

Sinks for Plant Surplus Carbon Explain Several Ecological Phenomena

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Research Article

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Abstract

Plants engage in many processes and relationships that appear to be wasteful of the high-energy compounds that they produce through carbon fixation and photosynthesis. For example, living trees keep leafless tree stumps alive (*i.e.* respiring) and support shaded understory trees by sharing carbohydrates through root grafts or mycorrhizal fungal networks. Plants exude a variety of organic compounds from their roots and leaves, which support abundant rhizosphere and phyllosphere microbiomes. Some plants release substantial amounts of sugar via extra-floral nectaries, which enrich throughfall and alter lichen communities beneath the canopy. Large amounts of photosynthetically fixed carbon are transferred to root associates such as mycorrhizal fungi and N-fixing micro-organisms. In roots, some fixed C is respired through an alternative non-phosphorylating pathway that oxidizes excess sugar. Each of these processes is most prevalent when plants are growing under mild-to-moderate deficiencies of nutrients or water, or under high light or elevated atmospheric CO₂. Under these conditions, plants produce more fixed carbon than they can use for primary metabolism and growth, and so have 'surplus carbon'. To prevent cellular damage, these compounds must be transformed into other compounds or removed from the leaf. Each of the above phenomena represents a potential sink for these surplus carbohydrates. The fundamental 'purpose' of these phenomena may therefore be to alleviate the plant of surplus fixed C.

Background

Under common environmental conditions such as moderate deficiencies of water, nitrogen (N) or phosphorus (P), high light, low temperatures, or elevated atmospheric carbon dioxide concentrations, plant leaf cells produce more photo-assimilates than they are able to use for primary metabolism, and so have 'surplus carbon' (Prescott et al. 2020). Accumulation of surplus carbohydrates can damage leaf cells and so must be either transformed to other compounds or removed from the leaf (Lambers and Oliveira 2019). Active carbohydrate sinks are essential for the transport and removal of surplus C. Many active sinks are organs or physiological processes within the plant, but other organisms (either internal or external to the plant) that take up and metabolize the surplus metabolites may also function as carbon sinks. In essence, any process that draws surplus carbohydrates away from sites of accumulation may serve as a sink and in so doing benefit the plant (under conditions of surplus C). Sinks for plant surplus carbohydrates may be behind several physiological and ecological phenomena that are difficult to explain, except through a lens of surplus C. Here, I discuss a few of these phenomena (alternative oxidase pathway, plant secondary metabolites, extra-floral nectaries, living stumps, root exudates) with special emphasis on forest ecosystems and a few of the many scientific contributions of Hans Lambers to our understanding of plant physiological and ecological processes.

Alternative Oxidase Respiratory Pathway

During his PhD research, Hans Lambers investigated a non-phosphorylating respiratory pathway within plant mitochondria, focusing on intact roots and leaves, rather than isolated mitochondria. Following analysis of experimental evidence, Lambers (1980) concluded that the alternative pathway functions as

an energy overflow to oxidize excess sugars (and NADH), which are not required for growth, maintenance, osmoregulation or storage. This 'Alternative Oxidase Pathway' (AOX) prevents the accumulation of reactive oxygen species in the mitochondrial electron transfer chain which would otherwise damage proteins, lipids and DNA (Lambers and Oliveira 2019). Alternative oxidase activity increases when carbon (NADH) supplies are plentiful and electron flow is restricted, which occurs under conditions such as high light, prolonged water deficit, low temperature, low P supply or high CO₂ concentration (Millenaar and Lambers 2003; Del-Saz et al. 2018; Selinski et al. 2018). The presence of this 'energy wasteful' respiratory pathway indicates that under common environmental conditions, plants produce more carbohydrates through photosynthesis than they require for their primary metabolism at that time, and that they dispose of these compounds to prevent cellular damage and reduced performance (Selinski et al. 2018).

Secondary Plant Metabolites

Lambers (1993) explored the influence of plant 'excess carbon' in determining concentrations of secondary plant metabolites, particularly phenolic compounds, in leaves. He noted that there was already a wealth of evidence that under nutrient- or water-limiting conditions, plants accumulate non-structural carbohydrates and produce more secondary metabolites of a phenolic nature. Two metabolic mechanisms explain this accumulation of secondary metabolites: sucrose levels increasing beyond those needed for protein synthesis, and insufficient N to convert phenylalanine into protein, causing more of the phenylalanine to be diverted into pathways that generate phenolic compounds. Based on this 'excess carbon' hypothesis, Lambers (1993) predicted that elevated CO₂ would only increase concentrations of secondary metabolites in plants if the higher CO₂ concentration was not matched by increased uptake of nutrients or water. This prediction has been borne out in many studies reporting negative correlations between levels of C-based secondary metabolites and N concentrations of plants exposed to high CO₂ (Wu et al. 2011; Ibrahim and Jaafar 2012) and heightened effects of elevated CO₂ on secondary metabolite levels in plants grown at low nutrient availability (Julkunen-Tiitto et al. 1993; Lavola & Julkunen-Tiitto 1994). The effect appears to be specific to a deficiency of N (not P) and limited to concentrations of phenylpropanoid-derived compounds (not hydrolyzable tannins or terpenoids) (Koricheva et al. 1998). In a study of a 2-million-year soil-development chronosequence in south-western Australia, phenolics accumulated in plants growing on young soils in which N was limiting for primary productivity, but not on old soils, where P was limiting and silica accumulated (de Tombeur et al. 2021). These findings are all consistent with the proposed metabolic mechanisms, supporting a causative link among N deficiency, excess fixed C and increased concentrations of some secondary metabolites in plants.

Starch granules

Young western hemlock trees on northern Vancouver Island are often severely deficient in N and P, with chlorotic foliage and slow growth (Prescott et al. 2013). Transmission electron microscopy of their needles revealed that a single large starch grain occupied 80% of the cross-sectional area of the chloroplasts (Fig. S1). The thylakoid membranes appeared to be mechanically distorted and the number

of thylakoid membranes per granum stack was reduced relative to that in trees that had been fertilized with N and P (White 2000). Starch accumulates in chloroplasts of P-deficient plants and, like sucrose production in the cytosol, is attributed to the production of fixed C in excess of that required by the plant, *i.e.* when sinks are not available (Hurewitz and Janes 1983; Fredeen et al. 1989). Although starch is usually considered to function as an energy store for the plant, C availability is unlikely to constrain production in highly nutrient-deficient trees. It is more likely that large accumulations of starch in leaves function as sinks where surplus carbohydrates can accumulate without osmotic consequences (Prescott et al. 2020).

Extra-floral nectaries

In sub-boreal spruce forests in British Columbia, foliose lichens with cyanobacterial bionts are disproportionately abundant and species-rich on conifer saplings beneath *Populus* trees (Campbell et al. 2010). The abundance of these lichens was linked to the fungal biont receiving sugars washed from poplar leaves (Campbell et al. 2013). These exogenous sugars allow the fungus to survive extended dry periods during which the cyanobacteria cannot produce sugars to support the symbiosis (Campbell et al. 2013). *Populus* species are among the 1–2 % of vascular plant species that produce extra-floral nectaries (EFN) at the base of their leaves (Weber and Keeler 2013). Extrafloral nectaries are plant glands that secrete sugar, water and amino-acids (Weber and Keeler 2013). High concentrations of saccharides have been measured in leaf wash and throughfall in *Populus* stands (Wildman and Parkinson 1981; Sanborn and Pawluk 1983). Release of sugars from EFNs and their removal via leaf wash may be a means of removing surplus carbohydrates from leaves. Several lines of evidence support this interpretation: 1) leaching of carbohydrates from leaves is greatest during periods of high light intensity (Tukey 1957; Bixenmann et al. 2011); 2) sugar is imported from older leaves into young leaves that generate EFNs (Radhika et al. 2008); and 3) rainfall washes the existing accumulation of sugar from the leaf surface and stimulates further release from EFNs (Trelease 1881, cited in Campbell et al. 2013). The finding that sugar release from EFN increases at the beginning of the rainy season (Calixto et al. 2021) could also result from sugar removal via rain stimulating its release from EFN. Phylloplane bacteria may also be an important sink for sugars and other metabolites released from leaves (Rodger and Blakeman 1984, Mercier and Lindow 2000).

Extra-floral nectaries are usually interpreted as adaptations for plant defense in that they entice invertebrates such as ants or wasps to act as “pugnacious bodyguards” (Bentley 1977) that protect the plants from herbivores (Koptur 1992). However, observations are not always consistent with this interpretation of the ‘purpose’ of EFNs. For example, in *Populustremuloides* trees, concentrations of phenolic glycosides, which deter insect feeding, were about 30% greater on leaves bearing EFNs than on leaves without EFNs (Young et al. 2010). This observation required a rather convoluted explanation on the basis of plant defenses, but is not unexpected when viewed through a surplus C lens, as both sugar exudation and elevated concentrations of secondary metabolites are expected under plant growth-limiting conditions (Prescott et al. 2020). The finding that nectar production by EFNs is stimulated by

phloem-sucking insects but not by mechanical damage by other insects (Escalante-Pérez et al. 2012) also indicates a strong sink control of nectar production in EFNs.

Belowground Carbon Flux

Up to half of the photosynthate produced by plants may be transported to belowground organs (Högberg and Högberg 2002; Pausch and Kuzyakov 2018), depending on environmental conditions. Much of it is used for root growth and maintenance or is stored, but 10-44% of photosynthetically fixed carbon is excreted by roots or transferred to mycorrhizal fungi (Bais et al. 2006; Pausch & Kuzyakov 2018). The C exuded from roots or from associated mycorrhizal fungi supports a large component of the soil biota, including invertebrates as well as micro-organisms (Pollierer et al. 2007; Drigo et al. 2008, Yarwood et al. 2009). Half or more of the soil activity in forests may be driven by photosynthate that is transported to mycorrhizal fungi and root-associated microbes within a few days of being fixed (Högberg et al. 2008). Why do trees export so much photosynthate to the belowground ecosystem?

The amount and proportion of fixed C transported belowground is related to the relative availabilities of C versus growth-limiting resources (N, P or water). In forests with high nutrient availability, a greater proportion of the photosynthates produced annually is used for plant biomass production, compared with forests with low nutrient availability (58% vs 42% in a synthesis of 49 forests; Vicca et al. 2012). In the loblolly pine stand at the Duke free-air CO₂ enrichment (FACE) experiment, elevated CO₂ conditions led to increases in total belowground C flux, root production, biomass and respiration, exudation and fungal allocation, microbial biomass, heterotrophic respiration and soil CO₂ efflux (Drake et al. 2011).

Belowground C flux in both ambient and elevated CO₂ plots was much lower where soil N availability was increased through N fertilization (Drake et al. 2011). Other FACE experiments have reported that in forests where growth is nutrient-limited, elevated CO₂ increases photosynthesis rates, but not tree growth, and the additional fixed C is respired and released back to the atmosphere, primarily from belowground organs (Körner et al. 2005; Reich et al. 2014; Ellsworth et al. 2017; Jiang et al. 2020).

In boreal pine forests, aboveground productivity is strongly limited by N and about 50% of tree photosynthate is transferred belowground and respired from the soil (Högberg and Högberg 2002).

Nitrogen additions to a boreal pine forest reduced the flux of tree photosynthate to roots and soil biota, including ectomycorrhizal (ECM) fungi, by as much as 60% (Högberg et al. 2010). Belowground C flux returned to pre-fertilization levels after N additions ceased, coincident with increased abundance of mycorrhizal fungi (Högberg et al. 2011). Belowground C flux (as a proportion of gross primary productivity, GPP) also increases under conditions of high light (Smith and Reynolds 2015), elevated CO₂ (Jackson et al. 2009; Drake et al. 2011) or reduced availability of P (Keith et al. 1997) or water (Stape et al. 2008; Preece & Peñuelas 2016; Hasibeder et al. 2015; Ledo et al. 2018). These observations are consistent with the amount of plant C transported belowground being strongly influenced by the need to remove surplus fixed C from plant leaves. Indeed, the rapid (1-day) link between GPP and respiration from roots and mycorrhizal fungi in forests prompted Heinemeyer et al. (2007) to propose that the mycorrhizal

CO₂ flux component represents an overflow 'CO₂ tap' through which surplus plant carbon can be returned directly to the atmosphere.

A strong seasonal pattern of photosynthate fluxes in boreal pine forests was also noted by Högberg et al. (2010). Belowground flux of photosynthate in August was 500% greater than that in June. They attributed this to developing leaves being a sink for fixed C early in the growing season (Horwath et al. 1994; Kagawa et al. 2006). Once leaves had fully expanded, much of the fixed C was translocated belowground, much of it to mycorrhizal fungi. Sporocarp production of ECM fungi was totally dependent on allocation of recent photosynthate in the late season. This late-summer flux of surplus photosynthate may underly the autumn peak in sporocarp production in boreal forests. Sporocarp production by mycorrhizal fungi may therefore function as an alternate sink for surplus carbohydrates once leaf expansion is complete.

Living stumps and carbon sharing among living trees

Leafless tree stumps, which are nevertheless 'alive' in the sense that they respire, have been observed in many forests. These stumps have a living root system, which is connected to that of other trees through root grafts and/or mycorrhizal fungal hyphae. These connections give them access to carbohydrates from the root systems of living trees, which sustains the remaining tissues of the leafless tree (Bader & Leuzinger 2019). Evolutionary rationales for the living plants investing carbohydrates in non-photosynthesizing neighbors are challenging, but it has been suggested that the stumps provide an extended root system for mechanical stability and uptake of water and nutrients (Bormann 1966, Keeley 1988, but see Loehl and Jones 1990). Alternatively, living stumps may result from surplus carbohydrates from living trees traveling to them through the phloem of connected roots, driven by the difference in hydrostatic pressure provided by phloem unloading and respiration in the surviving tissues of the stump tree.

Transfer of carbohydrates among *living* trees through root grafts (Fraser et al. 2006) or mycorrhizal fungi (Simard et al. 1997; Klein et al. 2016) have received considerable attention. Carbon fluxes have been traced from source trees growing in full light to sink trees growing in low light conditions (Fraser et al. 2006; Teste et al. 2009). The adaptive 'purpose' of the transfers through common mycorrhizal networks has been explained through kin selection processes, as neighboring trees have a high probability of being related (Gorzalak et al. 2015). Alternatively, these fluxes may represent the movement of plant surplus carbohydrates along pressure gradients through roots and fungal hyphae driven by phloem loading in source trees and phloem unloading in sink trees. The source plant benefits from the removal of surplus photo-assimilates and prevention of consequent physiological dysfunction, regardless of the relatedness of the sink plant.

Carboxylate exudation

Roots of plants growing under conditions of low P availability often exude more carboxylates, especially organic anions such as citrate and malate (Lambers et al. 2013; 2011). In the rhizosphere, carboxylates

compete with inorganic and organic P for binding sites which increases the availability of P for plant uptake (Lambers et al. 2011). Release of carboxylates is therefore widely considered to be part of a P-acquisition strategy that allows plants to survive in low-P environments (Lambers et al. 2006, 2010). However, several observations are inconsistent with this interpretation, such as increased carboxylate exudation at low N availability (Zhu et al. 2016) and inconsistent relationships between rates of carboxylate release and both P uptake and plant growth (Huang et al. 2017; He et al. 2021; Wang and Lambers 2020). Carboxylate exudation by roots of alfalfa (*Medicago sativa*) growing in an alkaline soil low in both N and P was studied by He et al. (2020, 2021). Root exudation of carboxylates (particularly tartrate) decreased with increasing P availability but also increased exponentially with increasing shoot N concentration. The closer association of root carboxylate release with N than with P concentration prompted He et al. (2021) to suggest that N addition resulted in increased production of photosynthates, which could not be used for primary metabolism and growth due to the lack of P, and so were discharged as carboxylates.

Metabolite profiling of root exudates (as well as of shoots and roots) of P-deficient and P-sufficient plants also supports the hypothesis that root exudates can be a means of removing surplus metabolites. Relative to P-sufficient soybean plants, root exudates of P-deficient plants had higher concentrations of TCA cycle intermediates and amino acids, and lower concentrations of phosphate esters (Tawaraya et al. 2014). Shoot and root extracts of P-deficient plants also had low levels of P-containing metabolites such as adenosine 5'-monophosphate and glycerol 3-phosphate and elevated concentrations of adenine, cytosine and adenosine, reflecting inhibition of nucleotide synthesis induced by P starvation. Remobilization of P from phosphate esters is common in P-deficient plants (Tawaraya et al. 2014). The higher concentrations of TCA cycle intermediates such as organic acids in root exudates from P-deficient plants may be a consequence of their accumulation in root cells as surplus metabolites. Plants exposed to very low P supply have very low concentrations of Pi and ADP which restricts the cytochrome pathway and causes TCA-cycle intermediates such as organic acids – especially citrate – to accumulate (Selinski et al. 2018). Increased carbon supply for organic acid synthesis in the TCA cycle in P-deficient roots has been demonstrated through transcriptome (Wasaki et al. 2003; Li et al. 2010) and proteome (Fukuda et al. 2007) analysis; this would lead to higher concentrations of organic acids in P-deficient roots (Tawaraya et al. 2014). Therefore, a primary function of organic acid exudation may be the disposal of surplus metabolites. Particular morphological and physiological traits such as releasing carboxylates in exudative bursts from specialized structures such as cluster roots or dauciform roots are more probably adaptations for P acquisition (Lambers et al. 2006).

The Belowground Ecosystem

The efficacy of root exudation as a means of disposing of surplus plant metabolites is largely attributable to the dynamic sink provided by the abundant microorganisms in the plant rhizosphere. The low-molecular-weight organic compounds exuded from roots are rapidly taken up and transformed by rhizosphere bacteria (Treonis et al. 2004; Ostle et al. 2003; Kastovska and Santuckova 2007), which are grazed by rhizosphere protists (Gao et al. 2019; Ceja-Navarro et al. 2021) and further transformed through

the soil food web (Pollierer et al. 2007). As a result, exudates in the soil solution have turnover times in the order of minutes or hours (Nguyen 2003; Butler et al. 2004). This maintains a steep concentration gradient right outside root tips which promotes exudation (Canarini et al. 2019) and generates a strong sink for plant C.

Carbohydrate sinks provided by root microbionts also stimulate photosynthesis, as evident in the faster photosynthetic rates of plants inoculated with rhizobia and/or mycorrhizal fungi (Wright et al. 1998; Kaschuk et al. 2009) and the decline in photosynthesis rate following removal of arbuscular mycorrhizal fungi (Gavito et al. 2019). Accumulation of carbohydrates is a key trigger for leaves to reduce photosynthetic C fixation rates (Drake et al. 1997; Ruiz-Vera et al. 2017), so the removal of carbohydrates from sites of photosynthesis can prevent or forestall down-regulation of photosynthesis. This has been demonstrated by shading some of the leaves on a plant, which can prevent down-regulation of photosynthesis (Pieters et al. 2001) or may even increase photosynthetic rates in unshaded leaves (McCormick et al. 2006). Therefore, the active sinks for surplus carbohydrates discussed in this article may cause plants to maintain rapid rates of photosynthesis when aboveground growth is restricted by resource supply. It is important to note that surplus carbohydrates are generated under mild-to-moderate deficiencies of N, P or water, and not under severe or prolonged deficiencies which constrain photosynthesis (Prescott et al. 2020; Lambers and Oliveira 2019).

Conclusion

The physiological and ecological phenomena discussed in this paper are challenging to explain if one invariably views fixed C as a scarce resource that plants must use efficiently. However, there is abundant evidence that C rarely limits plant production (Körner 2003, 2015; Millard et al. 2007); in fact, under common environmental conditions such as mild-to-moderate deficiencies of N, P or water, plants tend to produce more fixed C than they can use at that time. Accumulation of surplus fixed C could be problematic for the plant, but is not, due to the activity of multiple sinks for fixed C that plants have at their disposal. Some of these sinks provide additional benefits such as protection from herbivores and pathogens or improved access to nutrients and water. These added benefits could reduce selective pressure against the production of surplus C, but are not necessarily the 'purpose' of the fluxes. The foundational function of phenomena such as the alternative oxidase pathway, extra-floral nectaries, root exudation and mycorrhizas may be to allow the plant to dispose of surplus fixed C.

Declarations

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References

1. Bader MK, Leuzinger S (2019) Hydraulic coupling of a leafless auri tree remnant to conspecific hosts. *iScience* 19:255
2. Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu Rev Plant Biol* 57:233-266
3. Bentley BL (1977) Extrafloral nectaries and protection by pugnacious bodyguards. *Annu Rev Ecol Syst* 8:407-427
4. Bixenmann RJ, Coley PD, Kursar TA (2010) Is extrafloral nectar production induced by herbivores or ants in a tropical facultative ant–plant mutualism? *Oecologia* 165:417-425
5. Bormann FH (1966) The structure, function, and ecological significance of root grafts in *Pinus strobus* L. *Ecol Monogr* 36:1-26
6. Butler JL, Bottomley PJ, Griffith SM, Myrold DD (2004) Distribution and turnover of recently fixed photosynthate in ryegrass rhizospheres. *Soil Biol Bioch* 36:371-382
7. Calixto ES, Novaes LR, Santos DFB, Lange D, Moreira X, Del-Claro K, Züst T (2021) Climate seasonality drives ant–plant–herbivore interactions via plant phenology in an extrafloral nectary-bearing plant community. *J Ecol* 109:639-651
8. Campbell J, Bengtson P, Fredeen AL, Coxson DS, Prescott CE (2013) Does exogenous carbon extend the realized niche of canopy lichens? Evidence from sub-boreal forests in British Columbia. *Ecology* 94:1186-1195
9. Campbell J, Bradfield GE, Prescott CE, Fredeen AL (2010) The influence of overstorey *Populus* on epiphytic lichens in subboreal spruce forests of British Columbia. *Can J For Res* 40:143-154
10. Canarini A, Kaiser C, Merchant A, Richter A, Wanek W (2019) Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. *Front Plant Sci* 10:157
11. Ceja-Navarro JA, Wang Y, Ning D, Arellano A, Ramanculova L, Yuan MM, Byer A, Craven KD, Saha MC, Brodie EL, Pett-Ridge J, Firestone MK (2021) Protist diversity and community complexity in the rhizosphere of switchgrass are dynamic as plants develop. *Microbiome* 9:96-18
12. de Tombeur F, Laliberté E, Lambers H, Faucon M, Zemunik G, Turner BL, Cornelis J, Mahy G, van der Putten W (2021) A shift from phenol to silica-based leaf defences during long-term soil and ecosystem development. *Ecol Lett* 24:984-995
13. Del-Saz NF, Ribas-Carbo M, McDonald AE, Lambers H, Fernie AR, Florez-Sarasa I (2018) An in vivo perspective of the role(s) of the alternative oxidase pathway. *Trends Plant Sci* 23:206-219
14. Drake BG, Gonzalez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Annu Rev Plant Physiol Plant Mol Biol* 48:609-639
15. Drake JE, Gallet-Budynek A, Hofmockel KS, Bernhardt ES, Billings SA, Jackson RB, Johnsen KS, Lichter J, McCarthy HR, McCormack ML, Moore DJP, Oren R, Palmroth S, Phillips RP, Phippen JS, Pritchard SG, Treseder KK, Schlesinger WH, DeLucia EH, Finzi AC (2011) Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest

- productivity under elevated CO₂. *Ecol Lett* 14: 349-357 doi: <https://doi.org/10.1111/j.1461-0248.2011.01593.x>
16. Drigo B, Kowalchuk GA, van Veen JA (2008) Climate change goes underground: effects of elevated atmospheric CO₂ on microbial community structure and activities in the rhizosphere. *Biol Fert Soils* 44, 667–679
 17. Ellsworth DS, Anderson IC, Crous KY, Cooke J, Drake JE, Gherlenda AN, Gimeno TE, Macdonald CA, Medlyn BE, Powell JR, Tjoelker MG, Reich PB (2017) Elevated CO₂ does not increase eucalypt forest productivity on a low-phosphorus soil. *Nat Clim Change* 7:279-282
 18. Escalante-Perez M, Jaborsky M, Lautner S, Fromm J, Müller T, Dittrich M, Kunert M, Boland W, Hedrich R, Ache P (2012) Poplar extrafloral nectaries: two types, two strategies of indirect defenses against herbivores. *Plant Physiol* 159:1176-1191
 19. Fraser EC, Loeffers VJ, Landhäuser SM (2006) Carbohydrate transfer through root grafts to support shaded trees. *Tree Physiol* 26:1019-1023
 20. Fredeen AL, Madhusudana Rao I, Terry N (1989) Influence of phosphorus nutrition on growth and carbon partitioning in *Glycine max*. *Plant Physiol* 89:225-230
 21. Gao Z, Karlsson I, Geisen S, Kowalchuk G, Jousset A (2019) Protists: puppet masters of the rhizosphere microbiome. *Trends Plant Sci* 24:165-176
 22. Gauslaa Y, Goward T, Pypker T (2020) Canopy settings shape elemental composition of the epiphytic lichen *Lobaria pulmonaria* in unmanaged conifer forests. *Ecol Ind* 113:106294
 23. Gavito ME, Jakobsen I, Mikkelsen TN, Mora F (2019) Direct evidence for modulation of photosynthesis by an arbuscular mycorrhiza-induced carbon sink strength. *New Phytol* 223:896-907
 24. Gorzelak MA, Asay AK, Pickles BJ, Simard SW (2015) Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. *AoB Plants* 7:plv050
 25. Hartley SE, Jones CG, Couper GC, Jones TH (2000) Biosynthesis of plant phenolic compounds in elevated atmospheric CO₂. *Glob Change Biol* 6:497-506
 26. Hasibeder R, Fuchslueger L, Richter A, Bahn M (2015) Summer drought alters carbon allocation to roots and root respiration in mountain grassland. *New Phytol* 205: 1117-1127.
 27. He H, Wu M, Guo L, Fan C, Zhang Z, Su R, Peng Q, Pang J, Lambers H (2020) Release of tartrate as a major carboxylate by alfalfa (*Medicago sativa* L.) under phosphorus deficiency and the effect of soil nitrogen supply. *Plant Soil* 449:169-178
 28. Heinemeyer A, Hartley IP, Evans SP, Carreira de la Fuente, JA, Ineson P (2007) Forest soil CO₂ flux: uncovering the contribution and environmental responses of ectomycorrhizas. *Glob Change Biol* 13:1786-1797
 29. Högberg MN, Briones MJI, Keel SG, Metcalfe DB, Campbell C, Midwood AJ, Thornton B, Hurry V, Linder S, Näsholm T, Högberg P (2010) Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytol* 187:485-493

30. Högberg MN, Högberg P (2002) Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. *New Phytol* 154:791-795
31. Högberg P, Högberg MN, Göttlicher SG, Betson NR, Keel SG, Metcalfe DB, Campbell C, Schindlbacher A, Hurry V, Lundmark T, Linder S, Näsholm T (2008) High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. *New Phytol* 177: 220-228
32. Högberg P, Högberg MN, Göttlicher SG, Betson NR, Keel SG, Metcalfe DB, Campbell C, Schindlbacher A, Hurry V, Lundmark T, Linder S, Näsholm T (2007) High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. *New Phytol* 177:220-228
33. Högberg P, Johannisson C, Yarwood S, Callesen I, Näsholm T, Myrold DD, Högberg MN (2011) Recovery of ectomycorrhiza after 'nitrogen saturation' of a conifer forest. *New Phytol* 189:515-525
34. Horwath WR, Pregitzer KS, Paul EA (1994) ¹⁴C allocation in tree-soil systems. *Tree Physiol* 14:1163-1176
35. Huang G, Hayes PE, Ryan MH, Pang J, Lambers H (2017) Peppermint trees shift their phosphorus-acquisition strategy along a strong gradient of plant-available phosphorus by increasing their transpiration at very low phosphorus availability. *Oecologia* 185:387-400
36. Hurewitz J, Janes HW (1983) Effect of altering the root-zone temperature on growth, translocation, carbon exchange rate, and leaf starch accumulation in the tomato [*Lycopersicon esculentum*, relationship of growth response of seedlings to relative translocation and photosynthetic rates]. *Plant Physiol* 73:46-50
37. Ibrahim MH, Jaafar HZE (2012) Impact of elevated carbon dioxide on primary, secondary metabolites and antioxidant responses of *Eleais guineensis* Jacq. (oil palm) seedlings. *Molecules* 17:5195-5211
38. Jackson RB, Cook CW, Pippin JS, Palmer SM (2009) Increased belowground biomass and soil CO₂ fluxes after a decade of carbon dioxide enrichment in a warm-temperate forest. *Ecology* 90: 3352-3366.
39. Jiang M, Medlyn BE, Drake JE, Duursma RA, Anderson IC, Barton CVM, Boer MM, Carrillo Y, Castañeda-Gómez L, Collins L, Crous KY, De Kauwe MG, Dos Santos BM, Emmerson KM, Facey SL, Gherlenda AN, Gimeno TE, Hasegawa S, Johnson SN, Kännaste A, Macdonald CA, Mahmud K, Moore BD, Nazaries L, Neilson EHJ, Nielsen UN, Niinemets Ü, Noh NJ, Ochoa-Hueso R, Pathare VS, Pendall E, Pihlblad J, Piñeiro J, Powell JR, Power SA, Reich PB, Renchon AA, Riegler M, Rinnan R, Rymer PD, Salomón RL, Singh BK, Smith B, Tjoelker MG, Walker JKM, Wujeska-Klaue A, Yang J, Zaehle S, Ellsworth DS, Sveriges lantbruksuniversitet (2020) The fate of carbon in a mature forest under carbon dioxide enrichment. *Nature* 580:227-231
40. Julkunen-Tiitto, R. (Joensuu Univ. (Finland). Dept. of Biology), Tahvanainen J, Silvola J (1993) Increased CO₂ and nutrient status changes affect phytomass and the production of plant defensive secondary chemicals in *Salix myrsinifolia* (Salisb.). *Oecologia* 95:495-498

41. Kagawa A, Sugimoto A, Maximov TC (2006) Seasonal course of translocation, storage and remobilization of ^{13}C pulse-labeled photoassimilate in naturally growing *Larix gmelinii* saplings. *New Phytol* 171:793-804
42. Kaschuk G, Kuyper TW, Leffelaar PA, Hungria M, Giller KE (2009) Are the rates of photosynthesis stimulated by the carbon sink strength of rhizobial and arbuscular mycorrhizal symbioses? *Soil Biol Bioch* 41:1233-1244
43. Kaštovská E, Santruckova H (2007) Fate and dynamics of recently fixed C in pasture plant–soil system under field conditions. *Plant Soil* 300:61-69
44. Keeley JE (1988) Population variation in root grafting and a hypothesis. *Oikos* 52:364-366
45. Klein T, Siegwolf RTW, Körner C (2016) Belowground carbon trade among tall trees in a temperate forest. *Science* 352:342-344
46. Korenblum E, Dong Y, Szymanski J, Panda S, Jozwiak A, Massalha H, Meir S, Rogachev I, Aharoni A (2020) Rhizosphere microbiome mediates systemic root metabolite exudation by root-to-root signaling. *Proc Natl Acad Sci USA* 117:3874-3883
47. Koricheva J (1998) Regulation of woody plant secondary metabolism by resource availability: hypothesis testing by means of meta-analysis. *Oikos* 83: 212-226
48. Körner C (2003) Carbon limitation in trees. *J Ecol* 91:4-17
49. Körner C (2015) Paradigm shift in plant growth control. *Curr Opin Plant Biol* 25:107-114
50. Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Peláez-Riedl S, Pepin S, Siegwolf RTW, Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2 . *Science* 309:1360-1362
51. Lambers H (1980) The physiological significance of cyanide-resistant respiration in higher-plants. *Plant Cell Environ* 3:293-302
52. Lambers H, Oliveira RS (2019) *Plant Physiological Ecology*. Springer International Publishing, Cham
53. Lambers H, Ahmedi I, Berkowitz O, Dunne C, Finnegan PM, Hardy, Giles E. St J., Jost R, Laliberté E, Pearse SJ, Teste FP (2013) Phosphorus nutrition of phosphorus-sensitive Australian native plants: threats to plant communities in a global biodiversity hotspot. *Conserv Physiol* 1:cot010
54. Lambers H, Brundrett MC, Raven JA, Hopper SD (2010) Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant Soil* 334:11-31
55. Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ (2006) Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Ann Bot* 98:693-713
56. Lambers H (1993) Rising CO_2 , secondary plant metabolism, Plant-herbivore interactions and litter decomposition: theoretical considerations. *Vegetatio* 104/105:263-271
57. Lavola, A, Julkunen-Tiitto R (1994) The effect of elevated carbon dioxide and fertilization on primary and secondary metabolites in birch, *Betula pendula* (Roth). *Oecologia* 99:315-321

58. Ledo A, Paul KI, Burslem, David F. R. P., Ewel JJ, Barton C, Battaglia M, Brooksbank K, Carter J, Eid TH, England JR, Fitzgerald A, Jonson J, Mencuccini M, Montagu KD, Montero G, Mugasha WA, Pinkard E, Roxburgh S, Ryan CM, Ruiz-Peinado R, Sochacki S, Specht A, Wildy D, Wirth C, Zerihun A, Chave J (2018) Tree size and climatic water deficit control root to shoot ratio in individual trees globally. *New Phytol* 217: 8-11 doi: <https://doi.org/10.1111/nph.14863>
59. Li L, Liu C, Lian X (2010) Gene expression profiles in rice roots under low phosphorus stress. *Plant Mol Biol* 72:423-432
60. Loehle C, Jones RH (1990) Adaptive significance of root grafting in trees. *Funct Ecol* 4:268-271
61. McCormick AJ, Cramer MD, Watt DA (2006) Sink strength regulates photosynthesis in sugarcane. *New Phytol* 171:759-770
62. Mercier J, Lindow SE (2000) Role of leaf surface sugars in colonization of plants by bacterial epiphytes. *Appl Environ Microbiol* 66(1):369-374
63. Millard P, Sommerkorn M, Grelet G (2007) Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. *New Phytol* 175:11-28
64. Millenaar FF, Lambers H (2003) The alternative oxidase: in vivo regulation and function. *Plant Biol* 5:2-15
65. Nguyen C (2009) Rhizodeposition of organic C by plant: mechanisms and controls. In: Sustainable Agriculture, Lichtfouse E, Navarrete M, Debaeke P, Véronique S, Alberola C. (eds). Springer, Dordrecht, pp 97-123
66. Ostle N, Whiteley AS, Bailey MJ, Sleep D, Ineson P, Manefield M (2003) Active microbial RNA turnover in a grassland soil estimated using a $^{13}\text{CO}_2$ spike. *Soil Biol Biochem* 35:877-885
67. Pausch J, Kuzyakov Y (2018) Carbon input by roots into the soil: quantification of rhizodeposition from root to ecosystem scale. *Glob Change Biol* 24:1-12
68. Pieters AJ, Paul MJ, Lawlor DW (2001) Low sink demand limits photosynthesis under Pi deficiency. *J Exp Bot* 52:1083-1091
69. Pollierer MM, Langel R, Körner C, Maraun M, Scheu S (2007) The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecol Lett* 10:729-736
70. Preece C, Peñuelas J (2016) Rhizodeposition under drought and consequences for soil communities and ecosystem resilience. *Plant Soil* 409:1-17
71. Prescott CE, Rui Y, Cotrufo MF, Grayston SJ (2021) Managing plant surplus carbon to generate soil organic matter in regenerative agriculture. *J Soil Water Conserv* 76:99-104A
72. Prescott CE, Grayston SJ, Helmisaari H, Kaštovská E, Körner C, Lambers H, Meier IC, Millard P, Ostonen I (2020) Surplus carbon drives allocation and plant–soil interactions. *Trends Ecol Evol* 35:1110-1118
73. Prescott CE, Nery V, van Niejenhuis A, Sajedi T, Marshall P (2013) Nutrition management of cedar and hemlock plantations in coastal British Columbia. *New Forests* 44:769-784

74. Radhika V, Kost C, Bartram S, Heil M, Boland W (2008) Testing the optimal defence hypothesis for two indirect defences: extrafloral nectar and volatile organic compounds. *Planta* 228:449-457
75. Reich PB, Hobbie SE, Lee TD (2014) Plant growth enhancement by elevated CO₂ eliminated by joint water and nitrogen limitation. *Nat Geosci* 7:920-924
76. Rodger G, Blakeman J P (1984) Microbial colonization and uptake of ¹⁴C label on leaves of sycamore. *Trans Br Mycol Soc* 82:45–51.
77. Ruiz-Vera UM, De Souza AP, Long SP, Ort DR (2017) The role of sink strength and nitrogen availability in the down-regulation of photosynthetic capacity in field-grown *Nicotiana tabacum* L. at elevated CO₂ concentration. *Front Plant Sci* 8:998
78. Sanborn P, Pawluk S (1983) Process studies of a Chernozemic pedon, Alberta (Canada). *Geoderma* 31:205-237
79. Selinski J, Scheibe R, Day DA, Whelan J (2018) Alternative oxidase is positive for plant performance. *Trends Plant Sci* 23:588-597
80. Simard SW, Perry DA, Jones MD, Myrold DD, Durall DM, Molina R (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388:579-582
81. Smith LM, Reynolds HL (2015) Plant-soil feedbacks shift from negative to positive with decreasing light in forest understory species. *Ecology* 96:2523-2532
82. Stape JL, Binkley D, Ryan MG (2008) Production and carbon allocation in a clonal Eucalyptus plantation with water and nutrient manipulations. *For Ecol Manage.* 225: 920-930. doi: <https://doi.org/10.1016/j.foreco.2007.09.085>
83. Tawarayaya K, Horie R, Shinano T, Wagatsuma T, Saito K, Oikawa A (2014) Metabolite profiling of soybean root exudates under phosphorus deficiency. *Soil Sci Plant Nutr* 60:679-694
84. Teste FP, Simard SW, Durall DM, Guy RD, Jones MD, Schoonmaker AL (2009) Access to mycorrhizal networks and roots of trees: importance for seedling survival and resource transfer. *Ecology* 90:2808-2822
85. Trelease W (1881) The foliar nectar glands of *Populus*. *Bot Gaz* 6:284-290
86. Treonis AM, Ostle NJ, Stott AW, Primrose R, Grayston SJ, Ineson P (2004) Identification of groups of metabolically-active rhizosphere microorganisms by stable isotope probing of PLFAs. *Soil Biol Biochem* 36: 533-537. doi: <https://doi.org/10.1016/j.soilbio.2003.10.015>
87. Tukey HB., Wittwer SH, Tukey HB (1957) Leaching of carbohydrates from plant foliage as related to light intensity. *Science* 126:120-121
88. Vicca S, Luysaert S, Peñuelas J, Campioli M, Chapin III FS, Ciais P, Heinemeyer A, Högberg P, Kutsch WL, Law BE, Malhi Y, Papale D, Piao SL, Reichstein M, Schulze ED, Janssens IA (2012) Fertile forests produce biomass more efficiently. *Ecol Lett* 15: 520-526. doi: <https://doi.org/10.1111/j.1461-0248.2012.01775.x>
89. Wang Y, Lambers H (2020) Root-released organic anions in response to low phosphorus availability: recent progress, challenges and future perspectives. *Plant Soil* 447:135-156

90. Wasaki J, Yonetani R, Kuroda S, Shinano T, Yazaki J, Fujii F, Shimbo K, Yamamoto K, Sakata K, Sasaki T, Kishimoto N, Kikuchi S, Yamagishi M, Osaki M (2003) Transcriptomic analysis of metabolic changes by phosphorus stress in rice plant roots. *Plant Cell Environ.* 26:1515-1523
91. Weber MG, Keeler KH (2013) The phylogenetic distribution of extrafloral nectaries in plants. *Ann Bot* 111:1251-1261
92. White JB (2001) Studies of western hemlock nutrition. PhD Thesis, University of British Columbia
93. Wildman HG, Parkinson D (1981) Seasonal changes in water-soluble carbohydrates of *Populus tremuloides* leaves. *Can J Bot* 59:862-869
94. Wright DP, Read DJ, Scholes JD (1998) Mycorrhizal sink strength influences whole plant carbon balance of *Trifolium repens* L. *Plant Cell Environ* 21:881-891
95. Wu G, Chen FJ, Ge F, Xiao N (2011) Impacts of elevated CO₂ on expression of plant defensive compounds in Bt-transgenic cotton in response to infestation by cotton bollworm. *Agric For Entomol* 13:77-82
96. Yarwood SA, Myrold DD, Högberg MN, (2009) Termination of belowground C allocation by trees alters soil fungal and bacterial communities in a boreal forest. *FEMS Microbiol Ecol* 70:151-162
97. Young B, Wagner D, Doak P, Clausen T (2010) Within-plant distribution of phenolic glycosides and extrafloral nectaries in trembling aspen (*Populus tremuloides*; Salicaceae). *Am J Bot* 97:601-610
98. Zhu S, Vivanco JM, Manter DK (2016) Nitrogen fertilizer rate affects root exudation, the rhizosphere microbiome and nitrogen-use-efficiency of maize. *Appl Soil Ecol* 28:19021–19033

Figures

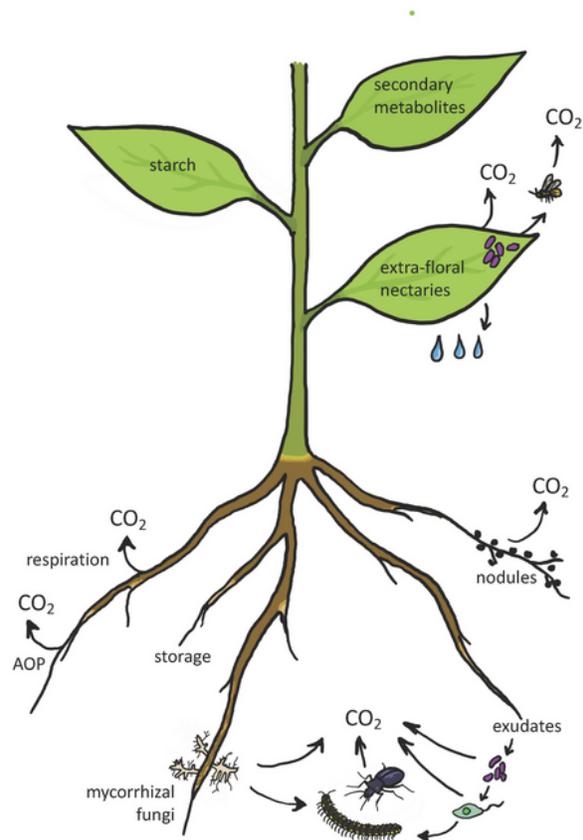


Figure 1

Sinks for surplus plant carbon generated when growth is constrained by availability of N, P or water. In the leaves, surplus carbohydrates can be stored as starch granules in chloroplasts, transformed into secondary metabolites, or exuded via extra-floral nectaries. On leaf surfaces, compounds can be removed via precipitation, assimilated by bacteria or consumed by insects. Surplus carbohydrates transported to roots can be stored, respired via phosphorylating or alternative oxidase pathway (AOP), exuded and

assimilated by rhizosphere bacteria, or transferred to endobionts such as N₂-fixing microorganisms or mycorrhizal fungi.

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