



Commentary

Fruiting and sink competition

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'Natural selection tends to make the energy flux through the system a maximum, so far as compatible with the constraints to which the system is subject', AJ Lotka (1922).

Introduction

The extent that photosynthesis is stimulated or suppressed in response to changing demands is a challenging topic for physiology. In part, the question is difficult to answer because there are so many sinks to keep track of, and they vary seasonally and inter-annually. Some sinks, like root exudates, are particularly difficult to measure, as is photosynthesis on large trees with varying canopy densities and physiological status.

It is well established that inadequate light, water or nutrients, along with suboptimal temperatures or herbivory, can limit photosynthesis and thereby reduce both vegetative and reproductive growth. At other times, vegetative and reproductive growth compete for carbohydrates. Similarly, demands for carbohydrates by roots and other respiring organs may affect growth aboveground. Seasonally, with plant dormancy, a lower sink demand can reduce photosynthesis or enhance the process when conditions are conducive for growth (Paul and Foyer 2001, Pinkard et al. 2011, Fatichi et al. 2014). A combination of any or all of these carbohydrate pathways could cause a trade-off between reproduction and growth (Figure 1).

Large production of fruits and seeds reduces vegetative growth in trees (Eis et al. 1965, DeJong and Grossman 1995, Thomas 2011), but the link between reproduction and vegetative growth has rarely been analyzed for components of the tree's carbon balance other than for wood and reproduction. Also poorly examined is the link between fruit production, shoot structure and branching

patterns. Two papers in this issue (Rosati et al. 2018a, 2018b) explore the link between fruit production, vegetative growth, shoot structure and branching using two cultivars of olive trees.

To assess competition between reproduction and vegetative growth, the authors manipulated fruit production of the cultivars, one fast- and the other slow-growing. They then proceeded to measure annual production of flowers, fruits, leaves, wood and roots under the range of controlled conditions after the cuttings were 2–3 years old. For two subsequent growing seasons, fruiting was controlled by imposing four treatments: (1) no flower removal, (2) flower removal for year one, (3) flower removal for year two and (4) flower removal for both years. The fast-growth cultivar did not flower in year one, so the design was not balanced for both cultivars (the fast-growth cultivar did not include plants for treatment 2 or 3).

Rosati et al. (2018b) report almost a 1:1 trade-off between annual production of biomass in reproductive tissue and vegetative growth. In other words, as fruit production increased, vegetative growth was reduced proportionately. Biomass fractions of the total for the four vegetative components were consistent across treatments for each cultivar. Because fruits had a greater energy content than other forms of biomass, when annual production was converted to the same energy (glucose) units, increased fruit production yielded a 73% reduction in vegetative growth. The authors suggest that the <1:1 trade-off between fruit and vegetative production indicates that the increased demand from growing fruits enhances photosynthesis, but not sufficiently to eliminate sink competition.

Increased fruit production also affected the structure of branches produced in the same year as the fruit, with shorter

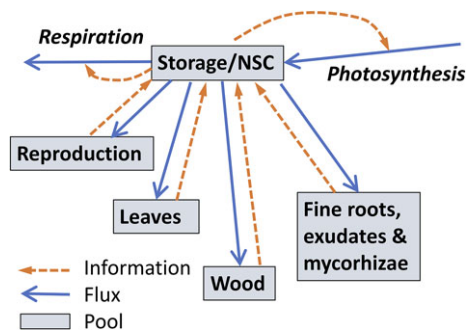


Figure 1. A conceptual diagram for sink competition and source-sink interactions. Pools are represented by boxes, fluxes by solid arrows and information by dashed arrows. Photosynthesis supplies carbohydrates to the storage or non-structural carbohydrate (NSC) pool (shared among all structural pools). The key addition to this simple flow diagram is the feedbacks between the sinks and the NSC pool. Sinks compete by being stronger or weaker—taking more or less from the NSC pool, or by having a higher priority (top to bottom in figure). Temperature and resources (water and nutrients) alter the sink strength of the pools and perhaps competition among them. An increase of NSCs increases respiration and decreases photosynthesis. A decrease of NSCs decreases respiration and increases photosynthesis.

branches occurring with increased fruit production. With increased fruit production, the new, shorter branches also had lower biomass, leaf area and ratio of shoot wood:leaf area (Rosati et al. 2018a). For the crown, new shoot length and wood and leaf biomass decreased with higher fruit production. The number of branches differed more among cultivars than with the amount of fruit, with the slow-growth cultivar having more branches.

The results of these two studies are important because they show that fruit production can alter tree size, growth and structure, yet most ecosystem, land surface and dynamic vegetation models do not incorporate fruit production (Walker et al. 2015 and references therein). These models also do not consider different sinks as competitors for limited carbohydrates, that there is a priority for different sinks, or that differences in sink strength might enhance or suppress photosynthesis, with potentially long-term effects (Drobyshev et al. 2010).

Ecosystem, land surface and dynamic vegetation models also differ in their consideration of autotrophic respiration, a large sink for about half of net photosynthesis. Some models consider autotrophic respiration as a competitor to growth, and subtract it first before distributing the remaining carbohydrate pool to growth (Running and Coughlan 1988, Running and Gower 1991), while others consider respiration as a fixed fraction of photosynthesis that has no effect on growth (Landsberg and Waring 1997). Models also differ in their treatment of respiration response to short- and long-term temperature exposure (Smith and Dukes 2013).

The analysis presented in these two papers offers important lessons for those attempting to measure and model tree carbon balances. The authors demonstrate that interactions between

different sinks must be considered as they affect the future structure and function of trees, whether or not fruit production has any effect on photosynthesis. Less apparent from the reported analyses, but equally important, is the recognition that it would be highly desirable to include all sources and sinks involved in a tree's carbon balance—admittedly a daunting task. In the two studies, neither photosynthesis nor respiration were measured, and changes in the flux of carbohydrates in and out of storage or that released as exudates from roots and mycorrhizae were not evaluated. To what extent might carbohydrates stored in roots be redistributed to enhance flowering? And, if the nutrition or water balance of leaves were altered, how might that affect flower and leaf production?

Although Rosati et al. (2018a, 2018b) have clearly demonstrated a strong reverse link between fruiting and vegetative production, other factors need to be monitored to make definitive statements regarding possible shifts in photosynthesis and competition between sinks. If photosynthesis per unit leaf area remained the same for all treatments, the carbohydrate for fruit production could be acquired from a reduction in carbohydrate stores from above- or below-ground sources or through a reduction in growth and maintenance respiration. Any changes in the sizes of the trees and their leaf areas among treatments could alter the total flux belowground (Giardina and Ryan 2002). Fruiting plants are known to have higher transpiration than non-fruited plants (Bustan et al. 2016), suggesting that photosynthesis might be higher as well. Non-fruited plants may have higher respiration if photosynthesis exceeded growth and carbohydrates accumulated (Robertz and Stockfors 1998), or more carbohydrates were exuded by roots for the same reason (Phillips et al. 2011).

If photosynthesis per unit leaf area changed with treatment, then inference is even more difficult because a relative increase or decrease in sink demand can, respectively, increase (Pinkard et al. 2011) or decrease photosynthesis (Paul and Foyer 2001). On the other hand, if non-fruited trees had higher leaf area, this would increase self-shading and potentially lower canopy photosynthesis per unit of leaf area compared with fruited trees.

Missing measurements and inference

One example illustrates the desirability to obtain a complete carbon balance to make definitive cause-and-effect inferences. Genet et al. (2010) found that wood growth (and growth per unit leaf area) decreased with tree age in both beech (*Fagus*) and oak (*Quercus*) (Figure 4 in the paper), which is a common observation (Ryan et al. 1997). Interestingly, the wood fraction of annual production, as well as that of carbohydrate and seed production, increased with age for beech, but not for oak. Genet et al. (2010) inferred that seed production and carbohydrate storage gained priority for carbohydrates over wood production as trees aged. Other possible explanations exist if other (unmeasured) changes

in partitioning of photosynthesis or photosynthesis itself are considered. If soil resources were to become less available as trees age (Gower et al. 1996, Ryan et al. 2004, Litton et al. 2007), more resources would be expected to be partitioned belowground, with a subsequent reduction in growth aboveground. Most belowground fluxes of carbohydrates go to maintain and replace fine roots and to sustain mycorrhizal fungi and free-living microbes in the rhizosphere. These sinks are ephemeral, highly seasonal and not recorded in simple assays of biomass. They need to be quantified.

Alternatively, Hsiao (1973) noted that growth is more sensitive to water stress than photosynthesis because cell expansion requires a higher turgor pressure than stomatal opening (Woodruff et al. 2004). As trees mature and grow in height and crown dimensions, the path for water movement becomes increasingly torturous as the ratio of foliage mass to branch production decreases exponentially (Figure 4 in Waring et al. (2016)). As a result, there is a linear relation between hydraulic supply of water to leaves and the maximum photosynthetic capacity (Brodrribb and Feild 2000). Reduction in growth could be caused by a combination of more limited soil resources and increased tortuosity of water movement through the xylem (Ryan et al. 2004), or diurnal trends in stomatal conductance that might have shown increased sensitivity to evaporative demand as branch length increases (Waring and Silvester 1994).

Other examples from carbon balance assessments over an age sequence (Ryan et al. 2004) and in whole-tree and free-air elevated [CO₂] experiments (Oren et al. 2001, Palmroth et al. 2006, McCarthy et al. 2010, Uddling and Wallin 2012, Sigurdsson et al. 2013) show a strong interaction of growth response with nutrition. These experiments confirm the difficulty of inferring cause and effect without measuring all of the components of the tree carbon balance.

In trees, photosynthesis can be uncoupled from photosynthetic capacity by hydraulic conductance and show responses to environmental drivers that differ from those where hydraulics are not considered (Waring and Silvester 1994, Hubbard et al. 1999). Still, the controls on respiration and belowground flux, beyond that influenced by temperature, remain poorly understood (Litton et al. 2007). Identifying source–sink tradeoffs without measuring all of the components of the tree carbon balance (Table 1) may lead to incorrect or incomplete inference. Even with a complete carbon balance, it may be difficult to identify cause and effect because the initial mechanisms that promote change are likely to be small while tree or stand measurements of carbon are accumulative and generally evaluated over timescales of months to a year.

Source control of sinks and sink competition

There is overwhelming evidence that photosynthesis is the primary supplier of carbohydrates, beginning with studies that relate

energy absorption by foliage to plant growth (Monteith 1972, 1977, Linder 1985). Photosynthesis has been demonstrated to control growth and respiration sinks over a broad range of distances and durations (Litton et al. 2007), and in many experimental manipulations (for example, Maier et al. 2004, Ryan et al. 2004, Forrester et al. 2006, Palmroth et al. 2006). Much evidence also shows that sink competition occurs (Litton et al. 2007), which also necessarily indicates a source limitation. The most dramatic sink competition occurs between wood production and total belowground flux, with wood production increasing and belowground flux decreasing as a consequence of greater availability of nutrients and water (Ryan et al. 2004, Stape et al. 2008). Wood growth also decreases in heavy, but not light seed years (Eis et al. 1965, Drobyshev et al. 2010, Thomas 2011, Hirayama et al. 2012, Rosati et al. 2018b, and many others), with managed fruit trees showing the most dramatic reductions.

For modeling, separation of sink response into differences in flux and differences in partitioning of photosynthesis to the sink is important because these processes are often treated separately. For example, elevated CO₂ or nutrient addition may alter photosynthesis (Nowak et al. 2004), partitioning (Ryan et al. 2004, Palmroth et al. 2006), both or neither. Whether the trade-off between wood growth and belowground flux or reproduction results from competition for a limited source or from an internal priority system (Waring and Schlesinger 1985) is unknown, though it may not matter for measurements and modeling.

The strong competition between reproductive flux and wood growth for fruit crop trees, together with the smaller size and uniformity of fruit trees and the ease of studying single genotypes suggests that greater interaction between horticulture and tree physiology would be fruitful for understanding whole-tree carbon balance and feedbacks. For example, horticulturists have devised a method for determining sink capacity by progressive fruit thinning (DeLong and Grossman 1995). In addition, horticulture studies would benefit from measurements of belowground flux by the carbon balance method (Giardina and Ryan 2002).

Sink–source feedbacks

Both positive and negative feedbacks from sink to source have been documented, but inference about these feedbacks remains difficult because of the lack of carbon balance measurements for most of these studies and the difficulty in interpreting the available measurements. Because growth (cell division and expansion) appears to be more sensitive to soil water potential, temperature and nutrition than photosynthesis (Hsiao 1973), drought studies often report an increase in non-structural carbohydrates (Muller et al. 2011, Piper et al. 2017). Inferences of source–sink behavior from non-structural carbohydrate (NSC) estimates are uncertain because these measurements vary greatly and are not comparable among laboratories (Quentin et al. 2015). Some NSCs are likely not accessible, or used for

Table 1. Components of a tree or stand carbon balance for annual or sub-annual estimates. Studies that have measured most of these components include Law et al. (1999), Maier et al. (2004), Ryan et al. (2004), Forrester et al. (2006) and studies cited in Litton et al. (2007).

Component	Measurements	Frequency	References
Total belowground C flux—root and mycorrhizae growth and respiration, exudates	Soil respiration – aboveground litter fall + Δ root biomass + Δ soil carbon	Per unit ground area soil respiration, aboveground litter fall: monthly or less; Δ root biomass, Δ soil carbon: annually or less	Raich and Nadelhoffer (1989), Davidson et al. (2002), Giardina and Ryan (2002)
Aboveground wood production	Tree height, diameter, local and validated allometric equation; biomass per ground area at time 2 – biomass at time 1	Annual or less for tree diameter	Clark et al. (2001), Ryan et al. (2004)
Aboveground foliage production	Aboveground litter fall + Δ foliar biomass (from local and validated allometric equation using tree diameter and perhaps tree height and crown depth estimate)	Per unit ground area aboveground litter fall: monthly or less; annual for tree diameter	Clark et al. (2001)
Reproduction	Sorted aboveground litterfall or branch sampling or harvest	Annual	Clark et al. (2001)
Foliar + reproductive respiration	Shoot or branch or fruit respiration throughout the canopy plus scaling measurements (mass, area, nutrient content of samples). Respiration temperature response and foliar and reproductive biomass also required	Monthly or less depending on seasonal variability	Ryan et al. (2004), Cavaleri et al. (2008), Ryan et al. (2009)
Wood respiration	Stem, branch and twig respiration plus scaling measurements (mass, area, nutrient content of samples)	Monthly or less depending on seasonal variability	Ryan et al. (2004), Cavaleri et al. (2006), Ryan et al. (2009)
Photosynthesis	Photosynthetic capacity from maximum photosynthesis under controlled light, humidity and [CO ₂] or from photosynthesis vs intercellular [CO ₂] curves. Environmental response of stomatal conductance vs free air vapor pressure deficit at controlled light and [CO ₂]. Detailed canopy gas exchange model such as MAESTRA	Monthly or less depending on seasonal variability	Zaehle et al. (2014), Walker et al. (2015)
Non-structural carbohydrate (storage) change	Assumed 0 for annual estimates. For sub-annual estimates, samples of foliage and wood throughout the canopy and fire roots for non-structural carbohydrate assay. Component biomass for extrapolating to area	Monthly or quarterly for sub-annual estimates	Smith et al. (2018)

other functions (Dietze et al. 2014). Accumulation of NSCs during drought may indicate a reduction in the growth sink yielding excess carbohydrates, or increased use of carbohydrates for osmotic and other physiological processes, or impeded transport or access to stored carbohydrates because of low plant water potential or reduced water content.

Branch pruning and adjacent branch girdling reduce source relative to sink and stimulate greater leaf-level photosynthesis (Pinkard et al. 2011, Asao and Ryan 2015), as does shading of the lower canopy (Whitehead et al. 1996). Phloem removal (Nebauer et al. 2011) and cold chilling phloem to slow or stop phloem transport (Johnsen et al. 2007) both reduce leaf-level photosynthesis (Paul and Foyer 2001). The mechanism for this photosynthetic reduction is currently unknown, given that changes in foliar non-structural carbohydrate concentrations are not necessarily related to changes in photosynthesis (Nebauer et al. 2011).

Despite this evidence, designing how models might represent sink to source is limited by our inadequate understanding of

feedback mechanisms. For example, lower-canopy shading or branch pruning might increase stomatal conductance by improving water availability (Ewers et al. 2007), by changing starch or sugar concentrations, or by altering hormonal signals, or through all of these (Paul and Foyer 2001). Slowing photosynthesis through feedback from carbohydrate increases seems logical (but may not be the correct interpretation (Nebauer et al. 2011)), and phloem removal can induce other negative effects, including water loss (Asao and Ryan 2015).

Current vegetation and ecosystem models assume that photosynthesis controls growth (Smith and Dukes 2013, Fatichi et al. 2014), by estimating photosynthesis from leaf area, environment, light absorption and photosynthetic capacity, and then partitioning these carbohydrates to different sinks. Most models incorporate some mechanism for changing both photosynthesis and the partitioning of photosynthesis to sinks in response to variation in nutrition and water availability. Modeling tree carbon balance with source controlling the sinks is simple, linear and often effective. For large areas and over longer time scales,

models using source control make reasonable predictions (Cramer et al. 1999, Xia et al. 2017). Experiments have shown that CO₂, nutrition, temperature, soil water and tree size interact with both sources and sinks, so source–sink feedbacks should be important for modeling forest response to global change. Incorporating some simple feedbacks into models, such as a labile carbohydrate pool with links to growth, photosynthesis and reproduction, may be a reasonable first step (Figure 1). This approach would require an independent growth model driven by carbohydrate availability and environmental drivers.

Much research has focused on determining if there is a source limitation in a higher-CO₂ world by determining growth and other responses to elevated [CO₂] (Körner 2003, Fatichi et al. 2014, Körner 2015). However, we question whether an elevated [CO₂] experiment really reflects a test of source control, given the dramatic increase in photosynthesis and growth observed following nutrient additions compared with the meager growth response to elevated [CO₂] alone (Oren et al. 2001, Sigurdsson et al. 2013).

We see in the research of Rosati et al. (2018a, 2018b) the opportunity to advance the field of tree physiology through experiments in orchards where fruit set can be modified and genetics carefully controlled. Reductions in growth in response to heavy seed production have been reported in native forest trees, although they are less extreme than in orchards. From our review of other field experiments, we identify additional interactions that affect carbon partitioning. We emphasize that the extent to which we can make definite statements about cause and effect relations between the environment and tree internal carbon balances is severely limited when not all fluxes and storage sites are monitored simultaneously. We recognize this is a daunting task, requiring collaboration among groups of specialists. Techniques are available to do this, however, and the need is great.

Conflict of interest

None declared.

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