachyose, fulfil a similar role in some species. Sucrose is exported from the photosynthetic mesophyll cells in mature leaves to the sieve elements of the phloem for transport to the growing or storage sinks. This process is called phloem loading and it occurs by symplastic and apoplastic routes (**Figure 3**). Plant species may be classified into groups as follows:

- type (1), largely symplastic loading facilitated by large numbers of plasmodesmata that connect neighbouring cells;
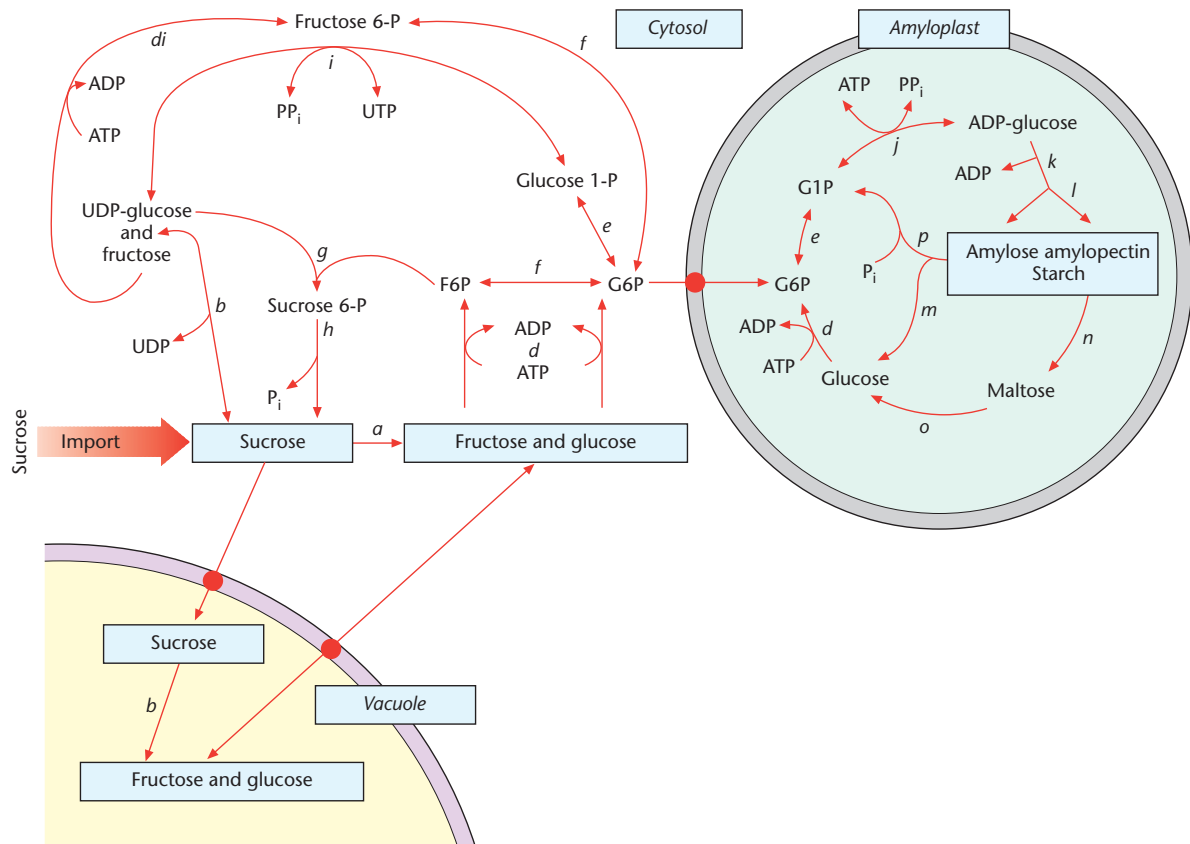
Figure 2 Carbohydrate metabolism in sink cells. Enzymes: *a*, alkaline invertase; *b*, sucrose synthase; *c*, acid invertase; *d*, hexokinase (includes glucokinase and fructokinase); *d*, fructokinase; *e*, phosphoglucomutase; *f*, phosphoglucose isomerase; *g*, sucrose-phosphate synthase; *h*, sucrose-phosphate phosphatase; *i*, UDP-glucose pyrophosphorylase; *j*, ADP-glucose pyrophosphorylase; *k*, starch synthase, *l*, starch-branching enzyme; *m*, α-amylase; *n*, β-amylase; *o*, α-glucosidase; *p*, starch phosphorylase.
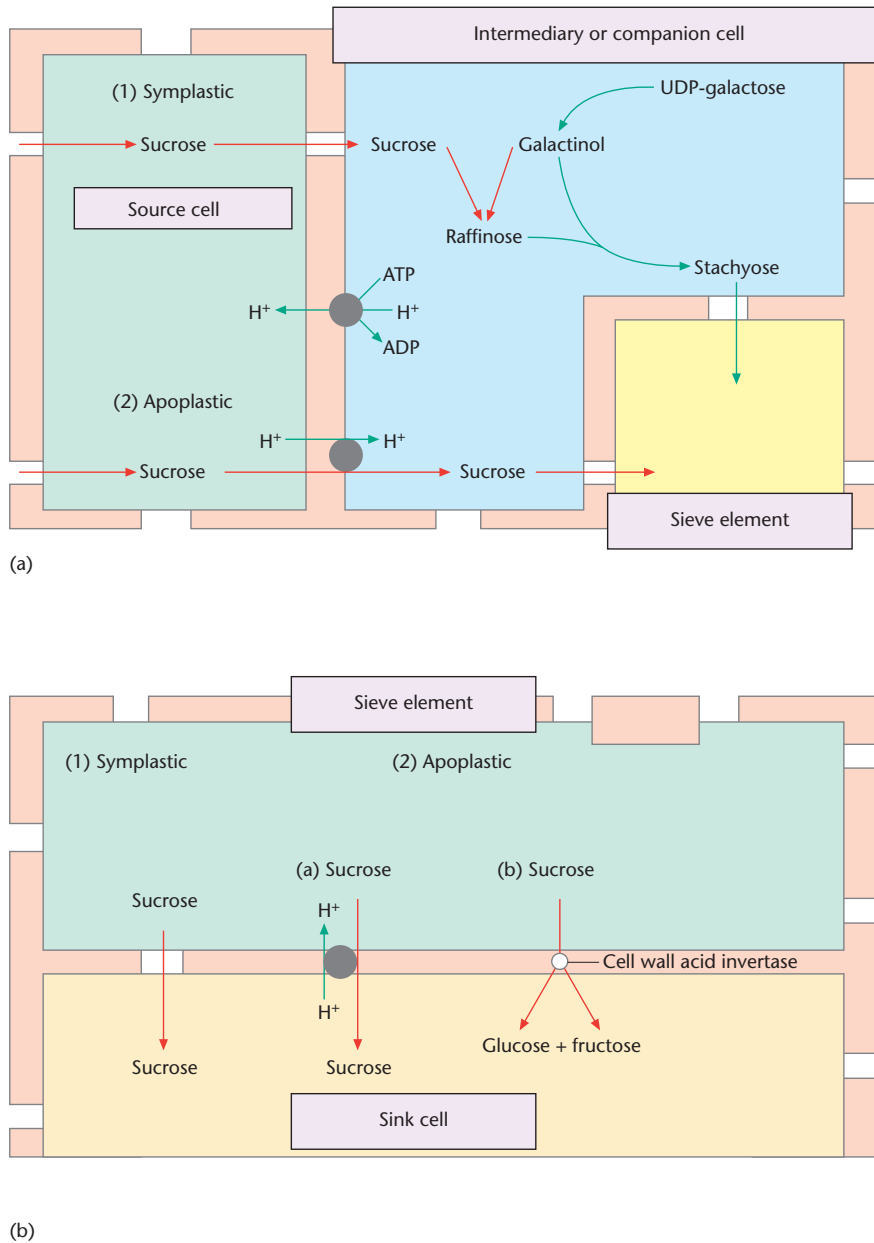
Figure 3 Phloem loading and unloading. (a) Pathways of phloem loading. (b) Pathways of phloem unloading.

- type (2a), symplastic, but including an apoplastic step;
- type (2b) as in (2a), but involving specialized transfer cells with highly invaginated cell walls;
- type (2c), as in type (2a) but with Kranz anatomy.

Apoplastic mechanisms require the participation of specialized sucrose transport proteins that carry sucrose across the cell membranes.

Sink Metabolism

The amount of starch produced and stored in leaves is species dependent. Most cereals store very little starch in their leaves, while other species such as snowdrop conserve most of the assimilate produced during the day in the leaves as starch. In general, over and above this genetic predisposition, leaves tend to synthesize and export sucrose early in the day. When the capacity for photo-

synthesis exceeds that of sucrose synthesis and export, excess assimilate is retained in the chloroplast and stored as starch in the light. In the subsequent dark period starch is degraded and the products of starch breakdown used for sucrose synthesis and export. Sufficient assimilate is stored in the leaves during the day to provide a constant supply of sucrose in the subsequent night, thus avoiding large diurnal fluctuations between supply from the source leaves.

Sugars and amino acids are transported through the phloem, the flow of sap through the sieve tubes being driven by a pressure gradient. The loading of osmotically active carbohydrates and amino acids at the source and the simultaneous unloading at the sink are the major contributors to the gradient. As in phloem loading, there are multiple paths of unloading that involve symplastic unloading, apoplastic unloading or combinations of the two. As with sink leaves, carbohydrate imported into other sinks is metabolized by either SS or invertase (**Figure 2**). Energy conservation considerations favour sucrose synthase rather than invertase in sucrose catabolism. Sucrose is a source of energy as well as carbon skeletons for biosynthetic purposes such as conversion to starch or other storage compounds. Unlike invertase, which converts sucrose to glucose and fructose, SS conserves energy in the form of UDP-glucose. However, SS catalyses a reversible reaction while the reaction catalysed by invertase is essentially irreversible. Invertase therefore acts as a much more powerful trap for sucrose. Recent evidence suggests that SS and invertase fulfil different roles in sink tissues. They are located in different compartments of sink cells. While SS is located in the cytosol, invertase is predominantly found in the vacuole and apoplast. Antisense technologies have shown that SS participates in the control of sucrose import and sink strength. This enzyme is therefore important in establishing processes such as fruit set and development. In general invertase is not as important as SS in determining sink strength but it may be important in ensuring that sucrose entering the vacuole is stored as hexoses. Hexoses are also key signal-transducing molecules, as discussed later.

## Regulation of Source–Sink Relationships in Photosynthetic Cells

Concepts of control within individual cells are also based on producer (source)–consumer (sink) relationships. In the case of the phosphorylating electron transport chains of the chloroplasts and mitochondria this control involves feedback effects of the high-energy state (the proton gradient across the membrane) on the rate of electron transfer. Photosynthesis and respiration each require the coordination of two discrete, spatially separated reaction sequences. In the chloroplast these are the electron transport processes occurring in the thylakoid membranes

(**Figure 4a**) and the reductive pentose phosphate cycle (also called the Calvin or Benson–Calvin cycle), which is housed in the chloroplast stroma (**Figure 4b**). The former comprises two photosystems operating sequentially to achieve light-driven reduction of $NADP^+$ with concomitant production of a proton gradient, which is used to generate ATP. NAPDH and ATP thus produced are consumed during the assimilation and reduction of carbon dioxide to the level of sugar phosphate and the reduction of nitrate to ammonium and its subsequent incorporation into amino acids. The producer–consumer relationship between electron transport and the assimilation of carbon and nitrogen ensures their tight coupling by virtue of the cycling of intermediates. Other associated reactions involve the supply of carbon skeletons for amino acid biosynthesis and require the participation of reactions in the cytosol and mitochondria. High ATP/ADP and NADPH/NADP favour high rates of carbon dioxide reduction but they hinder high rates of electron transport. Coordinate regulation reconciles these conflicting requirements of the thylakoid and stromal reactions. Several regulatory mechanisms are involved in the modulation of Calvin cycle enzymes to match their activities to the availability of the products of electron transport. As well as providing the assimilatory force that drives the cycle, light also activates component enzymes through alkalinization and an increase in free Mg^{2+} in the chloroplast stroma, and through the transfer of reducing equivalents from ferredoxin (Fd) to thioredoxin, which activates enzymes through thiol-disulfide exchange reactions.

Chloroplasts and mitochondria do not function in isolation; their reactions are integrated into the metabolic processes of photosynthetic cells. This is necessary to provide a flexible supply of energy and carbon skeleton sources for end-product synthesis that is essential to avoid detrimental effects of light (principally photoinhibition and photooxidation) in a hazardous and constantly changing environment. Furthermore, the coordination of reaction rates in each compartment of the cell prevents continuous oscillations in metabolite flux and allows optimization of resource use.

Surviving Environmental Change

The sessile nature of plants means that, unlike animals, they are unable to take refuge from adverse conditions. The wide range of environmental variables has driven the evolution of a complex network of acclimatory mechanisms that attempt to optimize resource use. Some environmental factors change dramatically in the course of a few seconds; others fluctuate in minutes, hours, days, or even, in the case of climate change, years. The amount of light a leaf receives, for example, may vary by three orders of magnitude between dawn and midday and by one order of
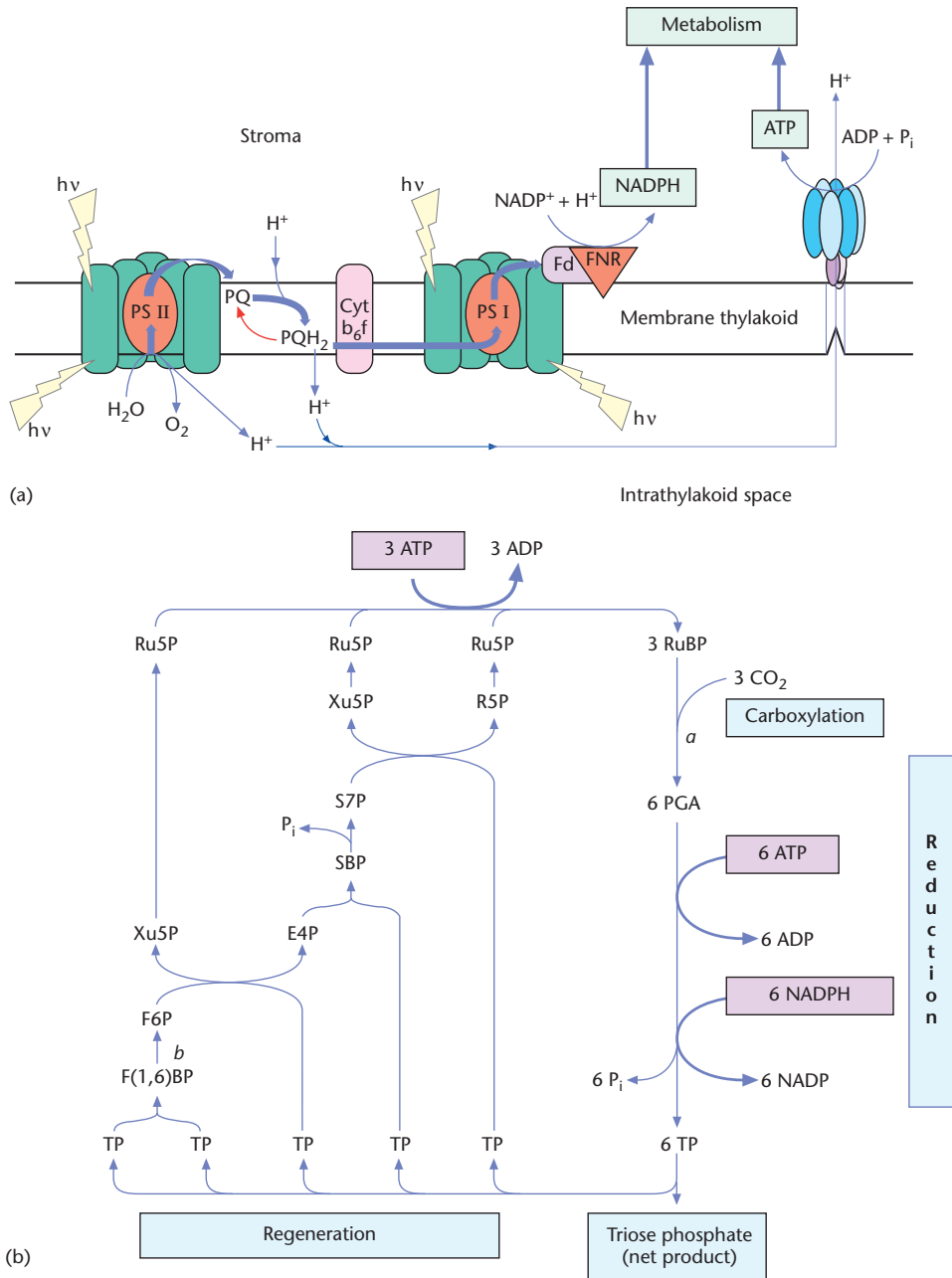
Figure 4 Photosynthesis. (a) Photosynthetic electron transport. (b) Photosynthetic carbon assimilation pathway (the Calvin cycle). Enzymes: *a*, ribulose-1,5-bisphosphate carboxylase/oxygenase; *b*, fructose-1,6-bisphosphatase. E4P, erythrose 4-phosphate; Fd, ferredoxin; FNR, ferredoxin-NADP reductase; F6P, fructose 6-phosphate; PQ, plastoquinone; R5P, ribose 5-phosphate; S7P, sedoheptulose 7-phosphate; SBP, sucrose bisphosphate; TP, triose phosphate; Xu5P, xylulose 5-phosphate.

magnitude within a few seconds as the sun passes in and out of cloud cover. Temperature can change within minutes and nutrient and water supply over hours and days. Over a longer time scale carbon dioxide levels in the atmosphere are rising by 1.5 ppm per year. The agricultural environment is more constant in that nutrients and water are supplied during the growing season in the form of fertilizer and irrigation, and weed control and spacing of crops ensure that there is less competition for resources. Nevertheless, we can probably make the general assertion that the metabolic machinery of plants possesses greater flexibility than that of animals.

# Short-term Regulation of Metabolism Balances Reactions of Photosynthesis with Carbohydrate Synthesis

In C_3 plants the Calvin cycle is the entry point for carbon dioxide from the atmosphere into plant metabolism. Photosynthesis in air is poised between a limitation by Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) activity and a limitation by the rate of production of the substrate for this reaction, ribulose-1,5-bisphosphate (RuBP). When carbon dioxide is scarce, photosynthesis is limited by the carboxylation rate and hence the activity of Rubisco. At high carbon dioxide levels and saturating light, photosynthesis is limited by the rate of production of ATP and NADPH in light-driven electron transport since this determines the rate of RuBP regeneration. ATP synthesis may also be restricted by the availability of inorganic phosphate, P_i. The P_i required for ATP synthesis is recycled from triose phosphates during the synthesis of sucrose and starch (**Figure 5**).

The product of photosynthesis in the chloroplast is triose phosphate. This is either retained temporarily in the chloroplast to produce starch or it is exported to the cytosol in exchange for P_i. In the cytosol, triose phosphate

is either used for synthesis of sucrose or to provide carbon skeletons for other reactions such as amino acid synthesis. Sucrose synthesis liberates P_i, which is returned to the chloroplast in exchange for more triose phosphate. In this way the processes of photosynthesis and sucrose synthesis are coordinated.

In general, either light and/or the availability of carbon dioxide limit photosynthesis. If these limitations are overcome, then the rate of photosynthesis is largely determined by the capacity of sucrose synthesis to regenerate P_i. In the short term, rapid regulation is achieved through the posttranslational control of enzyme activities. A predominant mechanism in this type of regulation is protein phosphorylation. Several key enzymes such as SPS, nitrate reductase (NR) (the first step of nitrate assimilation) and phosphoenolpyruvate (PEP) carboxylase (the first enzyme of the anapleurotic pathway) all undergo reversible changes in activation state mediated by changes in the phosphorylation of the enzyme protein.

Coordination of end-product synthesis with the rate of photosynthesis is essential. If triose phosphate is withdrawn from the Calvin cycle too quickly, photosynthesis is inhibited because Calvin cycle intermediates are depleted and RuBP cannot be regenerated. If they are withdrawn too slowly, photosynthesis will be inhibited because
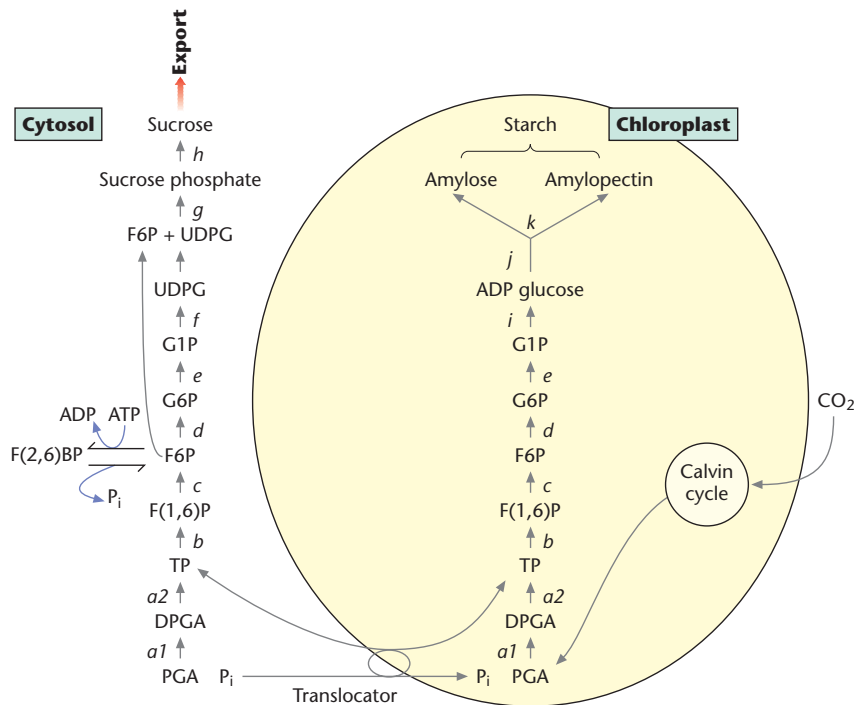

Figure 5 Pathways to sucrose and starch synthesis in source leaves. Enzymes: *a1*, phosphoglycerate kinase; *a2*, NAD(P)-glyceraldehyde 3-phosphate dehydrogenase; *b*, aldolase; *c*, fructose-1,6-bisphosphatase; *d*, hexose phosphate isomerase; *e*, phosphoglucomutase; *f*, UDP-glucose pyrophosphorylase; *g*, sucrose phosphate synthase; *h*, sucrose phosphatase; *i*, ADP-glucose pyrophosphorylase; *j*, starch synthase; *k*, starch-branching enzyme; DPGA, 1,3-bisphosphoglycerate; F6P, fructose 6-phosphate; G1P, glucose 1-phosphate; G6P, glucose 6-phosphate; PGA, 3-phosphoglycerate; UDPG, UDP-glucose.

phosphorylated intermediates accumulate in the Calvin cycle and P_i is depleted. Control of sucrose synthesis is achieved at two key regulatory steps, through cytosolic fructose-1,6-bisphosphatase (FBPase) and SPS. Enhanced rates of photosynthesis stimulate cytosolic FBPase by decreasing the concentration of the inhibitory metabolite fructose-2,6-bisphosphate (F(2,6)BP) and activating of SPS by dephosphorylation of the enzyme protein. There is a threshold concentration of triose phosphate below which sucrose synthesis is inhibited, preventing depletion of the triose phosphate pool and inhibition of Calvin cycle turnover. When triose phosphates rise above a threshold there is a strong activation of sucrose synthesis. This minimizes the risk that phosphorylated intermediates accumulate to the point where photosynthesis becomes P_i-limited. As sucrose begins to accumulate in the leaf, SPS deactivates and F(2,6)BP increases. As a result, export from the chloroplast decreases and starch synthesis increases.

The Coordination of Carbon Dioxide and Nitrate Assimilation in Photosynthetic Cells

Nitrate is the major source of nitrogen for most plants, at least in agricultural environments. It is taken up from the soil and is reduced and assimilated into amino acids in either roots or shoots (**Figure 6**). In higher plants the reductive assimilation of nitrogen differs from that of carbon in that it can occur in the dark or in heterotrophic tissues. In this case reductant is supplied by reoxidation of carbon through respiration. Photosynthesis is dependent on nitrogen assimilation as this process provides the building blocks for the synthesis of the proteins and pigments that comprise the photosynthetic machinery. Conversely, nitrogen assimilation requires a continuous supply of energy and carbon skeletons that are produced by photosynthesis (**Figure 6**). Carbon skeletons and energy must be partitioned between carbohydrate synthesis and the synthesis of amino acids in such a way as to prevent competition. Regulation of this partitioning must be flexible since both external nitrogen supply and internal demand for nitrogen may be variable. Decreases in carbon dioxide assimilation are accompanied by decreased rates of nitrate assimilation. This is achieved by rapid inhibition of the first enzyme of the pathway, NR, by phosphorylation of the NR protein, which allows binding of a protein inhibitor. Similar mechanisms also operate in response to changes in nitrate supply. Addition of nitrate leads to activation of PEP carboxylase and inhibition of starch synthesis that facilitates provision of carbon skeletons for amino acid synthesis. Increased nitrogen supply also inactivates SPS. In addition to these short-term regulatory
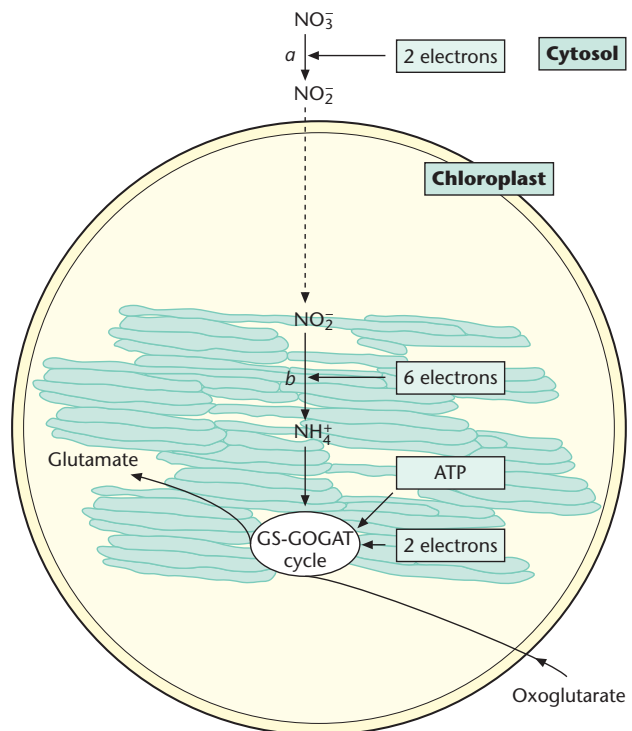
Figure 6 Reductive assimilation of nitrate in photosynthetic cells. Enzymes: *a*, nitrate reductase (NR); *b*, nitrite reductase; GS-GOGAT, glutamine synthetase-glutamate synthetase.

mechanisms, long-term acclimation to changes in nitrate supply are brought about by changes in gene expression.

Carbon and nitrogen compounds not only provide energy and the building blocks for biomass production but are also involved in the regulation of gene expression in both source and sink tissues. This regulation allows the integration of source and sink activities. Metabolic cross-talk between the pathways of carbon and nitrogen assimilation requires the concerted action of a repertoire of signals that allow graded molecular and physiological responses to provide sugars and amino acids in appropriate stoichiometries for growth, development and reproduction. The expression of genes encoding components involved in photosynthesis, carbohydrate biosynthesis, nitrate uptake and assimilation, as well as amino acid biosynthesis, are regulated by sugars, nitrate and amino acids. Carbohydrate accumulation in leaves, for example, decreases the expression of the genes encoding the subunits of the Rubisco protein. Nitrate reductase activity is increased as the expression of the gene coding for NR is increased by sugars. In a similar manner the expression of ADP-glucose pyrophosphorylase, a key enzyme of starch biosynthesis, is increased when the availability of nitrate is low and decreased as the nitrate supply is increased. Increased carbohydrate availability also favours higher

respiratory rates and increases carbon flow through the anapleurotic pathway (**Figure 7**).

Nitrate enhances the expression of nitrate transporter genes and those of enzymes involved in metabolizing nitrogen, particularly NR, nitrite reductase, glutamine synthetase and glutamate synthase. There are also major changes in carbon metabolism, to provide synthesis of carbon skeletons for amino acid synthesis. This involves the mobilization of starch reserves and organic acid synthesis to provide the carbon skeletons. Whole plant allocation and development are also modified by nitrate. Heterogeneous distribution of nitrate within the soil results in local stimulation of lateral root growth, whereas a more uniform abundance results in a stimulation of shoot growth and general inhibition of root growth. Plants growing on abundant nitrogen are able to devote these resources to maximize carbon acquisition and to produce large green leaves with high photosynthetic capacity. Under such conditions plants may have the luxury of investment of large amounts of nitrogen in Rubisco. In turn, the amino acids produced by the assimilation of

nitrate repress the expression of the genes encoding the enzymes of the pathway such as NR.

The Regulation of Gene Expression by Carbon and Nitrogen Metabolites is a Pivotal and Universal Mechanism for Coordination of Pathways in Source and Sink Tissues of Higher Plants

Carbon metabolites, principally sugars (such as glucose and fructose), regulate the expression of a wide range of plant genes. When sugars accumulate, genes for metabolism and storage of carbon are induced while those for photosynthesis and mobilization of stored reserves are repressed. Nitrogen deficiency results in carbohydrate accumulation in leaves. Resources are switched away from high photosynthesis towards acquisition of nitrogen and storage of carbohydrate. Genes involved in photosynthesis
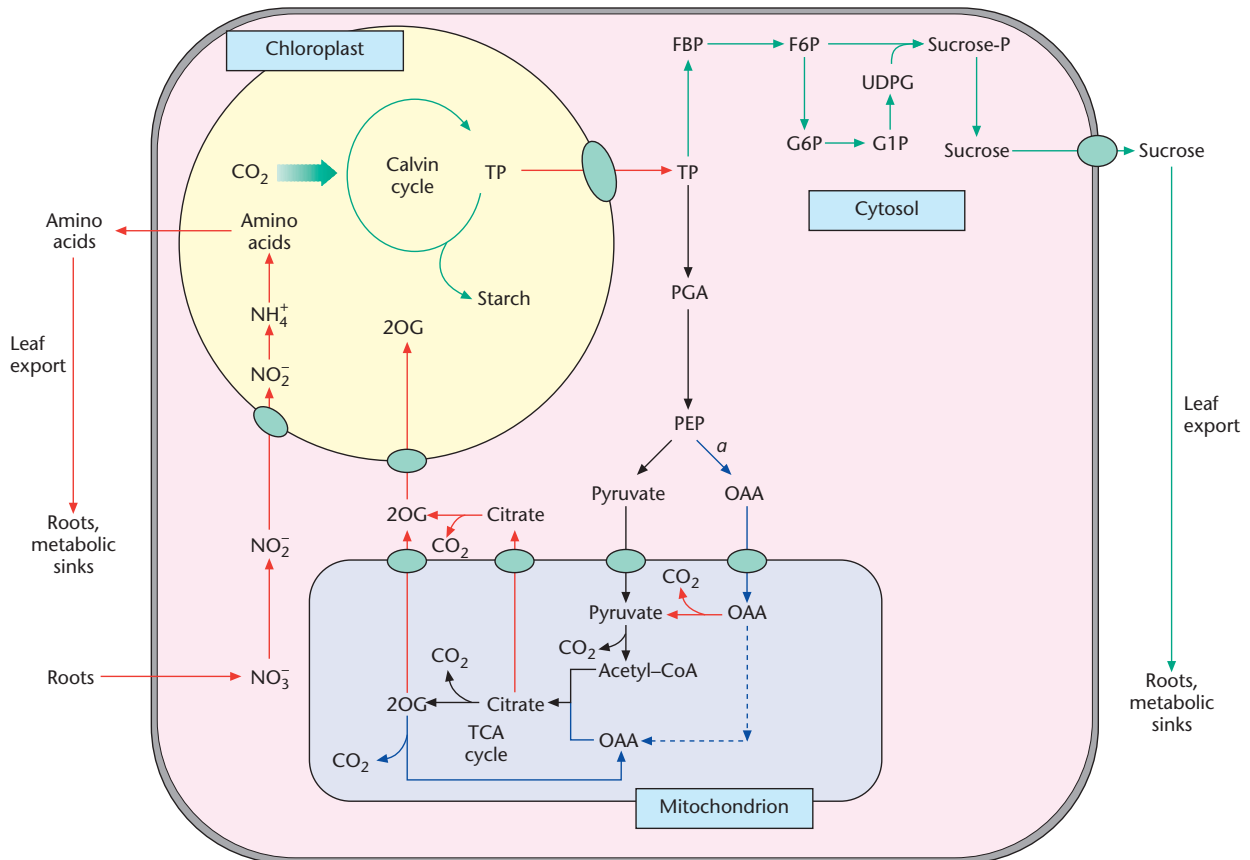
Figure 7 Integration of photosynthetic carbon and nitrogen assimilation in photosynthetic cells. The pathway of nitrogen assimilation is marked by red arrows, carbon respiratory flow by black arrows, carbon assimilation and carbohydrate production by green arrows, and the anapleurotic pathway by blue arrows. Enzyme *a*, phosphoenolpyruvate carboxylase; OAA, oxaloacetate; 2OG, 2-oxoglutarate.

and mobilization of carbohydrate and fat reserves are repressed. Root growth is stimulated. Carbohydrates induce genes for nitrogen assimilation and for the synthesis of starch and, in some species, other polysaccharides such as fructan. The mechanism of sugar-mediated repression of photosynthesis has received much recent attention because carbon dioxide is accumulating in the atmosphere at a faster rate than at any other time in history. Carbon dioxide enrichment results in enhanced photosynthesis and carbohydrate synthesis in the short term, but can cause a decline in the rate of photosynthesis in the long term, particularly if nitrogen is limiting. Carbohydrate repression of photosynthesis serves to resolve a carbon : nitrogen imbalance in this situation. Sugar repression of photosynthesis may only occur when there is an adaptive advantage in releasing nitrogen reserves from Rubisco and the photosynthetic apparatus.

Several different sugar-sensing systems appear to operate in plants (**Figure 8**). The best characterized, although not yet unequivocal, sugar-sensing mechanism requires a flow of carbon through the enzyme hexokinase. Other systems involve a hexose-transport-associated sensor and a sucrose-specific pathway, which may involve a signalling sucrose transporter. The hexokinase-mediated sugar-sensing pathway operates in both source and sink tissues. It regulates feedback inhibition of photosynthesis associated with carbohydrate accumulation in leaves, and also the induction of other genes such as NR. Sugar availability, signalling fat mobilization in early seedling growth by stimulation of the glyoxylate cycle, may involve hexokinase signalling. Hexose sensing is associated with the secretory Golgi endomembrane system in cells that distribute the products of biosynthetic reactions. Hexokinase signalling may therefore result from hexose import

into the cytosol. Hexose transport rather than hexose concentration may be sensed. Potential intermediary steps in the signal transduction cascades that lead to modulation of gene expression include protein phosphorylation–dephosphorylation changes, Ca^{2+} and calmodulin. In particular, a family of protein-serine/threonine kinases (including sucrose nonfermenting-1-related protein (SNF1) kinase) have been shown to be involved in the sensing of sucrose and sugar-mediated regulation of gene expression.

The disaccharide trehalose may also be involved in other steps of the pathway. With one exception (*Myrothamnus flabellifolius*) trehalose does not accumulate in angiosperms because of high activities of the enzyme trehalase that break down trehalose. However, the precursor of trehalose, trehalose 6-phosphate, is present in plants and inhibits hexokinase and hence has a possible sugar-sensing role. In addition to modulating sugar sensing it is also possible that regulation of hexokinase impacts on carbon flow and partitioning directly. Further, there is now compelling evidence that two plant hormones, abscisic acid (ABA) and cytokinin, are involved in coordinating source and sink activities. While ABA metabolism is implicated in sugar sensing, cytokinins are involved in the carbon : nitrogen balance of organs. Cytokinins are transported from roots to the shoot in the presence of nitrogen and are able to trigger re-greening of chlorotic shoots.

Limits to Biomass Production: Perspectives for Agriculture

Up until now increases in crop yield have been achieved through improved crop husbandry, fertilizers, pesticides and breeding. Breeding for yield of most crops has resulted in a change in the partitioning of biomass from non-harvestable parts to the harvested product, for example from stems to ears in cereals. Overall biomass has remained unchanged. The limit to which this improvement in harvest index can be extended has been reached for most crops and further increases in crop yield now depend on increasing overall biomass production. The need for innovative agriculture is real and perhaps has never been more urgent because the population of the world continues to increase and virtually all land suitable for agriculture is already under cultivation. Fortunately, increasing crop yield remains a realistic goal for plant breeding because of the application of the new biotechnologies.

The general positive response of crops to high carbon dioxide in terms of photosynthesis and yield adds further weight to the hypothesis that increasing photosynthesis, particularly in unfavourable environmental conditions, will improve yield. Plant growth and productivity is, however, not only determined by photosynthetic capacity,
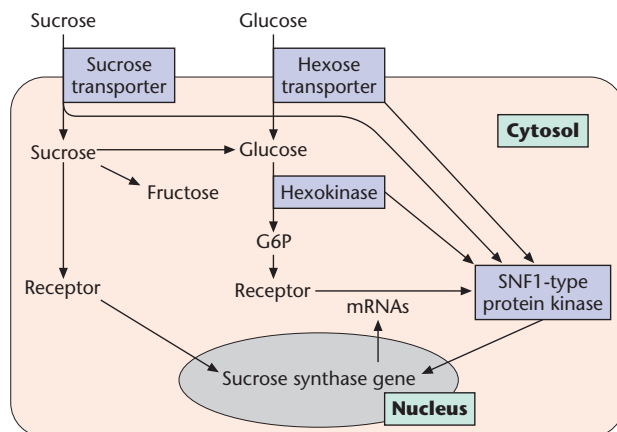
Figure 8 Sugar sensing leading to the expression of sucrose synthase. The predominant sugar transported is sucrose. Sucrose or hexoses (produced by sucrose hydrolysis) may be sensed. A sucrose nonfermenting-one-related protein kinase (SNF1) is required for sugar-induced expression of the sucrose synthase gene.

but also by the way in which the products of photosynthesis are allocated and utilized during plant growth and development. Plants possess sophisticated and complex mechanisms to enable adjustment of source and sink activity over the short and long term. Targeted changes in the amounts of proteins and activities of enzymes has been shown to redirect resources. At present, despite some successes, the plasticity of plant metabolism often leads to compensatory changes that negate the effect of the modification and restore the original pattern or home-ostasis. A rather different and potentially much more far-reaching and rewarding approach to manipulating plant metabolism and productivity is required. As discussed above, whole plant metabolism is orchestrated through regulated changes in gene expression by proteins that sense carbohydrates and amino acids. Thus, major features of plant growth and development can potentially be modified in a concerted way by changing the activity of individual signal transduction components.

Current knowledge of the mechanisms whereby meta-bolic regulation is achieved in the short term is relatively comprehensive. In contrast, relatively little is known about the components of the sensing and signal transduction pathways that mediate carbohydrate regulation of gene expression in source and sink organs. A detailed under-standing of these longer-term acclimatory control mechan-isms will allow control of carbohydrate production, utilization and plant yield. Hence, the sustainability of crop quality and yield can be improved. In recent years the application of genetic manipulation techniques has led to a dramatic increase in our understanding of plant metabo-lism. On this basis, strategies for manipulating plant metabolism may be formulated. These may represent the only real means of significantly improving crop production to feed the increasing population worldwide.

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