



Sinks for plant surplus carbon explain several ecological phenomena

Cindy E. Prescott

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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 diverse array 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. Plants also respire fixed C through an alternative pathway that does not generate ATP. Rates of each of these processes appear to be highest when plants are growing under mild-to-moderate deficiencies of nutrients or water. During

this stage of deficiency, aboveground plant growth is curtailed more than photosynthesis, causing leaves to produce surplus carbohydrates. Each of the above phenomena provide a sink for these surplus carbohydrates, thereby preventing feedback inhibition of photosynthesis, and perpetuating the influx of C. Because these processes incur little cost to the source plant, they need not provide a benefit beyond the removal of surplus carbohydrates.

Keywords Root exudates · Belowground carbon flux · Extra-floral nectaries · Living stumps · Alternative oxidase pathway

Under common environmental conditions such as deficiencies of water, nitrogen (N) or phosphorus (P), or low temperatures, aboveground plant growth is curtailed at an earlier stage of deficiency than is photosynthesis, and during this phase, leaves produce more photo-assimilates than they are able to use for primary metabolism (Prescott et al. 2020). This ‘surplus carbon’ phase occurs prior to the onset of severe or prolonged deficiencies which constrain photosynthesis (Körner 2013; Prescott et al. 2020, 2021). Nonstructural carbohydrates (soluble sugars and starch) also accumulate under high light intensity and elevated carbon dioxide concentrations, if growth is constrained by availability of water or nutrients (Sugiura et al. 2019; Prescott et al. 2020). Accumulation of carbohydrates is a key trigger for leaves to

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C. E. Prescott (✉)
Department of Forest and Conservation Sciences,
The University of British Columbia, 2424 Main Mall,
Vancouver, BC V6T1Z4, Canada
e-mail: cindy.prescott@ubc.ca

reduce photosynthetic C fixation rates (Drake et al. 1997; Ruiz-Vera et al. 2017), but removal of carbohydrates from sites of accumulation can forestall or postpone 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 presence of active sinks for surplus carbohydrates can cause plants to maintain rapid rates of photosynthesis when aboveground growth is restricted by resource supply. Several potential sinks for surplus carbohydrates exist (in addition to growth), including organs, physiological processes, and other organisms (either internal or external to the plant) that take up the surplus plant metabolites. In essence, any process that draws surplus carbohydrates away from sites of accumulation may serve as a sink 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 the lens of surplus C. Here, I discuss a few of these phenomena (alternative oxidase pathway, plant secondary metabolism, extra-floral nectaries, living stumps, and 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

Lambers (1980) investigated a non-phosphorylating respiratory pathway within plant mitochondria, which is not coupled to the production of ATP. Following analysis of experimental evidence, he concluded that the alternative pathway functions as an energy overflow to oxidize excess sugars (and NADH) that 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 intensity, 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). These are also the conditions under which surplus fixed C is generated (Prescott et al. 2020), supporting the suggestion that under these environmental conditions, plants produce more carbohydrates through photosynthesis than they require for their primary metabolism at that time.

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 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 and Julkunen-Tiitto 1994). The effect appears to be specific to a deficiency of N and limited to concentrations of phenylpropanoid-derived compounds (not hydrolyzable tannins or terpenoids) (Koricheva 1998). Along 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). Secondary metabolism also produces excess reducing equivalents, which can be oxidized through the AOX

pathway (Sakano 2001). These findings support surplus fixed C as a causative link between nutrient deficiency, secondary metabolism and the AOX pathway.

Starch granules

Young western hemlock trees on northern Vancouver Island are 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 2001). 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 adequate sinks are not available (Hurewitz and Janes 1983; Fredeen et al. 1989). Accumulation of large, irregularly shaped starch grains that distorted grana stacks were also reported in response to elevated CO₂ (Cave et al. 1981), further supporting a link to surplus fixed C. Starch is usually considered to function as an energy store for the plant, but C availability is unlikely to constrain production in 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). Cell-wall thickening as also been proposed as a mechanism by which plants consume surplus carbohydrates (Sugiura et al. 2020).

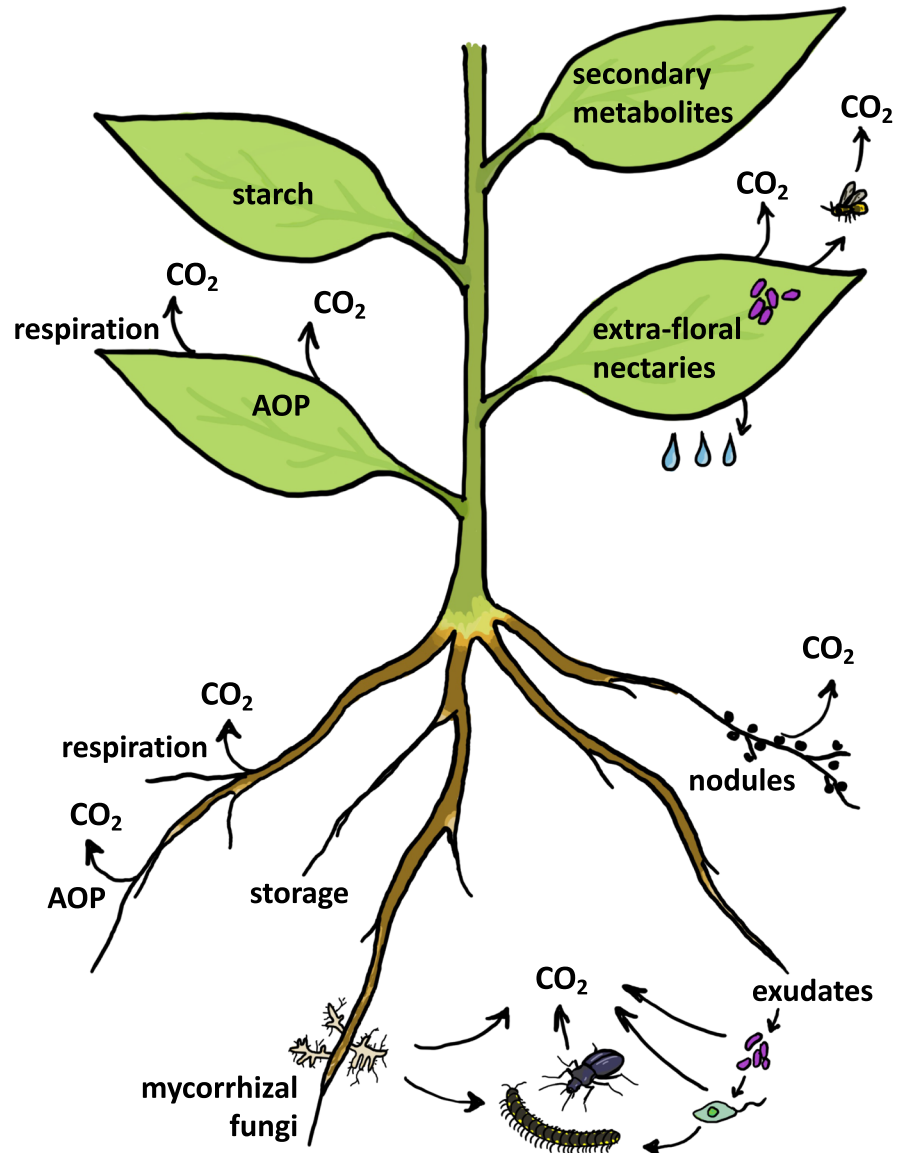
Extra-floral nectaries

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). The sugars released from EFNs and removed via leaf wash may be 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 et al. 1957; Bixenmann et al. 2010); 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) (Fig. 1).

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 *Populus tremuloides* 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-Perez et al. 2012) also indicates strong sink control of nectar production in EFNs.

Fig. 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, respired via phosphorylating or alternative oxidase pathways (AOP), 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, exuded and assimilated by rhizosphere bacteria, or transferred to endobionts such as N_2 -fixing micro-organisms or mycorrhizal fungi



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 and Kuzyakov 2018). The C exuded from roots or from associated mycorrhizal fungi supports a large component of the soil biota,

including micro-organisms and invertebrates (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 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). Increasing availability of C but not nutrients (via CO₂ enrichment) often induces a C allocation shift towards belowground compartments (meta-analysis by Dieleman et al. 2010). In the sweetgum stand at the ORNL free-air CO₂ enrichment (FACE) experiment, the only increases in NPP in elevated CO₂ plots (after the first year) were in fine-root production (Iversen et al. 2008; Norby et al. 2021). They attributed this to progressive N limitation in the stand (Norby et al. 2010), which is consistent with the generation and belowground transport of surplus C under nutrient-deficient conditions. In a hardwood forest at the Swiss FACE experiment, elevated CO₂ did not increase aboveground growth or respiration, but did increase C transport to below-ground sinks, as indicated by C transfer to ectomycorrhiza and neighbouring trees and by increased C export to soil (Klein et al. 2016a). 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). Increasing soil N availability through N fertilization reduced the belowground C flux in both ambient and elevated CO₂ plots (Drake et al. 2011).

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 and 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 amount of surplus fixed C in 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 and no longer served as a sink, the fixed C was translocated belowground, much of it to mycorrhizal fungi. Sporocarp production of ECM fungi was totally dependent on recent photosynthate in the late season. This late-summer flux of surplus photosynthate may underly the autumn peak in sporocarp production in boreal forests. 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 and 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 Loehle 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. Sharing

of surplus carbon does not entail a cost to the source tree, so this explanation does not require there to be a benefit to the living trees of maintaining a non-living neighbor.

Transfer of carbohydrates among *living* trees through root grafts (Fraser et al. 2006) or mycorrhizal fungi (Simard et al. 1997; Klein et al., 2016b) has 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, as neighboring trees have a high probability of being related (Gorzelaek 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. Sharing surplus carbohydrates with sink trees is of little cost to the source tree (Corrêa et al. 2012), and may actually benefit the source tree by providing a sink for surplus photo-assimilates.

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. 2011, 2013). 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, 2011). 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 (Tawarayama 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 (Tawarayama 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 (Tawarayama 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 likely adaptations for P acquisition (Lambers et al. 2006).

The belowground ecosystem

The abundant microorganisms in the plant rhizosphere provide a large and dynamic sink for surplus

plant metabolites. 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; Kaštovská and Santruckova 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, 2009; Butler et al. 2004). This maintains a steep concentration gradient immediately outside root tips, which promotes exudation (Canarini et al. 2019) and generates a strong sink for plant C. Root microbionts can 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 rates following removal of arbuscular mycorrhizal fungi (Gavito et al. 2019). These observations are consistent with root microbionts serving as active carbohydrate sinks, which prevents the accumulation of surplus carbohydrates and attendant suppression of photosynthesis in source leaves.

Conclusions

The physiological and ecological phenomena discussed in this paper are challenging to explain if fixed C is invariably viewed as a scarce resource that plants must use efficiently. However, under conditions such as mild-to-moderate deficiencies of N, P or water that reduce leaf growth more so than photosynthesis, plants tend to produce more fixed C than they can use at that time. Accumulation of surplus fixed C in the absence of the growth sink can generate photo-oxidative damage and induce end-product inhibition of photosynthesis, but these outcomes are prevented by the activities of multiple alternative sinks for fixed C such as the alternative oxidase pathway, starch synthesis, secondary metabolites, extra-floral nectaries, root exudation and mycorrhizal fungi. Activities of these sinks increase under the same conditions that result in generation of surplus C (mild-to-moderate deficiencies of N, P or water and high light and CO₂). Under these conditions, C ‘allocated’ to these sinks is not really an ‘investment’ as it does not entail a cost to the plant. Instead, these phenomena can be viewed

as downstream consequences of C flow from sites of accumulation to sites of removal.

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