

Source-sink relationships

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SOURCE-SINK RELATIONSHIPS

Abstract

Life on earth depends on the growth and survival of plants. In order for plants to grow and develop effectively, coordination between sources and sinks is required. Source organs provide a net uptake of resources whilst sink organs have a net drawdown of resources. Molecular mechanisms regulate the relationship between sources and sinks. These molecular mechanisms include carbon- and nitrogen-containing metabolites, plant hormones, and genes. Sources and sinks for both carbon and nitrogen are key contributors to plant growth, and these regulate themselves and one another *via* feedback, feedforward, and crosstalk mechanisms. Our understanding of the relationships between sources and sinks is increased by experimental manipulations of the source-sink balance. To bring about increases in crop growth and yield, a holistic view of sources and sinks must be developed, including the molecular mechanisms underpinning the relationships between them. Mathematical modelling can be an effective tool for providing this unified perspective.

Key words

Carbon, Growth, Nitrogen, Phytohormone, Signalling, Sink, Source

Key concepts

Sources have net uptake of a resource and sinks have net utilisation of a resource.

Plant growth is underpinned by sources and sinks.

Sources and sinks for both carbon and nitrogen are vital components of plant development.

Molecular mechanisms including metabolites, genes and phytohormones regulate the source-sink balance.

Introduction

In order for plants to grow effectively, the relationship between resource uptake and resource utilisation must be finely tuned. Plants take up a range of resources from the environment in order to sustain growth, including water, carbon dioxide, and mineral nutrients. Plant organs responsible for taking up a particular resource from the environment are known as the 'source' for that resource, whilst organs utilizing the resource for growth, metabolism or storage are the 'sink' for that resource. Source and sink organs must be in balance in order for plants to function effectively in their environment, and this balance depends upon a coordinated relationship between sources and sinks.

The strength of a sink or source depends upon the size of the organ and the rate at which it is taking up or utilising a particular resource:

$$\text{Source strength} = \text{source size} \times \text{source activity} \quad (\text{Equation 1}),$$

$$\text{Sink strength} = \text{sink size} \times \text{sink activity} \quad (\text{Equation 2}),$$

where strength is net transport (mol s^{-1}), size refers to the biomass of the organ (g) and activity is the specific resource uptake rate ($\text{mol g}^{-1} \text{s}^{-1}$) based on Geiger and Shieh (1993).

Source and sink organs for carbon and nitrogen

In the simplest case, consider a plant composed of two organs only: leaf and root. Leaves carry out photosynthesis and are net sources of carbon, whilst roots are net sinks for carbon. In contrast, roots are net sources for nitrogen which they take up from the soil, whilst leaves are net sinks for this element. These roles are outlined in Figure 1. Since both leaves and roots require both carbon and nitrogen, the net role played by each organ represents the overall balance of resource transfer. All plant cells use carbon for respiration, growth, and the building of essential metabolites, and nitrogen for building proteins, enzymes, and genetic material. Thus, mature photosynthetic leaves have a relatively small carbon sink activity and a relatively large carbon source activity, meaning that they are net sources for carbon. Roots have a small nitrogen sink activity and a greater nitrogen source activity making them net sources for nitrogen.

The reality is more complex, with plants being composed of multiple types of organs. For carbon, which is taken up by plants as carbon dioxide from the atmosphere, mature photosynthetic leaves are net sources whilst developing organs (young leaves, fruits, grains, tubers) and other non-photosynthetic organs (roots or woody tissues) are net sinks (Figure 2). In contrast, for mineral nutrients which are taken up from the soil, roots are net sources whilst leaves are net sinks. Multiple resources are required by plants, including a suite of macro- and micro-nutrients. The supply and demand of many mineral nutrients is critical for plant development. Phosphorus is a vital component of DNA, ATP, and phospholipids, making it an essential element for plant growth and metabolism (Schachtman *et al.*, 1998). Sulphur is another important mineral nutrient, required for building proteins and some secondary metabolites (Dijkshoorn and Van Wijk, 1967; Gigolashvili and Kopriva, 2014; Hawkesford, 2000). These, like nitrogen, are taken up from the soil making the root a net source for these mineral elements. This article focuses on carbon and nitrogen which are the elements required in largest quantities by plants; the patterns described here for nitrogen may be broadly applied to the suite of soil-derived macro- and micronutrients required for plant growth.

Key carbon and nitrogen metabolites

Carbon dioxide from the atmosphere is fixed by plants in the process of photosynthesis, to generate triose phosphate which is converted to sucrose – a readily available store of carbon, or starch – for longer-term storage. The amount of starch stored in leaves varies between different species; many temperate grass species also use the polymer fructan for long-term carbon storage (Pollock and Cairns, 1991; Scofield *et al.*, 2009). Structural components – such as cellulose, which is a major component of plant cell walls – are also important repositories for fixed carbon. Besides sucrose, which is the main carbohydrate used for transporting

photosynthate between different parts of the plant, some plant species transport oligosaccharides and sugar alcohols. See also: DOI: 10.1002/9780470015902.a0003198.pub2 and DOI: 10.1002/9780470015902.a0001309.pub2 (photosynthesis), DOI: 10.1002/9780470015902.a0021259.pub2 (sucrose metabolism) and DOI: 10.1038/npg.els.0003892 (cellulose).

Nitrate is the typical molecule by which plants take up nitrogen from the soil. Due to its strong osmotic effect, free nitrate is stored in the vacuole, and is returned to the cytosol when it is needed. Nitrogen is reduced and then used to create amino acids, the building blocks of proteins, a process which occurs in both root and shoot. Once assimilated into amino acids, nitrogen can be stored as protein for long-term storage, or amino acids for readily-available nitrogen to be combined with carbon fixed in photosynthesis. In tropical legumes, and some other species, nitrogen is stored as ureides (Pate *et al.*, 1980). Figure 3 shows key nitrogen metabolites and source-sink processes within the plant. Protein is a stable and efficient store for nitrogen in plant cells in both shoot and root, and in contrast to nitrate, does not pose an osmotic threat to cells. Photosynthetic proteins including Rubisco, the workhorse of photosynthesis, constitute a large nitrogen sink in the leaf, with Rubisco accounting for up to 50% of leaf nitrogen content (Ellis, 1979; Evans, 1989; Sage *et al.*, 1987). In vegetative tissue, vegetative storage proteins may account for 50% of soluble protein (Liu *et al.*, 2005). See also: DOI: 10.1002/9780470015902.a0023693 (storage proteins) and DOI: 10.1002/9780470015902.a0001293.pub2 (Rubisco).

The balance between carbon- and nitrogen-containing metabolites is an important indicator of source-sink status. For example, the ratio of free amino acids to sucrose expresses the relative availability of nitrogen and carbon, with a high ratio indicating an excess of available nitrogen and a low ratio indicating an excess of available carbon. This balance is attuned to enable plants to optimise their growth and development – for example, the rate of photosynthesis is correlated with the rate of nitrogen assimilation, whilst increased availability of nitrogen leads to a reduction of starch synthesis, making carbon available for assimilation into amino acids.

Transitions

The primary role – source or sink – carried out by each plant organ changes with ontogeny, i.e. the developmental changes which organs undergo during the life of the plant. Whilst leaves are net sources for carbon and net sinks for nitrogen overall (when resource uptake and utilisation is integrated across the lifespan of a leaf), this is not the case at all stages of development. For example, a very young leaf will have a much lower rate of photosynthesis than one which is more mature, and at this early stage of development respiration outstrips the rate of photosynthesis meaning that the young leaf is a net sink for carbon whilst, as discussed above, mature photosynthetic leaves are net sources for carbon. The transition from being a sink to a source leaf is linked to sucrose and its transport, with a change in metabolism as the leaf changes from being a net importer to a net exporter of sucrose alongside the development of the photosynthetic apparatus. As part of this transition, the expression of enzymes which cleave sucrose for use by the developing leaf is decreased, whilst the expression of enzymes for sucrose synthesis increases. Leaves are net sinks for nitrogen throughout much of their lifespan,

receiving nitrogen that has been taken up by the root and utilising it in respiration and growth. However, during leaf senescence in deciduous species, nitrogen reserves from dying leaves are remobilised, causing the leaf to become a net nitrogen source. See also: DOI:

10.1002/9780470015902.a0020133.pub2.

The degree to which a plant – as a whole organism – is primarily limited by carbon source or carbon sink capacity also changes during ontogeny. Growth in young plants is primarily limited by carbon source capacity, since the developing shoot has a small photosynthetic capacity with relation to the metabolic demand of the plant. Older plants are primarily limited by carbon sink capacity, when growth slows down and photosynthetic rates are high. The switch from being carbon source limited to carbon sink limited often occurs with the transition to reproductive growth (Arp, 1991), when metabolism is focused on producing grains or fruits. However, many cereal crops are co-limited for the carbon source and sink during grain filling (Acreche and Slafer, 2009; Álvaro *et al.*, 2008; Peterhansel and Offermann, 2012; Slewinski, 2012).

Co-limitation

Coordination of source and sink is required if plants are to grow, develop, survive, and reproduce efficiently. Therefore, plants must balance the regulation of sources and sinks so that resource uptake and demand are closely matched. A totally co-limited plant would be equally limited by source and sink for each resource, such that supply and demand were in perfect harmony. However, since plants are sessile and at the mercy of a plethora of changing environmental conditions, they must be readily able to adapt to new situations. Therefore, in reality, plants are not perfectly co-limited, meaning that increasing the source or sink capacity for a particular resource can often increase growth.

Experimental manipulations of source and sink

Experimental manipulations of source and sink capacity can reveal the primary factors limiting growth at a particular time in ontogeny, and thus provide information about the strategy employed by the plant. Table 1 summarises a variety of studies in which the carbon source or sink capacity – or both – was manipulated experimentally, in a range of plant species. The responses of plants to the experimental treatments shows that increasing the capacity of either the source or the sink may increase growth, which indicates that both source and sink may limit growth, and also shows that source and sink strengths can be altered in order to alleviate changes in the balance between source and sink. This regulation is achieved using a suite of sophisticated molecular mechanisms, discussed below.

An example of how sources and sinks interact can be seen by manipulations of photosynthesis (the carbon source). Efforts to increase crop yield often focus on improving photosynthesis, with elevated CO₂ studies being a popular and effective way of increasing the carbon source capacity and developing our understanding of how plants may react to future elevated atmospheric CO₂ levels. In theory, increasing atmospheric CO₂ would increase photosynthesis and therefore crop yield. However, increases in photosynthesis and yield are not always as

great as expected, when plants are grown in elevated CO₂. (Ainsworth *et al.*, 2008; Leakey *et al.*, 2009; Long *et al.*, 2006). This indicates carbon sink limitation, since the plant is unable to utilise the additional photosynthate in sink processes. Concurrent manipulations of source and sink can provide insights into the ways in which sources and sinks regulate each other. Elevated CO₂ increases the carbon source:sink ratio, and insufficient sink demand can cause a down-regulation of photosynthesis due to the plant's inability to utilise large amounts of additional fixed carbon. However, defoliation (leaf removal, which decreases the carbon source:sink ratio) can alleviate this effect, allowing elevated rates of photosynthesis to be maintained in the remaining leaves. When elevated CO₂ is combined with manipulations of the carbon sink, source activity is increased or decreased depending on whether the manipulation increases or decreases the capacity of the sink (Table 1).

Carbon- and nitrogen-derived signalling molecules regulate source and sink

Both carbon-derived signals and nitrogen-derived signals regulate sources and sinks for both carbon and nitrogen (Figure 4). This complex network of molecular interactions enables effective control of the source-sink balance for each element, both with respect to supply and demand of the element in question, and with respect to other important elements. For example, sugars influence sucrose transport, and the important regulator trehalose-6-phosphate (T6P) plays a variety of roles in modulating the metabolic response to sugar (Figure 4). T6P is a known 'feast-famine' signalling mechanism in cereals and signals sucrose availability in plant cells (Paul *et al.*, 2017). Sugars increase levels of T6P, which integrates sugar and growth and also lifts repression of growth (Figure 4), by acting upon the integrator SnRK1 (MacNeill *et al.*, 2017). T6P regulates allocation of sucrose such that starch synthesis is increased when sucrose availability is high (a 'feast' scenario), and sugar export is increased when availability is low ('famine') (Paul *et al.*, 2017). Figure 5 illustrates the integrative role of T6P signalling. Modification of T6P levels affects carbon allocation and use, and also increases plant yield. The protein TOR kinase is another feast-famine signaling molecule, linking energy supply and growth (Lastdrager *et al.*, 2014). Hexokinase is another regulator of sugar status, and has multiple actions in the plant (MacNeill *et al.*, 2017). In addition to the effect of sugars on sucrose transport, leaf sugars also affect the regulation of nitrate reductase – both its transcription and its post-translational regulation. Conversely, starch synthesis is regulated by sugar but also by nitrate, further illustrating the inter-dependent nature of carbon and nitrogen sources and sinks.

Like sugars, which are carbon repositories as well as signalling molecules, starch is more than a carbon storage molecule: as a signalling molecule it is important for developmental transitions such as the transition to flowering, reproductive development and grain filling (MacNeill *et al.*, 2017). Starch is also a point of signalling crosstalk with the environmental conditions, meaning that starch as a signal interacts with other players in a signalling pathway. Starch reserves are affected by the environment, and starch itself affects the plant's response to environmental stress (MacNeill *et al.*, 2017).

In addition to plant organs having the capacity to act as sources or sinks at different times during their development, even at the molecular level entities can assume source or sink roles. For example, starch can act as a source – it releases leaf carbon for growth and development – and is a sink – it stores carbon including temporary storage for other sink metabolites (MacNeill *et al.*, 2017). This switch from sink to source occurs on a diurnal basis in stores of transient starch (in contrast to starch used for longer-term storage): transient starch is a carbon sink during the day and a carbon source at night. This transition depends on the accurate perception of photoperiod (MacNeill *et al.*, 2017; Smith and Stitt, 2007). See also: DOI:

10.1002/9780470015902.a0020113.pub2 (the circadian clock) and DOI: 10.1002/9780470015902.a0020124.pub2 (starch metabolism).

The ratio of nitrogen to carbon (rather than the absolute amount of nitrogen) affects the production and degradation of starch; when nitrate is low, more starch is produced enabling carbon to be stored for future growth when nitrogen is available (MacNeill *et al.*, 2017). The sensing of ratios rather than simply absolute values of elements or molecules provides plants with the vital capacity to attune different resource types.

In terms of nitrogen sources and sinks, experiments show important regulatory effects of nitrate on nitrogen assimilation in the root as well as nitrogen sink activity in the shoot (Figure 4). Plants of *Arabidopsis thaliana* with an amino acid transporter knock-out, which resulted in increased nitrogen allocation to leaves, grew faster than wild-type plants and also had improved carbon storage, seed yield and nitrogen use efficiency (Perchlik and Tegeder, 2018). This study reveals that nitrogen transport is a critical element of the nitrogen source-sink relationship, and that manipulating nitrogen transport can increase nitrogen sink capacity and manipulate the nitrogen source-sink balance, which could translate into increased productivity in an agricultural setting. In order to draw meaningful conclusions about the agricultural relevance of such studies, it is important to translate research from *Arabidopsis thaliana* into crop species and the production environment. See also: DOI: 10.1002/9780470015902.a0023734.

Genetic regulation of source and sink

In addition to direct molecular effects mediated by carbon- and nitrogen-derived metabolites acting as signalling molecules, these metabolites can also cause regulation of gene expression to instigate effects higher up in the signalling pathway, which can have wider-reaching effects. For example, carbohydrates can repress the expression of photosynthetic genes in the leaf (such as the genes encoding the subunits which make up Rubisco) and regulate expression of nitrate reductase in the shoot (Figure 4). This reduces the carbon source activity and increases the nitrogen sink activity in the leaf, enabling additional photosynthate to be assimilated into amino acids. Sugars increase the expression of nitrate reductase, the enzyme responsible for nitrate reduction, making nitrate available as amino acids, whilst the expression of enzymes for starch biosynthesis is increased when nitrate levels are low to facilitate carbon storage.

The regulatory role of phytohormones

Phytohormones (plant hormones) are important mediators of plant signalling. For example, levels of the phytohormone cytokinin are modulated by nitrate and upregulate nitrate assimilation, photosynthesis, and growth (Figure 4). Signalling crosstalk often involves phytohormones interacting with other signalling molecules. This enables a greater range of responses, with differing degrees of sensitivity, to be achieved, due to a greater complexity in the network. For example, sugars interact with abscisic acid (Teng *et al.*, 2008) and auxin (Stokes *et al.*, 2013) as well as regulating development themselves (Eveland and Jackson, 2012) and regulating (and being regulated by) the circadian clock (Lastdrager *et al.*, 2014). See also: DOI: 10.1002/9780470015902.a0002091.pub2 (phytohormones), DOI: 10.1002/9780470015902.a0020088.pub3 (abscisic acid) and DOI: 10.1002/9780470015902.a0020090.pub2 (auxin).

Species differences and environmental conditions

Different plants have different capacities for source and sink, and also differ in their ability to show developmental plasticity (flexibility) in their source-sink balance. Plant species which transport sucrose via the apoplastic pathway, which uses developmentally plastic membrane transporters, are more readily able to increase sucrose transport out of the leaf and therefore are sometimes able to show a more flexible response to source and sink manipulations, than are species which use the symplastic pathway which uses developmentally fixed plasmodesmata for sucrose transport. 'Apoplastic loaders' include many herbaceous species, whilst trees and shrubs are often 'symplastic loaders' (Ainsworth and Bush, 2011). For more information on plasmodesmata, see: DOI: 10.1002/9780470015902.a0001681.pub3.

Legumes may have a greater capacity to increase the carbon sink under elevated CO₂ if nitrogen is plentiful (Rogers *et al.*, 2009). This is because legumes fix atmospheric nitrogen, via a symbiotic relationship with bacteria in legumes' root nodules, although this fixation of nitrogen is suppressed when soils are nitrogen-rich (Murray *et al.*, 2017). See also: DOI: 10.1002/9780470015902.a0003720.pub2

Regulating sinks and sources in concert with the availability of resources is an important factor contributing to the successful growth of plants in the natural environment. This is especially critical when plants are living in an environment of fluctuating resource availability, or when a species is adapted to grow in wide-ranging environments. Having a successful growth strategy enables plants to withstand stress, survive to reproduction, and compete effectively with neighbours.

Impact of sources and sinks on crop growth and yield

In order to maximise crop yield – which is an important element of future food security to support a burgeoning global population (FAO *et al.*, 2014) – source-sink relationships should be considered when breeding crops. Many cereal crops are sink-limited during the grain-filling stage, indicating that increasing sink capacity could facilitate increases in yield. Developing our

knowledge of source-sink relationships earlier in the lifetime of the plant, during the vegetative stage, could also increase subsequent yield: alleviating source or sink limitation during vegetative growth could contribute to the development of additional nutrient reserves and/or storage structures, which could in turn be used to increase yield. For example, experimental work in *Hordeum vulgare* (barley) has demonstrated both carbon sink limitation and mineral nutrient sink limitation during the vegetative growth stage; alleviation of these limitations is important for maximising the growth of elite cereal crops, especially under future elevated CO₂ levels (Burnett *et al.*, 2016, 2018). Comparing a wild perennial relative with this annual crop revealed carbon source limitation during the vegetative growth stage in the perennial, indicating a more flexible, opportunistic growth strategy in this wild species which is appropriate for the natural environment (Burnett *et al.*, 2016). Low nutrient levels were found to limit growth directly rather than by impacting carbon acquisition (which would occur *via* a reduction in the investment in leaves and therefore the carbon source capacity), since at high nutrient levels, carbohydrate storage did not increase, the ratio of free amino acids to sucrose increased suggesting that carbon was not limiting to growth, and shoot allocation increased, rather than decreasing if carbon had been the limiting factor to growth at lower nutrient levels, suggesting nutrient sink limitation (Burnett *et al.*, 2018).

Work in two cultivars of *Nicotiana tabacum* (tobacco) grown in the field showed that, under elevated CO₂ levels, photosynthesis was down-regulated to differing degrees depending on the carbon sink strength of the cultivar, with the faster-growing variety able to maintain greater rates of photosynthesis due to its larger sink (Ruiz-Vera *et al.*, 2017). Increasing the amount of nitrogen available to the plants – and therefore increasing carbon sink strength – partly mitigated this down-regulation of photosynthesis in some but not all cases, highlighting both the role of carbon sink strength in allowing plants to utilise additional CO₂ resources, and the complex nature of this relationship in which multiple factors contribute to sink strength and plant growth. Field experiments such as this are critical for crop improvement; it is important to note that experiments performed in glasshouses or growth chambers can be sink limited (Poorter *et al.*, 2012) and this can lead to an even greater down-regulation of the response to increased resource availability.

Increasing the source capacity for carbon, *via* photosynthesis, or for mineral nutrients such as nitrogen, *via* mineral uptake, can alleviate source limitations for these elements. However, as has been seen above, realising yield increases through manipulations of the source will require a concomitant increase in sink capacity. If, for example, photosynthesis is not integrated with sink processes, the resultant increase in sucrose will lead to a homeostatic reduction of photosynthesis (Paul *et al.*, 2017). The sink is influenced by a range of factors such as cell growth (DOI: 10.1002/9780470015902.a0020107 pub2), organ initiation rates at meristems, organ size, growth determinacy/indeterminacy, and the ratios of different organs and body parts such as the shoot:root ratio and the leaf area ratio.

In addition to the manipulation of source and sink organs and processes, molecular feedback mechanisms are a key target for improving the source-sink balance. For example, T6P is a master regulator and a useful target for boosting sinks for crop improvement (Paul *et al.*, 2017).

The signalling molecule SnRK1 is also a possible target for improving yield potential (Paul *et al.*, 2017). Metabolic engineering is notoriously difficult, with modelling being a vital tool for realising the potential of metabolic engineering – including the integration of metabolic models with whole-plant-level models (Sweetlove *et al.*, 2017). For maximal gains in crop productivity, an approach including engineering of both source and sink metabolism has been advocated (Sweetlove *et al.*, 2017).

Whilst changing the activity of individual components in a signalling pathway can bring about major changes in plant development, multi-gene transformations to manipulate source and/or sink function may be the best way to improve crops, and modelling is again an important tool for developing the necessary understanding to achieve such transformations (Sonnewald and Fernie, 2018). By improving the ways in which plants coordinate sink and source, greater efficiency of growth and increased yield may be achieved. To learn more about plant breeding, see also: DOI: 10.1002/9780470015902.a0002024.pub3.

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Root nodules <http://www.els.net/WileyCDA/ElsArticle/refId-a0003720.html>

DOI: 10.1002/9780470015902.a0003720.pub2

Glossary

Crosstalk signal transmission *between* different signalling pathways

Feedback signalling mechanism in which an increase leads to repression

Feedforward signalling mechanism in which an increase leads to an increase

Ontogeny development of an organism throughout its lifespan

Phytohormone plant hormone, a signalling molecule with regulatory effects on growth and development

Sink plant organ with net drawdown of resources

Source plant organ with net uptake of resources

Figure legends (files attached separately)

Figure 1 Net sources and sinks for carbon (green) and nitrogen (blue), in a simplified plant system. Deepening colour illustrates the gradient for each element, indicated by the grey arrows. Sugars and amino acids are transported in the phloem.

Figure 2 Sources (a, b, c) and sinks (d, e, f) of three glasshouse-grown crop plants: *Helianthus annuus* (sunflower) leaves (a) and flower with developing seeds (d); *Raphanus sativus* (radish) leaves (b) and edible tuber (e); *Curcubita pepo* (courgette) leaves (c) and flowers with edible fruits (f). Photographs taken at Brookhaven National Laboratory by Angela C Burnett (a, b, c, e, f) and Erin O'Connor (d).

Figure 3 Schematic overview of nitrogen (N) transport processes and source–sink relationships at the whole-plant level. N fluxes from soil to root to leaf to sinks involve short- and long-distance transport of inorganic N (nitrate (NO_3^-), ammonium (NH_4^+) and di-nitrogen (N_2)) and organic N (amino acids (AA) and ureides (Ur)). The xylem and phloem connect sources with sinks and are essential for N mobilization. The smaller font size of xylem NH_4^+ and phloem NO_3^- refers to their lower concentration compared with other transported N compounds. Grey arrows indicate feedback controls exerted by source and sink on N uptake and partitioning, respectively. Figure originally published by Tegeder and Masclaux-Daubresse (2017) and reproduced with permission from John Wiley and Sons.

Figure 4 A range of feedback mechanisms enables fine-tuning of the balance between sources and sinks for carbon (green) and nitrogen (blue). These mechanisms include metabolites derived from carbon and nitrogen; genetic regulation; and control by phytohormones. Feedbacks operate at the tissue level (arrows 1-4 and 6-9) and at the whole-plant level (arrows 5 and 10). Figure originally published by White *et al.* (2016) and reproduced with permission.

Figure 5 Trehalose 6-phosphate (T6P), synthesized by trehalose phosphate synthase (TPS) and subsequently catalysed to trehalose by trehalose phosphate phosphatase (TPP), signals sucrose availability through the feast–famine protein kinase, SnRK1, which regulates genes involved in metabolism, growth, and development. An intermediary factor (IF) is necessary for inhibition of SnRK1 by T6P (Zhang *et al.*, 2009). Low T6P results in activation of genes for famine responses; high T6P results in activation of genes for feast responses. Decreases in T6P through genetic modification (Nuccio *et al.*, 2015) and marker-assisted selection (Kretzschmar *et al.*, 2015), or increases in T6P through chemical intervention (Griffiths *et al.*, 2016), have resulted in improved performance and large yield improvements in maize, rice, and wheat. Figure originally published by Paul *et al.* (2017). Publisher permission pending.

Table 1. Experimental manipulations of the carbon source:sink balance, illustrating that: (a) both sources and sinks affect plant growth; (b) sources and sinks regulate each other by feedback mechanisms; (c) source and sink strength can be altered by the plant, to alleviate perturbations of the source:sink balance.

Species	Manipulation	Effect	Key Result	Reference
SOURCE MANIPULATIONS				
<i>Eucalyptus globulus</i>	Defoliation + Debudding	Reduces source Reduces sink	Defoliation increases photosynthesis in other leaves; source:sink biomass ratio is main driver of this change	(Eyles <i>et al.</i> , 2013)
Three chalk grassland species	Defoliation + Elevated CO ₂	Reduces source Increases source	In two species, photosynthetic acclimation to elevated CO ₂ was alleviated by defoliation, which restores the source:sink balance	(Bryant <i>et al.</i> , 1998)
<i>Lolium perenne</i>	Canopy-cutting + Elevated CO ₂	Reduces source Increases source	Photosynthetic acclimation to elevated CO ₂ was alleviated by cutting the canopy which restores the source:sink balance	(Rogers <i>et al.</i> , 1998)
<i>Phaseolus vulgaris</i>	Defoliation / Reduced light + Elevated CO ₂	Reduces source Increases source	At ambient and elevated CO ₂ : defoliation increases photosynthetic rate in other leaves, reduced light decreases photosynthetic rate	(von Caemmerer & Farquhar, 1984)
<i>Lolium perenne</i>	Elevated CO ₂ + Canopy-cutting + Low nitrogen	Increases source Reduces source Reduces sink	Photosynthetic rate decreased in low nitrogen, but this effect was reduced when the source:sink balance was restored by canopy-cutting	(Ainsworth <i>et al.</i> , 2003)
<i>Dactylis glomerata</i>	Elevated CO ₂	Increases source	Shortening of cell cycle in shoot and root meristems	(Kinsman <i>et al.</i> , 1997)
<i>Triticum aestivum</i>	Elevated CO ₂	Increases source	Cell division and expansion affected	(Masle, 2000)
SINK MANIPULATIONS				
Various species	Elevated CO ₂ + Removal of sinks / Low nitrogen / Low temperature	Increases source All reduce sink	Reducing sink capacity increases acclimation of source activity	(Arp, 1991)

<i>Arabidopsis thaliana</i>	Low temperature + Genetic manipulation of T6P/ SnRK1 signalling pathway	Reduces sink Affects integration of sucrose levels and growth	Altered signalling pathway reduced plant capacity to recover from sink limitation	(Nunes <i>et al.</i> , 2013)
Various species	Inhibition of sucrose export from source leaves	Reduces apparent sink demand	Inhibition of photosynthesis	(Ainsworth and Bush, 2011)
<i>Glycine max</i>	Elevated CO ₂ + Genetic modification to make a determinate line of a cultivar normally showing indeterminate growth	Increases source Reduces sink	Reduced sink capacity and decreased photosynthesis, due to increase in source:sink balance	(Ainsworth <i>et al.</i> , 2004)
<i>Solanum tuberosum</i>	Transgenic reduction of ADP-glucose pyrophosphorylase	Reduces sink capacity by reducing starch synthesis	Tuber sinks adapted by increasing sucrose content	(Müller-Röber <i>et al.</i> , 1992)
<i>Solanum tuberosum</i>	Transgenic reduction of ADP-glucose pyrophosphorylase + Transgenic expression of fructan biosynthesis enzymes	Reduces sink capacity by reducing starch synthesis Increases sink	Plants avoided yield reductions by synthesising fructan instead	(Zuther <i>et al.</i> , 2011)
<i>Triticum aestivum</i>	Transgenic modification to increase sucrose uptake in developing grains	Increases sink	Storage protein synthesis increased	(Weichert <i>et al.</i> , 2010)
<i>Triticum aestivum</i>	Elevated CO ₂ + Addition of nitrogen in proportion to growth	Increases source Increases sink	Acclimation of photosynthesis did not occur when nitrogen was added in this way	(Farage <i>et al.</i> , 1998)
<i>Abutilon theophrasti</i> and <i>Setaria faberii</i>	Elevated CO ₂ + Large size / High nutrients	Increases source Both increase sink	Increase in growth and yield in response to elevated CO ₂ was higher when sink capacity was also increased	(McConnaughay <i>et al.</i> , 1993)
<i>Triticum aestivum</i>	Elevated CO ₂ + Cultivars with high and low harvest index	Increases source Different sink sizes	Increase in photosynthesis and growth was dependent on high sink strength: only seen in cultivar with high harvest index	(Aranjuelo <i>et al.</i> , 2013)
<i>Brassica</i> spp.	Elevated CO ₂ + Species had different sink sizes	Increases source Different sink sizes	Long-term growth increases were dependent (to an extent) on species-specific sink size	(Reekie <i>et al.</i> , 1998)

‘+’ denotes treatments applied in combination; ‘/’ denotes alternative treatments. Table originally published by White *et al.* (2016) and reproduced with permission.

Figure 1

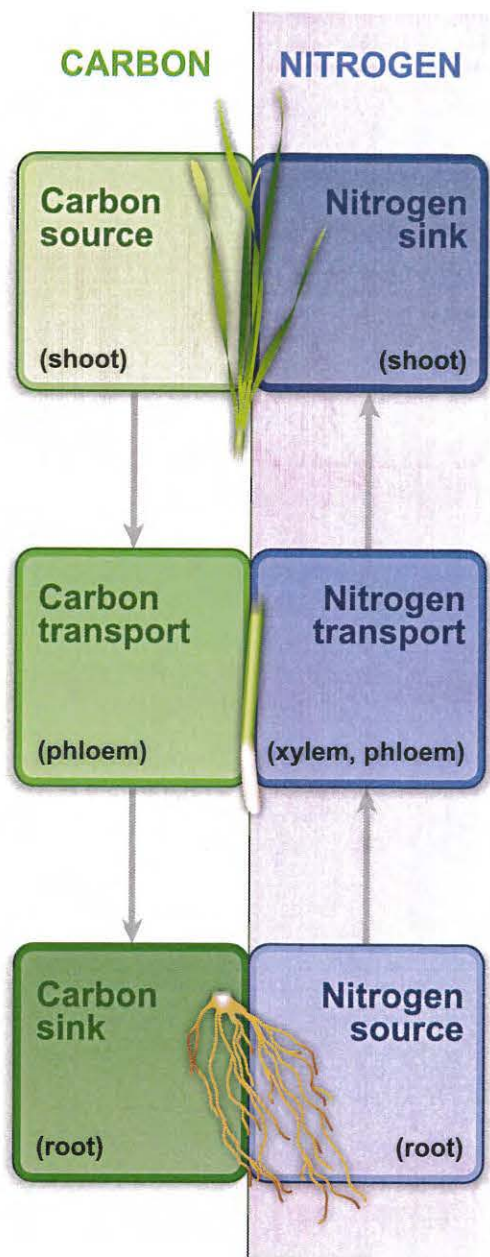


Figure 2

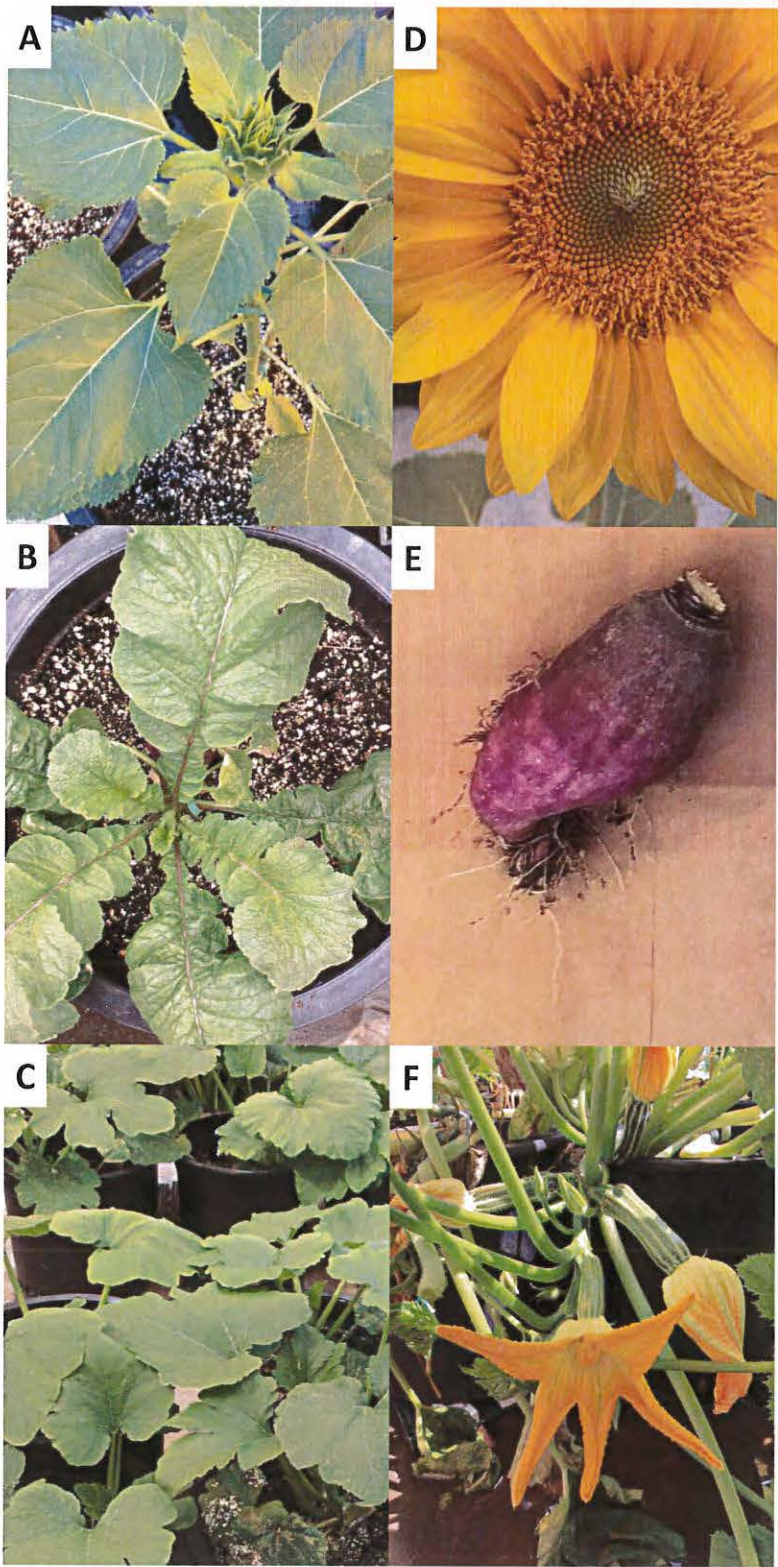


Figure 3

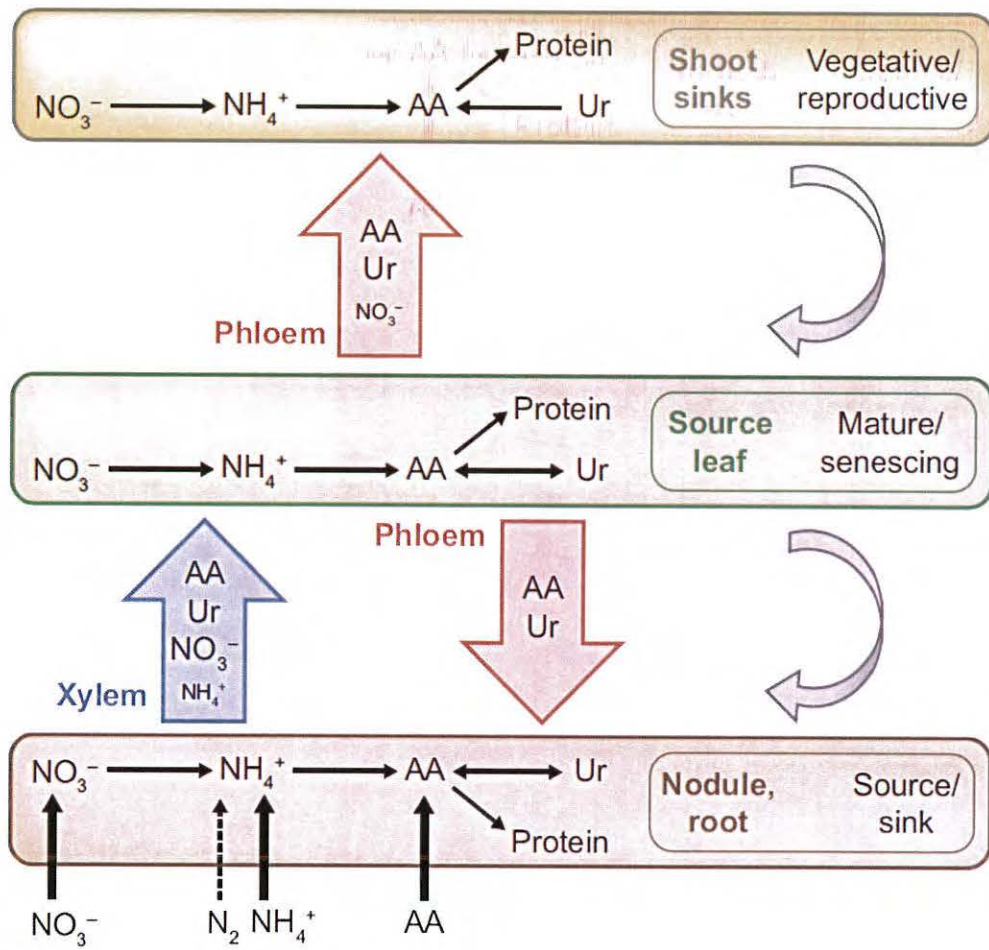


Figure 4

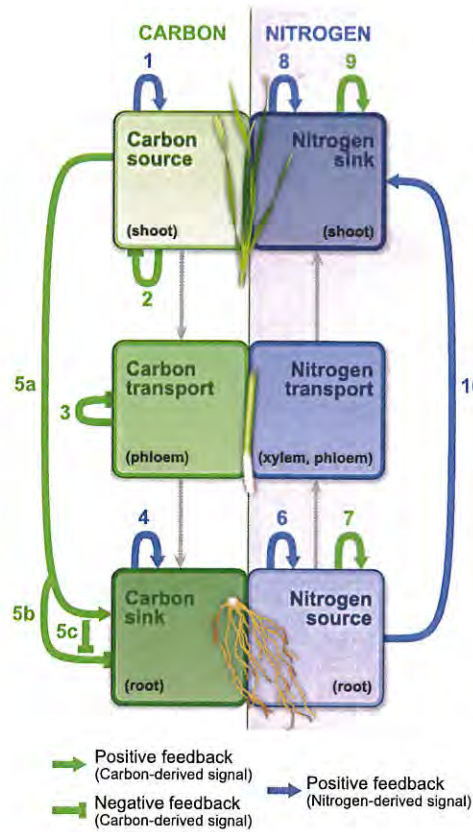


Figure 5

