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REVIEW PAPER

How can we make plants grow faster? A source–sink perspective on growth rate

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Abstract

Growth is a major component of fitness in all organisms, an important mediator of competitive interactions in plant communities, and a central determinant of yield in crops. Understanding what limits plant growth is therefore of fundamental importance to plant evolution, ecology, and crop science, but each discipline views the process from a different perspective. This review highlights the importance of source–sink interactions as determinants of growth. The evidence for source- and sink-limitation of growth, and the ways in which regulatory molecular feedback systems act to maintain an appropriate source:sink balance, are first discussed. Evidence clearly shows that future increases in crop productivity depend crucially on a quantitative understanding of the extent to which sources or sinks limit growth, and how this changes during development. To identify bottlenecks limiting growth and yield, a holistic view of growth is required at the whole-plant scale, incorporating mechanistic interactions between physiology, resource allocation, and plant development. Such a holistic perspective on source–sink interactions will allow the development of a more integrated, whole-system level understanding of growth, with benefits across multiple disciplines.

Key words: Carbon, crops, models, nitrogen, plant growth, regulation, sink, source.

Introduction

Growth rates of plants vary widely: even in constant environmental conditions, relative growth rate can vary six-fold among species (Grime and Hunt, 1975). This is not surprising given the astonishing variety of ecological niches occupied by plants in all the major biomes, where adaptation comes in part from matching growth rate to available resources (Díaz *et al.*, 2004). Growth is controlled by proximate physiological and developmental mechanisms, but ultimately depends upon ecological adaptations and evolutionary history: plants with different growth strategies succeed in different ecosystems, and in different niches within those ecosystems. For example, in the dynamic, diverse rainforest environment, rapidly growing seedlings and lianas will quickly colonize gaps, while slow-growing epiphytes often stay poised and wait for a gap in the canopy before upregulating their rates of photosynthesis and growth (Hubbell and Foster, 1992). Ecological life history theory points towards a growth-survival trade-off (e.g. Baraloto *et al.*, 2010), which helps to explain species differences in growth rate (Metcalf *et al.*, 2006), and leads to niche partitioning (Wright *et al.*, 2010). Growth rate therefore represents a major axis of ecological variation among species, which correlates with changes in resource availability and risk of mortality, but trades off against defence and storage (Grime, 1977; Herms and Mattson, 1992; Rose *et al.*, 2009; Turnbull *et al.*, 2012).

Proximate causes of growth rate variation include both external and internal factors (Körner, 1991). Externally,

plants are affected by a plethora of abiotic and biotic factors including nutrient and light levels, temperature, competition, and herbivory, all of which influence the supply and demand for essential resources, and plants must ensure that growth rates are attuned accordingly (Bloom *et al.*, 1985; Coley *et al.*, 1985). Internally, plant growth is constrained by molecular, physiological, and developmental processes: metabolic rates determine the capacity to take up and store resources, while allocation during development, rates of cell division and expansion, and developmental transitions from vegetative to reproductive growth all have important effects on resource use and partitioning. These internal processes can all be understood within the framework of source–sink interactions: source activity refers to the rate at which essential external resources are acquired by the plant and made available internally, while sink activity refers to the internal drawdown of these resources. This drawdown encompasses resource sequestration in growth and storage, plus resource losses through respiration or exudation. By necessity, the relationships between sinks and sources are both finely tuned and tightly regulated by feedback and feedforward mechanisms, many of which are now well characterized within tissues at the molecular level (e.g. Smith and Stitt, 2007; Lawlor and Paul, 2014). Since plants are sessile and can only influence external factors to a limited degree, the internal factors are well controlled. As a consequence, it is these internal interactions of source and sink activity that must be responsible for the large intrinsic variation in relative growth rate among species under common environmental conditions.

The general principles governing the diversity in intrinsic growth rate among wild species also underpin the variation in yield potential among crop genotypes. The current need to increase crop productivity for food and fuel, due to a rapidly increasing global population, is urgent and well-documented (FAO *et al.*, 2014). Yield increases in rice and wheat due to breeding and genetic techniques are currently around 1% per year—a trajectory too low to meet future requirements, and this has motivated the development of global consortia for crop improvement (von Caemmerer *et al.*, 2012; Reynolds *et al.*, 2012; Ort *et al.*, 2015). The primary focus for many of these is boosting photosynthetic carbon acquisition (source activity), yet sink activity is also believed to limit grain development in many major crops (Acreche and Slafer, 2009; Peterhansel and Offermann, 2012; Slewinski, 2012). Global efforts to elucidate the responses of crop photosynthesis and yield to future elevated atmospheric CO_2 conditions show that the translation of a large and sustained stimulation of photosynthesis into growth and yield differs markedly between species and often falls short of the expected response (Long *et al.*, 2006*a*). Achieving future yield targets requires that this translation of improved photosynthesis into yield is made effectively through enhanced sink development. To achieve the 70% increase in crop productivity required by 2050, a greater understanding of the relationships between photosynthesis and growth, and the factors underpinning growth rates, is therefore essential.

This review discusses current understanding of plant growth rates, considering a range of factors from molecular to ecological, with a particular focus on source–sink interactions. It emphasises the importance of sources and sinks as determinants of growth and as targets for crop improvement. For the first time, this review argues the case for a fully integrated network analysis of physiology, allocation, and development when considering growth across the diversity of wild and crop plants. It highlights source and sink limitation as key areas where understanding could be improved, and suggests that quantitative estimates are required of how sources and sinks limit growth, the extent to which these limitations change at different stages of development within the same species, and their differences in species, which vary in allocation and life history strategies.

Source and sink definitions

Source tissues are net exporters of an elemental resource required for plant growth, such as carbon or nitrogen, while sink tissues are net importers and are responsible for resource assimilation. Mature leaves are net sources of carbon but sinks for nitrogen, while root tissues are net sources of nitrogen but sinks for carbon. Cells require carbon and nitrogen for growth and development; nitrogen to maintain protein turnover; and carbon for respiration to fuel metabolic processes. Other elements are also vital for growth, such as oxygen obtained from the air, hydrogen from water, and minerals found in soil including the macronutrients potassium and phosphorus, and numerous micronutrients. This review focuses on carbon and nitrogen only, because these elements are commonly limiting for growth, and effectively illustrate the balance between source and sink tissues. Carbon is usually exchanged between sources and sinks as simple sugars, typically sucrose. The equivalent currency of exchange for nitrogen includes both inorganic ions (NO_3^-) and organic forms (typically amino acids).

Source tissues are generally responsible for the acquisition of resources from the external environment, although the remobilization of stored resources (e.g. to subsidize reproduction or regrowth after disturbance) may also turn a sink into an internal source. A general definition of source strength should therefore consider the export rate of a particular resource from the source tissue. However, C- or N-uptake from the external environment is more commonly and easily measured than internal fluxes of sucrose or inorganic and organic nitrogen. Consequently, the term ‘source strength’ usually refers to the net rate of uptake (mol s^{-1}) for a particular resource from the external environment:

$$Source\ strength = source\ size \times source\ activity \qquad (1),$$

where source size refers to the total biomass of source tissue (g), and source activity is the specific uptake rate of the resource (mol g^{-1} s^{-1}; based on Geiger and Shieh, 1993).

Sink tissues are net receivers of resources from source tissues (Doehlert, 1993). While all tissues have some sink activity, leaves are net sinks for nitrogen transported from the root system, and roots are net sinks for sucrose exported from leaves. Sink strength refers to the net rate of uptake (mol s^{-1}) for a particular resource by a defined tissue within the plant:

$$Sink\ strength = sink\ size \times sink\ activity \quad (2),$$

where sink size is the total biomass of sink tissue (g), and sink activity refers to the specific uptake rate of the resource (mol g^{-1} s^{-1}). Sink activity involves the utilization of resources for the synthesis of new tissues, including the synthesis of structural components such as cell walls, or the maintenance and modification of existing tissues, including the synthesis of non-structural components including enzymes, storage and defence compounds. Sink activity also encompasses the expenditure of resources in respiration or root exudation. In practice, therefore, it is usually quantified via the net accumulation rate of a particular resource in a tissue over time, after accounting for the losses from respiration and exudation.

Source tissues thus take up resources from the environment and export them to sinks, which draw down resources within the plant. The parallels with financial transactions are clear in this conceptualization of plant function, and the next section considers the molecular currencies traded between sources and sinks.

Source and sink tissues

Carbon

Mature leaves are net sources of carbon. Carbon dioxide is fixed to generate triose phosphate in photosynthesis, which is then converted to starch for diurnal storage in the chloroplast (Smith and Stitt, 2007; Gibon *et al.*, 2009; Stitt and Zeeman, 2012; Pilkington *et al.*, 2015), or to sucrose for export from the leaf or storage in the vacuole.

Net carbon sink tissues include roots, tubers, reproductive structures, and young leaves. Sucrose may itself be stored directly, or it may first be converted to storage polymers. These polymers are typically starch or fructans, depending on the species; some plants store additional compounds such as raffinoses (Atkinson *et al.*, 2012). Starch is stored in the amyloplasts and chloroplasts of many higher plants (Müller-Röber *et al.*, 1992); amyloplasts are found in seeds, shoot storage tissues, and roots, while chloroplasts are found in leaves and stems (and are the only repository for starch within leaves). Starch is also the primary carbohydrate in the grains of many crops, including wheat, rice, and maize, and in the tubers and storage roots of vegetables (Pollock and Cairns, 1991; Zeeman *et al.*, 2010). Carbon storage in the stems of many temperate grasses consists primarily of fructans (Pollock and Cairns, 1991; Scofield *et al.*, 2009), water-soluble fructose polymers which confer some resistance to low temperatures (Sandve *et al.*, 2011). Typically, fructans and sucrose are stored together in the stem, as in wheat, barley, and oat (Slewinski, 2012). Significant stem storage of starch is rare in cereals—rice being a notable exception, storing sucrose in leaves and starch in stems (Murchie *et al.* 2009), and being unable to synthesize fructans naturally (Kawakami *et al.*, 2008). Stem storage of carbohydrates is an important buffering system for recovery after grazing and for supplying photosynthate to cereal ears during grain-filling, especially during drought (Schnyder, 1993; Ruuska *et al.*, 2006; Slewinski, 2012), and is thus a relatively labile sink. For growth, a major use of photosynthate is the synthesis of cell wall polysaccharides such as cellulose and hemicellulose, in all parts of the plant. Indeed, almost half of plant cell wall biomass is composed of carbon (Körner, 2012).

In addition to the assimilation of resources in sink tissues, the utilization of resources in respiration and exudation constitute a further sink, since these processes also contribute to resource drawdown. Maintenance respiration can represent a significant carbon cost to the plant (Penning de Vries, 1975); for example, respiration constitutes 70% of the carbon sink in *Pinus halepensis* (Klein and Hoch, 2015). Carbon and nitrogen are released through root exudation of a variety of compounds including organic acids, sugars, polysaccharides, ectoenzymes such as acid phosphatase, and sloughed-off cells and tissues (Marschner, 1995). Exuded metabolites have many functions (Badri and Vivanco, 2009) such as modifying the rhizosphere to provide a desirable environment for beneficial microorganisms and providing signals to aid recruitment of arbuscular mycorrhizal fungi, contributing to immunity (Cameron *et al.*, 2013). These processes may be substantial—one meta-analysis of annuals found that 30–60% of net photosynthetic carbon is allocated to roots, of which 40–90% is lost in respiration and exudation (Lynch and Whipps, 1990).

Nitrogen

In contrast to carbon, roots are net sources for nitrogen, while shoot tissues are net nitrogen sinks until senescence when their nitrogen is remobilized (Aerts and Chapin, 2000). Annuals remobilize nitrogen for reproduction while perennials may remobilize nitrogen for reproduction or for growth and storage in subsequent years. Inorganic nitrogen is taken up by roots as nitrate (NO_3^-) or ammonium (NH_4^+), and may be utilized in growth or exported from the root. Assimilation of nitrogen into amino acids takes place in both roots and shoots, although the relative proportions depend on the species and are still debated (Nunes-Nesi *et al.*, 2010). Approximately 80% of wild plant species benefit from mycorrhizal associations in which specialised fungi aid the uptake of phosphorus and sometimes organic nitrogen (Read, 1991). Organic nitrogen may also be taken up from the soil in the form of free amino acids. Nitrogen is exported from roots as nitrate (transported in the xylem), amino acids or amides (both transported in the phloem).

Root and leaf nitrogen concentrations are positively correlated, but a global survey of wild grassland species found that leaf nitrogen concentration is more than double that of roots in the same species (Craine *et al.*, 2005). The main use of nitrogen for growth is in proteins and there is a particularly high demand in leaves, where the complex, enzyme-rich photosynthetic machinery is assembled and maintained. Photosynthetic proteins encompass the majority of leaf nitrogen—for example, Rubisco (EC 4.1.1.39) typically accounts for between 10% and 30% of leaf nitrogen content but can account for up to 50% of leaf nitrogen content (Ellis, 1979; Sage *et al.*, 1987; Evans, 1989). Through Rubisco, carbon

source activity is directly connected with leaf nitrogen sink activity, providing one way in which source and sink activity are intrinsically coordinated. Nitrogen partitioning into photosynthetic proteins is a flexible trait, varying between species and as resource availability changes (Evans, 1989).

Nitrogen may be stored as nitrate in the vacuole, or as proteins (Millard, 1988). Vegetative storage proteins (VSPs) may comprise up to 50% of soluble protein in vegetative tissues (Liu *et al.*, 2005). Protein storage occurs primarily in seeds, although some legumes, tuber-formers, and deciduous trees species have additional storage proteins (Shewry, 1995). VSPs have been well-studied in soybean, and the nitrogen sink-to-source transition occurring in leaves during ontogeny is correlated with a decrease in VSP gene expression in this species (reviewed by Staswick, 1990). In both potato and soybean, removal of nitrogen sink tissues upregulates nitrogen storage in other parts of the plant, indicating a buffering role for VSPs in maintaining source:sink balance (Staswick, 1990). In contrast, grasses such as wheat and rice (usually grown as annuals) are less reliant on protein stores beyond those in the seed, yet can still accumulate nitrogen when conditions are favourable. For example, excess nitrogen in wheat accumulates in the lamina of upper leaves or the true stem of the peduncle, and just as stem carbohydrate reserves are important for grain-filling in grasses, this stored nitrogen is thought to provide a nitrogen buffer for use during grain-filling (Pask *et al.*, 2012). Non-leaf nitrogen stores, such as the culm in grasses, may also play a role in plant recovery after grazing.

Co-limitation and optimization

A plant that has optimized its source:sink ratio can grow using balanced allocation of source and sink sizes and activities (Equations 1–2), facilitated by molecular feedbacks. However, at any point in time, most plants are not fully optimized, meaning that the creation of either more source or sink tissue could increase growth: in these cases, the potential source or sink strength (Equations 1–2) has not been realized (Patrick, 1993). The extent to which these potentials are met may be investigated using environmental or genetic manipulations, and are discussed later in this review.

Resource uptake changes over time due to fluctuations in the external environment, such that the total supply of a particular resource over the lifetime of the plant cannot be predicted in advance. The plant reacts to these fluctuations in resource availability by modifying its investment in resource acquisition and consumption (Freschet *et al.*, 2015). At the most general level, a suitable balance between leaf and root tissues is critical for balancing the acquisition of carbon and mineral nutrients. Allocation to shoot and root is adjusted depending on available resources so that, for example, the allocation of resources to root growth is increased in low nitrogen soil conditions. Co-limitation by carbon and nitrogen has been demonstrated experimentally and optimization of these resources has been considered in models (Woodrow, 1994; Iwasa, 2000; Guilbaud *et al.*, 2015) yet, due to environmental and developmental constraints, plants do not always achieve perfect co-limitation *in vivo*.

Greater insights into this balancing of sources and sinks at the whole-plant scale can be gained by analogy with metabolic systems within cells or tissues. In plant metabolic networks, control of the overall flux is typically shared between several enzyme steps, although many elements in the system exert only a limited effect (Fell and Thomas, 1995; e.g. Raines, 2003; Araújo *et al.*, 2012). If the dynamic internal system of resource fluxes among source and sink tissues is analogous to such a metabolic system, then overall control of the flux of materials into growth is also likely to be shared among multiple elements. This flux control analogy generates two predictions.

The first prediction is that multiple elements in the system share control of the growth rate, and growth will increase if their sizes or activities are raised together. In contrast, most elements exert limited control, and are present in excess. The most resource-efficient solution for the developing plant is therefore to tune down investment in those components with little influence, and increase allocation to the elements exerting a high degree of control. Such regulation must be a dynamic process that balances fluctuations in external resource availability with ontogenic changes in the demand for resources. Analogous examples from metabolism show how such reallocation among elements in the system can optimize enzyme activities to increase fluxes (Woodrow, 1994; Zhu *et al.*, 2007). However, in a whole-plant system, this optimization process must operate within the context of life history strategies of investment in growth versus defence or storage (the growth–survival trade-off).

The second prediction generated by the flux control analogy is that development of new source and sink organs during ontogeny shifts the overall control of growth to different elements in the system. This effect is expected because changes in the number, size, and activity of plant organs during development alters the internal capacity of a plant to acquire and consume resources, and is well supported by experimental evidence. For example, some plants transition from sink to source limitation during the shift from vegetative to reproductive growth (examples within Arp, 1991; Marschner, 1995; Rogers and Ainsworth, 2006). Equivalent effects arise when plants are exposed to external environmental conditions which change resource acquisition rates, or if the numbers or activities of source or sink organs are manipulated experimentally. The evidence for such effects is considered in the next section of this review.

In combination, these external and internal factors mean that the acquisition and consumption of resources must be balanced over time by a combination of coarse and fine internal regulatory controls. This control, in turn, operates within a general life history strategy of investment in growth versus storage or defence, which means that the growth rate is not necessarily maximized under particular internal and external constraints.

The situation for crop plants is simpler, since breeders aim to maximize lifetime growth and reproductive allocation within monospecific communities (Denison, 2012). Current

views on source–sink relations in crop plants point towards a co-limitation of growth by sources and sinks during grain-filling (Álvaro *et al.*, 2008; Acreche and Slafer, 2009; Peterhansel and Offermann, 2012; Slewinski, 2012) yet growth could be further optimized. One line of evidence for the lack of optimization of source and sink to maximize growth comes from experiments where plants are grown at elevated CO_2 (discussed later, in Table 1). Such experiments aim to predict the responses of plants to future climatic conditions, and increase the carbon source activity of plants in a non-invasive manner. The increase in photosynthesis under elevated CO_2 demonstrates that source activity typically limits growth under ambient CO_2 levels. However, the increases in photosynthesis and yield seen when plants are grown under elevated CO_2 do not match the magnitude of those predicted from theoretical modelling and extrapolation of chamber experiments (Long *et al.*, 2006*a*; Ainsworth *et al.*, 2008; Leakey *et al.*, 2009). These results suggest a degree of sink limitation of growth, which could be due to nitrogen limitation. Responses to CO_2 do vary between species (Poorter, 1993) and some plants are able to upregulate source and sink in concert. For example, high CO_2 can stimulate nitrate uptake to balance source and sink capacity (Stitt and Krapp, 1999). When external nitrate levels are low, elevated CO_2 levels cause an increase in both the rate of nitrate uptake and the activity of a high affinity nitrate transport system in wheat roots (Lekshmy *et al.*, 2009), representing an upregulation of nitrogen source strength through increased activity [Equation (1)].

In order to improve crop yields, a greater, more integrated understanding of how plant growth rates are limited by sinks and sources for carbon and nitrogen, and the shifts in limitation that occur during the lifetime of a plant, is required. Only by grounding modelling and experimental work in mechanistic knowledge of source:sink relationships will plant growth be effectively understood—and potentially manipulated—at every stage of development in order to maximize yield.

Sources and sinks affect growth and yield

Evidence that growth may be controlled by both source and sink strengths comes from manipulation experiments and studies of natural variation among species.

Manipulation experiments

Manipulating the source:sink balance shows that source and sink strengths often operate below their full potential, due to the limitations imposed by environmental and developmental changes discussed above. Historically, such manipulations involved physically manipulating the plant or its environment: for example, source activity may be altered by elevated CO_2, defoliation, or shading, while sink activity may be altered by sink removal or sink chilling. However, modern genetic approaches may now be used to alter source and sink activity with greater elegance. Table 1 outlines a range of source:sink manipulations and summarizes their results. Broadly speaking, increasing either source or sink may increase growth, suggesting that both can limit growth to a certain extent. Sources and sinks regulate each other by molecular feedback mechanisms (discussed later), and evidence for these is seen at the whole-plant scale when manipulation of the source affects sink activity, and *vice versa*.

Elevated CO_2 increases the potential carbon source activity of the plant by stimulating photosynthesis, and this typically translates into faster growth (Table 1; e.g. McConnaughay *et al.*, 1993; Christ and Körner, 1995; Masle, 2000; see also Taylor *et al.*, 1994; Ranasinghe and Taylor, 1996; Long *et al.*, 2006*b*; Ainsworth and Rogers, 2007; Leakey *et al.*, 2009), also affecting cell patterning, cell expansion, and plant architecture (Kinsman *et al.*, 1997; Pritchard *et al.*, 1999; Masle, 2000). Growing plants in large pots increases the potential carbon sink activity, due in part to increased nitrogen availability, generally leading to increased growth (Table 1; McConnaughay *et al.*, 1993; Poorter *et al.*, 2012), and experiments comparing species or cultivars with different sink sizes reveal that growth is faster when sinks are larger (Table 1; Reekie *et al.*, 1998; Aranjuelo *et al.*, 2013).

Reduction of source leaf area by defoliation usually leads to an increase in photosynthesis in the remaining leaves, to maintain source activity within the plant and support the sinks (Table 1; von Caemmerer and Farquhar, 1984; Eyles *et al.*, 2013). This could indicate sink limitation of growth because leaves are not carrying out their maximal potential rates of photosynthesis under normal conditions. In contrast, decreasing sink capacity—for example, by inhibiting sucrose export from leaves to reduce the apparent sink demand—leads to an inhibition of photosynthesis (Table 1; Ainsworth and Bush, 2011) mediated by an increase in leaf carbohydrates (Sheen, 1990).

Combining experimental treatments that affect both source and sink provides evidence that sources and sinks work together and feed back on each other. Photosynthetic acclimation at elevated CO_2 concentration is a decrease in photosynthetic capacity that reduces the magnitude of the CO_2-induced stimulation in photosynthetic rate at elevated CO_2. Acclimation acts to reduce the ratio of source:sink activity and thus adjust source:sink balance towards equilibrium. Combining defoliation and elevated CO_2 treatments (which decrease and increase the source, respectively) shows that photosynthetic acclimation under elevated CO_2 is alleviated by defoliation, supporting the hypothesis that it is sink-mediated (Table 1; e.g. Bryant *et al.*, 1998; Rogers *et al.*, 1998; Ainsworth *et al.*, 2003). The alleviation of acclimation occurs because defoliation opposes the effect of elevated CO_2 by decreasing the source:sink ratio, and higher levels of photosynthesis can thus be maintained in the remaining leaves. The opposite effect is seen when the source is increased but the sink is reduced. For example, when physical removal / restriction of sinks or genetic manipulation to reduce sink size is combined with elevated CO_2, leading to an increase in the source:sink balance, source activity is decreased in order to return towards equilibrium (Table 1; Arp, 1991; Ainsworth *et al.*, 2004). Combining low nitrogen or low temperature—which restrict sink development—with elevated CO_2 has a similar effect (Table 1; Arp, 1991). In contrast, increasing

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				
Eucalyptus globulus	Defoliation + Debudding	Reduces source Reduces sink	Defoliation increases photosynthesis in other leaves; source:sink biomass ratio is main driver of this change	(Eyles *et al.*, 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 *et al.*, 1998)
Lolium perenne	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 *et al.*, 1998)
Phaseolus vulgaris	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)
Lolium perenne	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 *et al.*, 2003)
Dactylis glomerata	Elevated CO_2	Increases source	Shortening of cell cycle in shoot and root meristems	(Kinsman *et al.*, 1997)
Triticum aestivum	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)
Arabidopsis thaliana	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 *et al.*, 2013)
Various species	Inhibition of sucrose export from source leaves	Reduces apparent sink demand	Inhibition of photosynthesis	(Ainsworth and Bush, 2011)
Glycine max	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 *et al.*, 2004)
Solanum tuberosum	Transgenic reduction of ADP-glucose pyrophosphorylase	Reduces sink capacity by reducing starch synthesis	Tuber sinks adapted by increasing sucrose content	(Müller-Röber *et al.*, 1992)
Solanum tuberosum	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 synthesizing fructan instead	(Zuther *et al.*, 2011)
Tricitum aestivum	Transgenic modification to increase sucrose uptake in developing grains	Increases sink	Storage protein synthesis increased	(Weichert *et al.*, 2010)

Table 1. *Continued*

Species	Manipulation	Effect	Key result	Reference
Triticum aestivum	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 *et al.*, 1998)
Abutilon theophrasti and *Setaria faberii*	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 *et al.*, 1993)
Triticum aestivum	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 *et al.*, 2013)
Brassica 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 *et al.*, 1998)

'+' denotes treatments applied in combination; '/' denotes alternative treatments.

carbon sink capacity under elevated CO_2, by using high-yielding cultivars or adding nitrogen, facilitates increased photosynthesis (Table 1; Farage *et al.*, 1998; Aranjuelo *et al.*, 2013).

Differences among species

In some species, developmental plasticity allows for greater flexibility when the source:sink balance is perturbed. Potato and citrus may easily increase their sink size, so tend to suffer less from feedback inhibition of photosynthesis (Paul and Foyer, 2001), and nitrogen-fixing legumes are easily able to increase their sink size in response to elevated CO_2 (Rogers *et al.*, 2009).

The physical mechanism of carbon export is important for the coordination of source and sink. Growth determinacy in soybean prevents an increase in photosynthesis at high CO_2, while poplar trees have high photosynthate export and maintain elevated photosynthesis at high CO_2 (Table 1; Ainsworth *et al.*, 2004; Ainsworth and Bush, 2011). Species which are symplastic loaders (many trees and shrubs) transport sucrose from source tissues into the phloem through developmentally fixed plasmodesmata, whereas apoplastic loaders (many herbaceous species) use developmentally plastic membrane transporters (Ainsworth and Bush, 2011). Therefore, at high CO_2, symplastic loaders cannot upregulate photosynthate export to the same extent as apoplastic loaders. As a result they tend to accumulate more non-structural carbohydrates in their leaves (Körner *et al.*, 1995) and can show a smaller increase in photosynthesis under elevated CO_2. However, despite their symplastic loading strategy, trees are generally well able to maintain photosynthetic stimulation under elevated CO_2 (Ainsworth and Rogers, 2007) although some species are capable of both symplastic and apoplastic loading and many species have not yet been characterized.

Taken together, this evidence clearly demonstrates that sources and sinks can both limit growth, and that feedbacks enable a degree of compensation. Species with greater plasticity can be more flexible in their response to manipulations of source and sink.

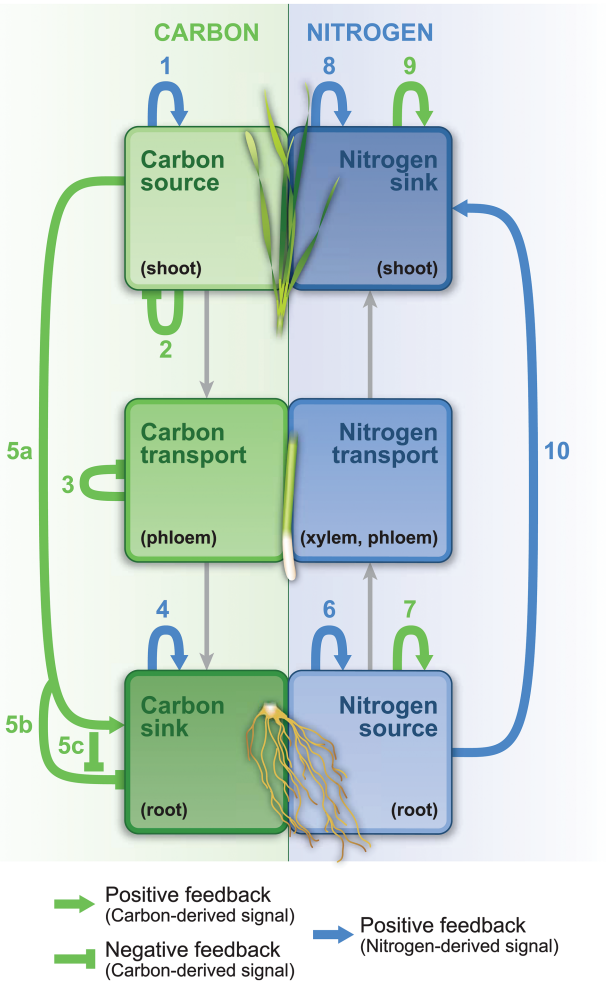
Regulation of sinks and sources

Regulation of source:sink balance is essential for enabling plants to maintain a growth rate appropriate for a given availability of resources. Storage allows the assimilation of more resources than are needed in growth, to create a reserve for future development in a fluctuating environment or recovery from disturbances such as herbivory. However, carbon assimilation must be appropriate for the available sink strength, in order to create a sufficiently large store that is still within the limits imposed by sink potential—thus sinks must feed back on sources to regulate their activity. Similarly, source activity must influence sink strength so that appropriate sinks may develop and plants can fully realize their growth potential for a given resource availability. Furthermore, the high metabolic costs of carbon and nitrogen assimilation mean that regulation of source and sink is vital to avoid wasting energy.

A complex molecular network including carbon- and nitrogen-derived signals and phytohormones has evolved to integrate the uptake, assimilation, and allocation of resources (Nunes-Nesi *et al.*, 2010). Many mechanisms of these molecular interactions are now well established although the puzzle remains incomplete at the whole-plant scale. Figure 1 illustrates key feedforward and feedback mechanisms regulating the source:sink relationship. Carbon- and nitrogen-derived feedforward and feedback signals act on sources and sinks of both carbon and nitrogen. This allows sources and sinks to modify their own activity, and also to regulate that of other tissues, creating molecular signalling links between source and sink.

Carbon feedbacks

Leaf carbohydrates feed into a complex network, affecting transcription, translation, and post-translational processes in order to balance carbon supply and demand (reviewed in Fig. 1). For example, a high carbon status upregulates nitrogen source and sink activity (Fig. 1; arrows 7 and 9) and carbon sink activity (arrows 5a and 5c), while downregulating photosynthesis



KEY:

1. If sink strength for carbon is high, **nitrogen-derived signals** increase carbon source activity. **Cytokinins** travel from root to shoot (10) and upregulate photosynthetic genes when the root nitrogen concentration – and thus the capacity for carbon usage – is high (Paul and Foyer, 2001). **Nitrogen-derived signals** also modulate feedback of **sugars** on photosynthesis (2) (Stitt and Krapp, 1999).
2. When **sugars** accumulate in the leaf they repress the expression of photosynthetic genes (reviewed by Smith & Stitt, 2007); the glucose sensor **hexokinase** leads to stomatal closure when sucrose production exceeds drawdown by phloem loading and thus reduces photosynthesis (Kelly et al., 2013); **carbohydrate accumulation**, **redox signals**, and **phosphate recycling** enable sink regulation of photosynthesis in the short term (Paul and Foyer, 2001).
3. **Sugars** in the phloem regulate export of leaf carbohydrates (Ainsworth and Bush, 2011). Inhibition of sucrose loading can increase the concentration of sucrose in the leaf, leading to a reduction in source activity (2). For example, a proton-sucrose symporter in sugar beet is regulated by sucrose, allowing high sucrose levels in the phloem to influence export from the leaf by negative feedback (Vaughn et al., 2002).
4. **Cytokinins** increase cell division and sink strength, increasing growth when nitrogen is plentiful (Kuiper, 1993; Ghanem et al., 2011; Thomas, 2013).

5a. The glucose sensor **hexokinase**, the primary metabolite **trehalose-6-phosphate (T6P)** and the **TOR protein kinase signalling pathway** provide three major ways in which sugar levels upregulate plant growth (Smeekens et al., 2010). Sucrose levels upregulate **T6P** and **TOR**; **TOR** increases growth and **T6P** appears to be an important integrator of sucrose and growth although its role is still debated (Xiong et al., 2013; Nunes et al., 2013; Lastdrager et al., 2014; Lunn et al., 2014). This leads to a positive feedback between source activity and sink activity.

5b. The **protein kinase SnRK1** and the **C/S1 bZIP transcription factor network** inhibit growth (reviewed by Lastdrager et al., 2014; Smeekens et al., 2010) and are regulated by metabolite status, allowing source to repress sink by reducing growth when carbon resources are scarce.

5c. **Sucrose** and **T6P** repress the action of **bZIP transcription factors** and **SnRK1** respectively, lifting repression of growth (5b) when photosynthate is plentiful (Lastdrager et al., 2014).

6. **Nitrate** and **cytokinins** increase transcription of nitrate reductase (NR), a key enzyme in nitrogen assimilation (Stitt and Krapp, 1999). This allows plants to exploit high soil nitrogen. NR transcription is induced by **nitrate** and repressed by downstream metabolites such as **glutamine** (Klein et al., 2000).
7. **Sugars** are thought to positively regulate NR in the root (Stitt and Krapp, 1999).
8. **Nitrate** and **cytokinins** upregulate NR, and thus nitrogen assimilation, in the shoot as in the root (6).
9. **Sugars** regulate shoot NR at a transcriptional and post-translational level; low sugar levels can override control of NR by nitrate and repress NR transcription (Stitt and Krapp, 1999; Klein et al., 2000; Kaiser et al., 2002; Reda, 2015).
10. **Nitrogen** increases **cytokinin** levels and these are exported to the shoot. When plant nitrogen levels are high, **nitrogen-derived signals** have a range of effects at both local (e.g. increasing lateral root growth) and whole-plant (e.g. increasing shoot:root allocation) levels (reviewed by Stitt & Krapp, 1999).

Fig. 1. A range of feedback mechanisms fine-tunes the source:sink balance and therefore plant growth. Signals derived from both carbon (green) and nitrogen (blue) regulate source–sink relationships. Feedbacks operate at the tissue level (arrows 1–4 and 6–9) and at the whole-plant level (arrows 5 and 10). Narrow grey arrows represent net movement of carbon and nitrogen from source (lighter) to sink (darker) tissues within the plant.

(arrows 2 and 3). In contrast, a low carbohydrate content in the leaf leads to the repression of carbon sink activity (arrow 5b). The presence of such a regulatory feedback loop in the leaf has long been investigated: in 1868, Boussingault first proposed that assimilate accumulation could decrease photosynthesis by feedback (Neales and Incoll, 1968), yet the precise mechanism for sucrose signalling remains unknown (Reda, 2015).

The partitioning of carbon into starch and sucrose is an important point of carbon source–sink regulation (directly affecting arrows 2 and 5 in Fig. 1) and is controlled by several factors. For example, trehalose-6-phospate is believed to influence starch synthesis by redox-regulation of AGPase, a key enzyme in starch synthesis, while the degradation of starch is regulated by a variety of enzymes, by the circadian clock, and possibly by starch-derived signals or even the level of starch itself (Smith and Stitt, 2007). It is important to note that most research into sugar and starch regulation has been carried out in *Arabidopsis* and it is therefore necessary to expand current knowledge of regulatory mechanisms in crop plants, which may not share the same mechanisms. For example, the starch degradation pathway in the endosperm of cereal grains differs from that in *Arabidopsis* leaves (Smith, 2012), while mutation of PGM, an enzyme important in starch synthesis and essential for normal growth in *Arabidopsis*, does not affect all species equally, suggesting the use of different metabolic pathways or storage compounds (Stitt and Zeeman, 2012).

Nitrogen feedbacks

Just as carbon availability impacts both on carbon and nitrogen source and sink activities, nitrogen availability regulates the uptake and storage of carbon (reviewed in Fig. 1). A high nitrogen status increases the rate of carbon acquisition in photosynthesis and also upregulates carbon sinks (Fig. 1; arrows 1 and 4). Nitrogen also increases the assimilation of nitrate by the enzyme nitrate reductase, to upregulate nitrogen source and sink activity (Fig. 1; arrows 6 and 8), and increases shoot:root allocation, enabling the plant to acquire more carbon and make use of the available nitrogen (arrow 10). Furthermore, nitrate increases root cytokinin production and export (Fig. 1, arrow 10), important for meristem generation and function in shoot and root (Su *et al.*, 2011).

Crosstalk

Tight control of the source–sink relationship is facilitated by points of crosstalk between carbon- and nitrogen-signalling

pathways. This enables plants to maintain a degree of co-limitation for sources and sinks, and carbon and nitrogen. Starch synthesis is regulated by nitrate as well as by sugar: nitrate downregulates transcription of the gene encoding the regulatory subunit of AGPase, an enzyme involved in starch synthesis. This negative regulation by nitrate lowers starch accumulation and allows more leaf sugar to be exported for growth when nitrate levels are high (discussed by Stitt and Krapp, 1999). Leaf sugars are involved in the transcription and post-translational regulation of nitrate reductase (Fig. 1, arrow 9), enabling plants to coordinate carbon and nitrogen supply (Stitt and Krapp, 1999; Kaiser *et al.*, 2002): sugars increase the level of nitrate reductase (Reda, 2015) while low sugar levels repress its transcription (Klein *et al.*, 2000).

Coordination is enhanced still further by crosstalk between sugars and phytohormones [for recent review, see Lastdrager *et al.* (2014)]. This contributes to developmental processes such as meristem activity (which is generally upregulated by cytokinins, e.g. Fig. 1, arrow 4) and lends an added layer of complexity to growth regulation (Eveland and Jackson, 2012). For example, sugars interact with abscisic acid (Teng *et al.*, 2008) and with auxin (Stokes *et al.*, 2013). Sugars can also act directly on development, independently of phytohormones, and are believed to be important for regulating meristem activities (Eveland and Jackson, 2012). Furthermore, sugar levels influence the transcription of thousands of genes; sugars and the circadian clock regulate each other; and sugars induce phytochrome-interacting factors, which regulate growth (Lastdrager *et al.*, 2014).

In summary, molecular feedbacks including carbon- and nitrogen-derived signals regulate sources and sinks for carbon and nitrogen. Crosstalk exists both between these signals and with growth regulators. With such elaborate molecular mechanisms in place—and given sufficient resources—increasing the sink activity of a plant might be expected to increase its source activity, and vice versa. However, as discussed above, experimental manipulations of sink strength and of source strength reveal that growth cannot always be altered as expected (e.g. Long *et al.*, 2006*a*). It has thus become important to increase knowledge of the potential strengths of source and sink, the limits to their physiological interactions, and to better incorporate known molecular mechanisms of the source–sink relationship into models of whole-plant growth. Moreover, in order to effectively increase crop yield, it may be necessary to manipulate the molecular feedback mechanisms between source and sink, in addition to manipulating the strengths of source and sink themselves. A source–sink-based perspective on growth is therefore an essential cross-disciplinary tool for understanding and increasing the growth and yield of crops.

Alternative perspectives on growth

Different disciplines have alternative perspectives of plant growth. Advancing the mechanistic understanding of growth that is necessary to realize improvements in crop growth will require a unification of these disciplinary perspectives. Here, a parsimonious model of plant growth which unites these different perspectives is presented. An extremely simplified system is used for illustration. Various factors have been omitted for simplicity, clarity, and ease of unification. These are both intrinsic (additional resources and tissue types within the plant, and feedbacks between internal processes) and extrinsic (environmental limitations on physiological and developmental processes), since plant growth and development are the product of genetic and environmental processes (e.g. Prusinkiewicz *et al.*, 2009; Pantin *et al.*, 2012). Rather than provide comprehensive models of growth, this section highlights key processes of interest for each of the three perspectives on growth, and uses equations to demonstrate the focus of each. In each perspective, the processes of interest depend on source and sink activities and tissues, and the equations are finally united to form a basic holistic model of plant growth which is underpinned at every level by source–sink interactions.

Growth may be conceptualized in a number of different ways, and may be viewed through different lenses depending on the perspective adopted. Three classic perspectives on growth are based on: the physiology of resource acquisition and loss; the internal allocation of resources to source and sink organs; and the morphogenetic development of source and sink tissues. Crucially, these three alternative perspectives, adopted by communities of scientists from different disciplines are all readily conceptualized within the context of source–sink interactions.

Here, equations have been used to illustrate each definition of growth, by considering a highly simplified system in which a single resource (carbon) is acquired by a source tissue (leaves) and used by sinks (in both leaves and roots). This system enables the limitations on growth to be formally defined in a readily interpreted form, yet still allows growth to be viewed through the three alternative lenses presented. Each of the three perspectives presented is, by mathematical definition, true. However, each is based implicitly upon an alternative hypothesis about the critical intrinsic controls on growth.

At its most fundamental level, growth may be defined as an increase in plant mass over time. For simplicity, growth is considered equivalent to net organic carbon gain, and the acquisition of other resources is ignored. The dry weight of organic carbon in the plant is W_P, referred to in this section as mass, and absolute growth rate (AGR) is thus net carbon gain over time, in g d^{-1}:

$$\frac{dW_P}{dt} = Absolute\ growth\ rate \qquad (3).$$

Growth may now be defined in various ways according to the perspective adopted, but the central definition [Equation (3)] is retained. The different approaches to explaining growth focus attention on different primary limitations.

Physiology

The first approach is physiological: a flux balance of organic carbon for the plant based on the loss and acquisition of this

essential resource to and from the atmosphere via the processes of respiration and photosynthesis (Lambers *et al.*, 1989; Poorter and van der Werf, 1998).

This carbon-based balance viewpoint on growth is adopted widely in crop production models and in Ecosystem and Earth System Models (EESMs), which simulate the physical properties and carbon exchange of the vegetated land surface (e.g. Knorr, 2000; Sitch *et al.*, 2003; Lu and Ji, 2006; Zaehle and Friend, 2010), and are ultimately used to project future global change (Friedlingstein *et al.*, 2014; IPCC, 2014). This flux balance approach expresses the AGR as the difference between photosynthesis and respiration:

$$\frac{dW_P}{dt} = A \times W_L - R \times W_P \qquad (4a),$$

where A is gross photosynthetic carbon uptake in g C d^{-1} g^{-1} leaf mass, W_L is total leaf mass (g), and R is respiratory carbon loss in g C d^{-1} g^{-1} plant mass. Note that not all of the inorganic carbon captured by photosynthesis is converted to biomass, and so R includes the metabolic costs of biosynthesis, translocation, exudation, and the uptake and assimilation of nitrogen needed for growth ('growth respiration'), as well as those associated with maintaining existing tissues ('maintenance respiration') (reviewed by Amthor, 2000).

Respiration may be partitioned between photosynthetic and non-photosynthetic tissues:

$$\frac{dW_P}{dt} = (A \times W_L) - (R_L \times W_L) - (R_R \times W_R) \qquad (4b),$$

where the subscripts L and R denote leaf and root tissues, respectively. A simple case is considered here, but this approach may be easily extended to include other sink tissues such as storage organs, stems, and reproductive tissues.

This basic model views growth as the net accumulation of organic carbon. However, the approach is limited because, while respiration is one component of sink activity, the sink activities of growth and storage are not explicitly considered, and accounting for sink limitation requires modifications to the model (Fatichi *et al.*, 2013). Furthermore, recent authors have argued that A and R do not control plant growth rate. Instead, it is argued that growth is controlled by the supply of mineral nutrients and water, and the plant regulates A and R to meet its growth requirements (Körner, 2012; Fatichi *et al.*, 2013; Körner, 2013). Without accounting for sink activities and their feedbacks on photosynthesis, the approach illustrated by Equations (4a) and (4b) cannot provide a complete description of the processes controlling growth.

Allocation

A second approach considers the internal allocation of resources to either photosynthetic or non-photosynthetic tissues. These tissues represent net carbon sources and sinks, respectively.

The philosophy underlying this approach is that allocation of resources to leaves (especially to leaf area) accelerates growth, whereas allocation to non-photosynthetic tissues (in this case, roots) has an opposing effect. Allocation is an important determinant of growth rate, and this viewpoint is classically adopted by ecologists when considering the ecological strategies of plants (Grime and Hunt, 1975), resource limitations on growth (McConnaughay and Coleman, 1999; Yang and Midmore, 2005), and the growth-allocation trade-off as a constraint on life history decisions (Bazzaz *et al.*, 1987). It is also considered dynamically in relation to resource limitation in global vegetation models (e.g. Higgins and Scheiter, 2012) and in crop simulation models (e.g. Weir *et al.*, 1984; Brisson *et al.*, 1998; Jamieson *et al.*, 1998).

The change in plant mass over time is the product of leaf area ratio, net assimilation rate, and plant mass:

$$\frac{dW_P}{dt} = LAR \times NAR \times W_P \qquad (5a),$$

where LAR is leaf area ratio (m^2 leaf area g^{-1} plant mass) and NAR is net assimilation rate (g carbon m^{-2} leaf area d^{-1}), remembering that carbon is equivalent to mass in these examples.

Viewed through the lens of carbon allocation, growth depends critically on the availability of photosynthetic tissue, expressed as the LAR. The LAR is in turn a product of SLA, the ratio of leaf area to leaf mass (efficiency of leaf area deployment, m^2 g^{-1} leaf mass), and LMR, the ratio of W_L to W_P (dimensionless):

$$LAR = SLA \times LMR \qquad (5b),$$

Both SLA and LMR vary with W_P. At any point in time, by definition, leaf area (L, in m^2) is therefore given by the following equation:

$$L = SLA(W_P) \times LMR(W_P) \times W_P \qquad (5c),$$

where $SLA(W_P)$ and $LMR(W_P)$ denote W_P-dependent values of SLA and LMR. The LAR changes over time in accordance with changes in allocation during growth, and the components of LAR therefore vary with plant mass, W_P:

$$\begin{aligned}\frac{dL}{dt} = &\frac{\partial SLA}{\partial W_P}\frac{\partial W_P}{\partial t} LMR \times W_P \\ &+ \frac{\partial LMR}{\partial W_P}\frac{\partial W_P}{\partial t} SLA \times W_P \\ &+ \frac{\partial W_P}{\partial t} SLA \times LMR\end{aligned} \qquad (5d),$$

where $\partial SLA / \partial W_P$ and $\partial LMR / \partial W_P$ describe the effects of allocation changing over time as plant mass changes.

The allocation perspective on growth, like the physiological perspective, can be interpreted in terms of source–sink interactions. For carbon, leaves constitute a net source while roots constitute a net sink. Thus Equation (5d) describes the change in the carbon source over time, and equivalent equations for roots would describe the change in the carbon sink.

These first two perspectives, which look at growth through the lenses of physiology and allocation, are ultimately resource-driven. The physiological perspective defines growth as being driven by carbon acquisition from, and losses to, the external environment, although in reality sink feedbacks are

also important here. The allocation perspective is driven by the allocation of carbon to structures that are responsible for its net acquisition or consumption.

Development

The third perspective encompasses the developmental processes of organ initiation, growth, and termination. These processes represent carbon sinks.

In contrast to the first two approaches, which are resource-driven, the third perspective considers the developmental process explicitly, and this is the approach applied by developmental biologists working on growth in *Arabidopsis* and crop plants. This perspective also impinges on large-scale macroevolutionary comparisons among species, since the evolution of development must inevitably drive changes in potential growth rate, for example, in transitions between woody and herbaceous life forms (Dodd *et al.*, 1999) or in transitions between determinate and indeterminate growth (Shishkova *et al.*, 2008).

Cells divide and expand at a rate that is ultimately limited not by the speed of resource acquisition from the external environment (although this does influence meristem activity, e.g. Pritchard *et al.*, 1999; Granier *et al.*, 2007) but by intrinsic constraints set by the internal resource balance, the cell cycle and developmental programme. Again, internal source–sink interactions underpin these processes. Because cell division and expansion, and the creation of new meristems through branching constitute sinks for carbon, modelling growth from a developmental perspective places greater emphasis on the limitation of growth by sink rather than source activity. Ultimately, cell division rate is limited by molecular constraints: for example, plant genome size is negatively correlated with cell cycle time (Francis *et al.*, 2008) and with root meristem growth rate (Gruner *et al.*, 2010).

Complex formulations for organ initiation, expansion, and termination have been developed, but a simple case is considered, for illustrative purposes. If growth is considered in terms of morphogenetic constraints and development, without taking into account environmental parameters, it can be expressed as a function of the number and mass of cells:

$$\frac{dW_P}{dt} = \frac{dC}{dt} \times m \qquad (6a),$$

where C is the number of cells in the plant, dependent on the division rate dC/dt in cells d^{-1}, and m is the mass of organic carbon in each cell, g $cell^{-1}$.

As in Equation (4b), this can be partitioned into developmental processes occurring in leaves and in roots, where W_L and W_R refer to the dry mass of organic carbon in the leaf and root, respectively:

$$\frac{dW_P}{dt} = \frac{dW_L}{dt} + \frac{dW_R}{dt} = \frac{dC_L}{dt} \times m_L + \frac{dC_R}{dt} \times m_R \qquad (6b).$$

Unification

The three perspectives on growth can be unified to show their interrelated nature, and to illustrate the overarching dependence of growth on source–sink relationships. While the physiological perspective focuses on metabolic processes which exchange carbon with the external environment, the allocation perspective focuses on the tissues that carry out net acquisition and drawdown of carbon, and the developmental perspective focuses on the rate of cell division in these tissues, all three perspectives are underpinned by source:sink interactions.

The mass of leaf and root tissues, seen in Equations (4b) and (6b) (relating to physiology and development, respectively), are dependent on allocation and can be expressed as follows:

$$W_L = LMR \times W_P \qquad (7a),$$

$$W_R = (1 - LMR) \times W_P \qquad (7b).$$

Substituting for dW_P/dt in Equation (6b) using Equation (4b) unifies the physiological and developmental perspectives:

$$(A \times W_L) - (R_L \times W_L) - (R_R \times W_R) = \frac{dC_L}{dt} \times m_L + \frac{dC_R}{dt} \times m_R \qquad (8a),$$

and substituting in the definitions of W_L and W_R seen in Equations (7a) and (7b) incorporates the allocation perspective, to give:

$$A \times LMR \times W_P - R_L \times LMR \times W_P - R_R \times (1 - LMR) \times W_P = \frac{dC_L}{dt} \times m_L + \frac{dC_R}{dt} \times m_R \qquad (8b),$$

where the dependence of SLA and LMR on W_P has been suppressed for ease of presentation.

This unifies the three lenses for looking at growth, and can be rearranged as:

$$A \times LMR \times W_P = \left[\frac{dC_L}{dt} \times m_L + R_L \times LMR. \times W_P \right] + \left[\frac{dC_R}{dt} \times m_R + R_R \times (1 - LMR) \times W_P \right] \qquad (9a),$$

which is an expression of, for carbon:

$$Source\ strength = leaf\ sink\ strength + root\ sink\ strength \qquad (9b).$$

Equation (9) illustrates an important point: it is relatively easy in a single mathematical formulation to encapsulate the intrinsic limitations on growth imposed by the physiology of resource capture, internal resource partitioning, and morphogenetic constraints on organ development. Equation (9) is not intended to be a realistic and detailed representation of growth—as discussed, it makes manifold simplifying assumptions and ignores several important components. Rather, it is intended to illustrate the potential value of taking such a unifying approach, as in the more realistic, detailed representations of the plant system developed by Chew *et al.* (2014) and Evers *et al.* (Evers *et al.*, 2010; Vos *et al.*, 2010). This unification is conceptually useful for understanding how the critical

processes of source and sink development and activity interact to limit growth in different species. A key step forwards will be model representation of the mechanisms that govern the crosstalk and interactions between different components.

Crucially, Equation (9) shows that source–sink interactions underpin all the aspects of growth described in the preceding equations. A balance between source and sink is essential for plants to grow and develop efficiently. Increased organ initiation, faster cell growth, and larger organ size will strengthen sinks; changes in the root:shoot ratio or leaf area ratio can alter the balance between carbon and nitrogen source and sink tissues; while uptake rates of carbon and mineral nutrients are primary determinants of source strength. A holistic understanding of growth rate should therefore draw on the concepts of source and sink strength, recognizing that each depends on the size and activity of the relevant tissue [Equations (1) and (2)]. Integrating molecular interactions at the tissue level (Fig. 1) with the behaviours of whole plants in terms of physiological regulation, allocation to different tissues and developmental processes will be critical for building a picture of the interactions between the three components discussed above. In order to increase crop yield effectively, it will be essential to build comprehensive growth models in which the source:sink balance is the cornerstone underpinning physiological, allocation-based, and developmental mechanisms for growth limitation. This will create an integrated perspective that allows the effects of this vital determinant of growth to be realized.

Conclusions and recommendations

An integrated understanding of source–sink relationships, growth, and yield is a vital next step in ongoing efforts to increase crop productivity, and requires a number of key 'unknowns' to be addressed: (1) Which components in the plant system of sources and sinks exert the strongest control over growth in major crops? (2) How do these source and sink limitations change during the crops' lifetimes? (3) Through what developmental or physiological mechanisms do these limitations arise? (4) Via genetic modification or selective breeding, to what extent is it possible to manipulate these processes to upregulate source and sink together, at the appropriate stage of development, to improve crop production?

We advocate the development of an integrated perspective, unifying physiological limitations on fluxes, controls on growth allocation, and the development of sink tissues, to successfully improve crop growth. A holistic view of the mechanistic interactions between sinks and sources is needed at the whole-plant scale during the trajectory of growth and development, in order to identify bottlenecks limiting growth rate. To address this knowledge gap, it will be vital to develop a greater understanding of the physiological processes operating at intermediate scales between molecular mechanisms and whole-plant traits. Ideotypes for future crops have been proposed (Sreenivasulu and Schnurbusch, 2012; Bennett *et al.*, 2012; von Caemmerer *et al.*, 2012; Reynolds *et al.*, 2012; Ort *et al.*, 2015), but reaping the maximum possible gains from these approaches requires a parallel effort in understanding how and when source and sink capacity limit growth and yield.

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