Trends in Ecology & Evolution

CellPress REVIEWS

Opinion

Surplus Carbon Drives Allocation and Plant–Soil Interactions

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Plant growth is usually constrained by the availability of nutrients, water, or temperature, rather than photosynthetic carbon (C) fixation. Under these conditions leaf growth is curtailed more than C fixation, and the surplus photosynthates are exported from the leaf. In plants limited by nitrogen (N) or phosphorus (P), photosynthates are converted into sugars and secondary metabolites. Some surplus C is translocated to roots and released as root exudates or transferred to root-associated microorganisms. Surplus C is also produced under low moisture availability, low temperature, and high atmospheric CO_2 concentrations, with similar below-ground effects. Many interactions among above- and below-ground ecosystem components can be parsimoniously explained by the production, distribution, and release of surplus C under conditions that limit plant growth.

Highlights

Plant growth is normally constrained by nutrients, water or temperature, not photosynthesis, and plants often have surplus carbohydrates.

Secondary metabolites are produced in N-limited plants primarily to dispose of surplus carbon, although they may subsequently help reduce browsing damage.

Surplus carbohydrates are translocated from leaves and below ground some are discharged via exudates and mycorrhizal fungi.

Root exudates contain more of the elements that plants have in surplus, and less of those in short supply.

The abundance and type of mycorrhizal fungi is influenced by the amount and composition of surplus carbon in roots.

Surplus carbon provides an alternative lens though which to view interactions between plants and soil organisms.

What Drives Carbon Allocation in Plants?

A pervasive practice in studies of carbon (C) allocation (both distribution of plant biomass and C between above- and below-ground parts and between primary and secondary metabolism) is interpreting the observed patterns in terms of optimisation [1], economic theory [2,3], or trade-offs between investments and returns of energy, water, and nutrients [4,5]. Similarly, explanations regarding the considerable quantity and variety of C-rich compounds exuded from plant roots and their manifold effects on soil biota commonly assume that these effects on other organisms are the purpose of the fluxes [6,7]. This implies that plants allocate C specifically to gain other resources (such as nutrients or water) and that such responses were selected for during the course of evolution. In both of these interpretations of the flux of C-containing compounds from leaves to roots and soil, C is used as the 'currency', with the implicit assumption that the C fixed in **photosynthates** (see Glossary) is 'traded' for other resources. As the currency for plant growth, the assumption persists that the availability of fixed C limits plant growth, despite abundant evidence to the contrary [8,9].

Plants in natural habitats frequently contain high levels of **nonstructural carbohydrates (NSCs)** [8,10] and do not exhibit a sustained growth response to elevated CO_2, unless replete with nutrients and water [11,12]. Together, these suggest that under natural conditions, plants often have surplus C, relative to other resources such as nutrients or water. A state of surplus C is also consistent with findings from numerous fertiliser-addition experiments that show that plant biomass production in most terrestrial ecosystems is primarily limited by the availability of nutrients – usually nitrogen (N) and/or phosphorus (P) [13,14]. Plant responses to N or P limitation may actually be activated by the associated increase in shoot carbohydrate concentrations, given the large similarities in gene expression triggered by N and/or P deficiency and high shoot carbohydrate concentrations [15]. Under conditions of inadequate availability of N and/or P [16,17], or water [18], plant growth tends to decrease at an earlier stage of limitation than does photosynthesis. This has profound consequences for both leaf C metabolism (Box 1) and C allocation within the plant. Here, we present an alternative view of C allocation that it is largely driven by disposal of surplus C.

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 https://doi.org/10.1016/j.tree.2020.08.007

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Box 1. Consequences of Nutrient Limitation on Leaf C Metabolism

When N or P are in short supply, rates of leaf cell division and elongation decline, while photosynthesis continues [16,17,63], resulting in leaves having surplus photosynthates. The photosynthetic machinery depends on photosynthate removal from the site of synthesis in order to avoid feedback inhibition [11,64] and consequent photodamage. In P-deficient plants, photosynthesis produces triose-P, which is converted into sucrose through a series of reactions that liberate inorganic P, which is retained and reused [65]. In leaves of N-deficient plants, surplus photosynthates are converted into sucrose or starch, or shunted into secondary metabolic pathways through which they are converted into C-based secondary metabolites such as flavonoids, terpenoids, hydrolyzable tannins, and phenylpropanoid derivatives [52]. During the synthesis of phenylpropanoids, ammonium is released and reused, while the N-free C skeletons of t-cinnamate are shunted into various phenylpropanoid pathways [66]. Therefore, N-deficient plants have higher concentrations of phenolic compounds than plants subjected to N deposition [52]. Elevated concentrations of phenolic compounds such as flavanols, anthocyanins, and coumarins in plants growing with N limitation [67] are metabolic consequences of plants eliminating surplus photosynthates, while conserving N. Therefore, the primary function of secondary metabolites in N-deficient plants may be to prevent photodamage by removing surplus photosynthates. Leaf secondary metabolites can make foliage less palatable to herbivores, so their production has often been interpreted as C allocation to defend leaves, thereby protecting the plants ability for photosynthesis [68]. Instead we suggest secondary metabolites are primarily produced for disposal of surplus C, although they may subsequently reduce the risk of browsing damage to the plant.

Consequences of Nutrient Limitation on Whole-Plant C Allocation

Growth limitations by N or P do not interfere with the process of **phloem loading**, so any surplus photosynthates can be exported out of the source leaf to sink organs such as twigs, stems and roots [19], thereby alleviating the **accumulation** of fixed C in the leaf and preventing biochemical end-product inhibition and associated phototoxicity. Many nutrient-limited plants accumulate NSCs in roots [20,21]. Accumulation of NSCs stimulates root growth; **phloem transport** of sucrose and subsequently increased sucrose concentrations in roots are the primary trigger for changes in root metabolism, growth, and gene expression in P-deficient plants [19]. Over time, this transport of fixed C to roots leads to greater **root:shoot ratios** of nutrient-limited plants [15,22] or of trees growing on nutrient-poor sites [23]. These phenomena are commonly interpreted as plants adjusting their root: shoot ratio or investing more photosynthates in roots and root symbionts in order to increase nutrient acquisition [4,24]. Alternatively, we argue that these shifts in biomass allocation reflect the plant discharging surplus photosynthates belowground when aboveground growth is curtailed by insufficient N or P.

The greater flux of photosynthates to roots when aboveground growth is constrained by N or P enhances **root exudation** (Box 2) and the abundance and growth of root-associated organisms such as **ectomycorrhizal (ECM)** and **arbuscular mycorrhizal** fungi [25,26]. Consistent declines

Box 2. C Surplus and Root Exudation

Plants exude a considerable proportion (20–40%) of their assimilated C from their roots [6], these root exudates include a wide range of compounds such as simple sugars, amino and organic acids, and a multitude of secondary compounds. Increased flux of photosynthates to roots in nutrient-limited plants can increase rates of exudation. For example, there is a close relationship between the quantity of root exudates and root import of soluble sugars [68] and a positive linear relationship between sugar concentrations in fine roots and exudation rates of organic C [15]. Exudate composition also varies with plant nutritional status; for example, slower release of amino acids from N-depleted plants has been reported for *Zea mays* (maize) [69], *Pinus radiata* (pine) [70], and *Phaseolus vulgaris* (bean) [71]. P limitation increases the release of carbohydrates in *Z. mays* [69] and *Gossypium hirsutum* (cotton) [72]. The exudation of amino acids by cotton roots also increases under P deficiency [72], consistent with both N and C being available in surplus when P is limiting. Likewise, *Glycine max* (soybean) roots release more metabolites including amino acids and organic acids when grown with limited P [73]. Roots may also release a large spectrum of plant secondary metabolites [74,75], particularly when plants are nutrient limited [76,77]. Increased concentrations of phenolic compounds [68], flavanoids [78], and organic acids [79] have been reported in root exudates from nutrient-deficient plants. These differences in exudate profiles are consistent with plants discharging compounds containing the elements that they have in surplus, while retaining those in short supply. There are situations in which specific compounds are produced and exuded in order to produce a specific effect. For example, cluster or dauciform roots that release carboxylates in an exudative burst when P availability is low [80]. Here, carboxylate exudation is probably a way to acquire P, rather than a way to dispose of surplus C. However, roots may also release carboxylates with a high availability of P [81,82]; in such cases, carboxylate exudation may be a way to remove surplus C.

in the abundance of **mycorrhizal** fungi following additions of N or P [27] can be attributed to reduced below-ground fluxes of C when nutrient limitation is alleviated. For example, addition of N to a N-limited boreal pine forest resulted in a 60% reduction in below-ground flux of recent photosynthate, and a concomitant reduction in biomass of ECM fungi [28]. N addition also causes shifts in relative abundance of fungal taxa. In severely N-limited temperate and boreal forests, ECM fungi dominate, particularly taxa with extensive extramatrical mycelia that form hydrophobic rhizomorphs, and possess proteolytic capacity and potential for organic matter degradation by enzymatic and oxidative activities [29]. N input reduces the abundance of ECM fungi and shifts the community towards short-distance and contact exploration types with much smaller biomass, often with no proteinase activities [29,30]. Shifts in arbuscular mycorrhizal fungal associates of plants also occur in response to N addition: from communities dominated by *Gigaspora* species, which have extensive **extramatrical hyphae** and possess enzymes capable of degrading recalcitrant compounds under low-N conditions, to dominance by *Glomus* species, which have minimal extramatrical hyphae and few recalcitrant compound-degrading enzymes [31].

These shifts in the composition of the mycorrhizal fungal community under changing nutritional conditions are predictable consequences of surplus C. When availability of N or P is low, mycorrhizal fungi receive plant photosynthates that are rich in C but poor in the limiting nutrient, so akin to the plant, have surplus C. Under these conditions, the fungus has a high demand for the limiting nutrient for its own metabolism. Fungi possessing the enzymatic capability to access the limiting nutrient have an advantage over those that do not. For example, northern coniferous forests are primarily poor in N [32], have large fluxes of fixed C below-ground (28) and are dominated by ECM and ericoid fungi, which have enzymes able to degrade complex organic compounds [33]. This relationship may be further strengthened by the ability of these fungi to degrade and metabolise the **secondary metabolites** generated by N-limited plants. Instead of plants selecting fungi that provide the most nutrients in return for C, shifts in abundance and composition of mycorrhizal fungi may reflect the size and composition of the surplus C flux under different nutritional conditions (Box 3).

Through the lens of surplus C, root exudates (and hyphal exudates from mycorrhizal fungi [34]), are the final step in the process through which plants dispose of surplus photosynthates (Figure 1). Root and hyphal exudates have stimulatory effects on associated soil microbial communities [34], which are commonly assumed to be the purpose of the fluxes [7]. However, many such effects may simply reflect heterotrophic organisms responding to a usable energy source (plant surplus C), and we suggest considering this explanation, rather than assuming that exudates are released for the purpose of the particular effect that we observe. This view of root exudation does not require economic rationalisation about plants 'investing' C or trading C for nutrients. Likewise, the phenomenon of C compounds being transferred from one plant to another via mycorrhizal fungal connections can be interpreted as material that is available in surplus in one organism being discharged and taken up by another. We suggest that the

Box 3. Are Mycorrhizal Associations Investments in Trading Partners or Consequences of Surplus C Disposal?

Shifts in the abundance and composition of mycorrhizal fungi under varying nutritional conditions are commonly interpreted via market theory as nutrient-limited plants enhancing mycorrhizal colonisation in order to obtain more nutrients, that is, trade C for nutrients [2,3], and nutrient-replete plants reducing their investment in mycorrhizas in order to retain C [5]. Implicit in this concept of 'biological markets' is that plants are 'choosing' their mycorrhizal partners by a trading strategy (shaped by natural selection), with C invested to gain some other resource [83]. This is essentially a C-centric view of plant–microbial interactions, based on the view that C is invariably a valuable resource for the plant. We suggest that when plants have excess C, instead of trading, they are disposing of it. Surplus C transferred to mycorrhizal fungi under nutrient-limited conditions is not a cost to the plant [84,85]; this is one of several shortcomings of market theory explaining mycorrhizal symbioses [86]. From the fungal perspective, there would be an evolutionary advantage of being able to provide a growth-limiting resource back to the host: maintaining the supply of surplus C for the plant to dispose of by alleviating without removing the nutrient limitation.

Glossary

Accumulation: allocation of C to storage pools, even when conditions for growth are favourable.
Active storage: storage pools increase, even when conditions for growth are favourable.
Arbuscular mycorrhiza: symbiotic structure exhibiting arbuscular (tree like) fungal structures in cortical cells.
Ectomycorrhiza (ECM): symbiotic structure exhibiting a large amount of fungal tissues outside the roots which is typical for many woody species.
Extramatrical hyphae: the collection of filamentous fungal hyphae emanating from ectomycorrhizas.
Mycorrhiza: symbiotic association between a root and a fungus, in which the plant provides C to the fungus, and the fungus provides nutrients, water, and protection against pathogens for the plant.
Nonstructural carbohydrates (NSCs): sugars that do not play a role in cellular structures, but are used for, for example, transport, storage, signalling, or osmoregulation.
Passive storage: allocation of C to storage pools when the conditions for growth are unfavourable.
Phloem loading: process involving the transport of products of photosynthesis from photosynthetically active cells into sieve tubes.
Phloem transport: movement of solutes inside sieve tubes from a location where they have been loaded into the phloem (source) to a location where they are unloaded and used (sink).
Photosynthate: product of photosynthesis.
Root exudation: release of organic solutes, enzymes, or protons from roots into the rhizosphere.
Root:shoot ratio: the ratio of the amount of biomass invested in roots divided by that invested in shoots.
Secondary metabolite: organic compound that does not play a role in primary metabolism, which occurs in all plants; secondary metabolites may be species specific and may be produced only under certain conditions.
Sequestration: accumulation in a pool that is a metabolic dead end from which it cannot be reused by the plant.
Storage: allocation of C to a pool that is not metabolically active, from which it can subsequently be reused for growth, maintenance, or reproduction.

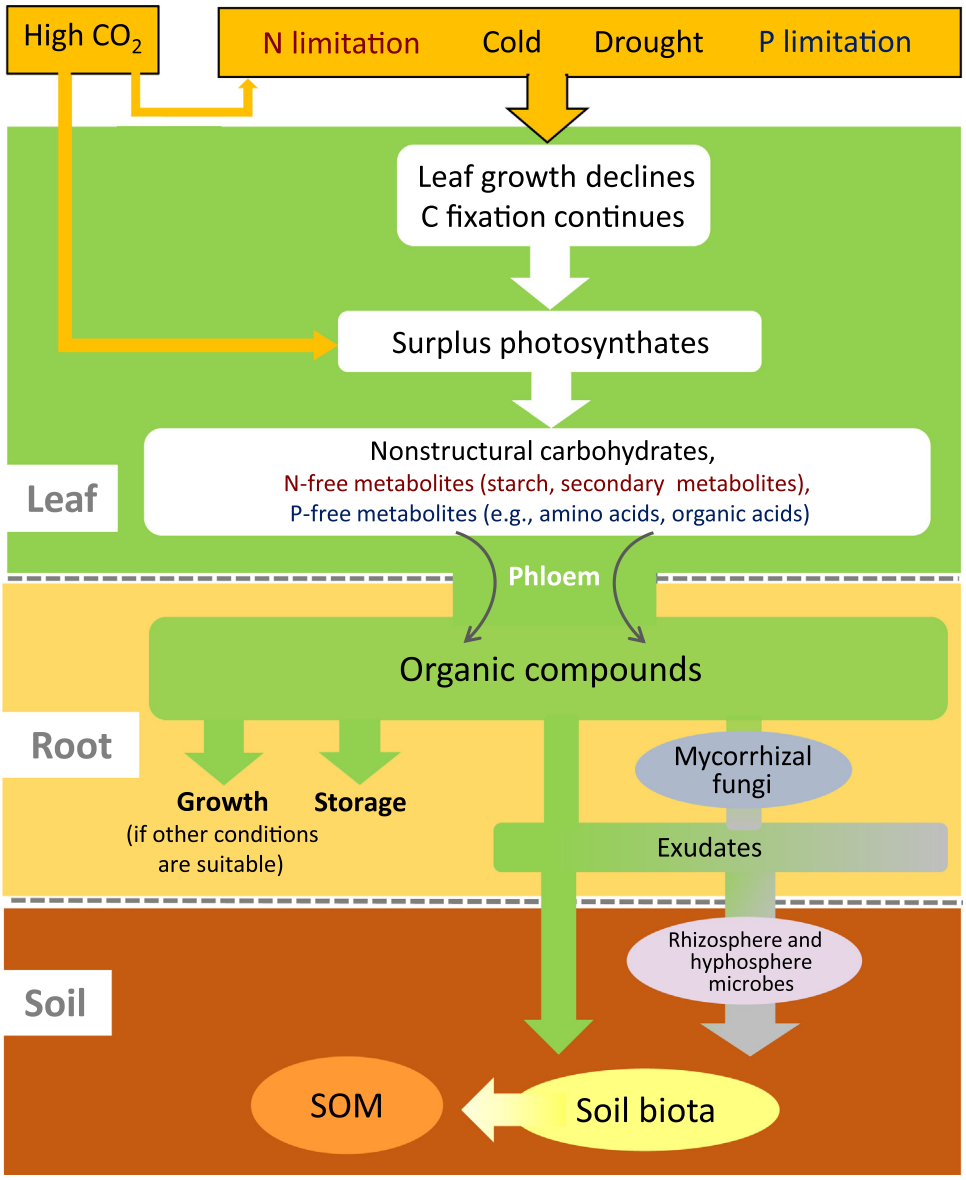

Figure 1. Surplus Carbon (C) Hypothesis. External factors such as insufficient nitrogen (N), phosphorus (P,) or water, or adverse temperatures cause growth to decline while C fixation continues (albeit at a reduced rate), resulting in surplus photosynthates. Elevated CO_2 concentrations also lead to surplus photosynthates, directly or through induced nutrient deficiencies. Surplus nonstructural carbohydrates (NSCs) are produced along with other C-rich metabolites; the nature of which varies according to whether N or P are most limiting. Some of the surplus NSCs and metabolites are transported through phloem and further metabolised in roots. If other conditions are suitable, root growth may increase and a portion of the surplus NSCs is stored. Remaining surplus C is exuded from the roots (green) or taken up and metabolised by mycorrhizal fungi, which exude materials they have in surplus (grey). Exudates from roots and fungal hyphae may be metabolised by microbes associated with their structures which in turn release surplus metabolites. Consequently, in many ecosystems, surplus photosynthates are largely metabolised and transformed by microorganisms prior to release into the soil. The flow, transformation, and release of surplus fixed C provides energy sources for heterotrophic soil organisms whose residues and metabolites may be important precursors of soil organic matter (SOM).

compounds that plants discharge via exudates or via root associates be considered first as indicators of the resources that the plant has 'in surplus' to its immediate requirements, rather than indications of what the plant 'needs'.

Other Evidence for C Surplus Driving Allocation

There is evidence for production of surplus photosynthates under other conditions in which growth is curtailed, but photosynthesis continues. This is often studied through measuring NSC levels in plants and interpreted as C **storage** by plants (Box 4).

During water limitation, plant growth declines before photosynthesis [18,35], resulting in a build-up of NSCs [36]. For example, water-limited *Populus tremuloides* (aspen) trees show elevated sucrose levels in branches, xylem, bark, and roots, and higher concentrations of starch in roots than nonlimited trees [37]. Elevated NSCs may contribute to osmoregulation during water limitation, but starch, which is not osmotically active, also builds up when growth is curtailed by water limitation [38]. Root growth and root: shoot ratios often increase in response to water limitation [38,39], as does root exudation [40,41]. Exudates of *Quercus ilex* (holm oak) under experimental water limitation mainly comprise secondary metabolites, while exudates of nonlimited plants are dominated by primary metabolites [42]. Each of these responses is a predictable metabolic consequence of the production and transport of surplus C when growth is constrained by lack of water, analogous to the exudate response to nutrient limitation.

Low temperatures constrain plant growth long before photosynthesis declines [15,43] which is related to the low temperature dependency of C_3 photosynthesis [44]. As a consequence, concentrations of NSCs (including starch and sugars such as glucose, fructose, and sucrose) rise in response to growth-limiting temperatures [45]. *Populus tremuloides* seedlings grown in cold soils have the highest fine-root sugar levels, and exude organic C at a faster rate than control seedlings [21]. Low, growth-limiting temperatures enhance phenylpropanoid metabolism and activate genes involved in phenolic metabolism [46]. Low temperatures may, therefore, also lead to production of surplus photosynthates (NSCs and secondary metabolites) [8].

Elevated CO_2 Concentrations

If plants were C-limited, elevated atmospheric CO_2 levels should result in faster growth. However, plants show faster growth rates under CO_2 enrichment only when they are well supplied with

Box 4. NSC Storage and Sequestration

NSCs can provide C and energy for plant growth and respiration. In perennial plants, NSCs accumulate during periods of photosynthesis, but are depleted during periods of rapid growth, or when respiration exceeds photosynthesis [10]. Thus, NSCs act as a storage pool for C, with remobilisation of the C from storage being driven by sink strength. There is a continuing debate whether NSC storage is an active or passive process [87,88]. **Active storage** means that NSC pools increase, even when conditions for growth are favourable, whereas **passive storage** indicates that NSC pools increase when the conditions for growth are unfavourable. There is overwhelming evidence for active storage, and that storage and growth compete for photosynthates, with storage often prioritised over growth [87,89]. The amount of NSC accumulating is often used as a measure of storage, although several authors have pointed out that while starch may be considered purely a storage compound, soluble sugars are involved in a wide range of other physiological functions, including drought and cold tolerance [10]. However, is all starch actually stored? The concept of storage implies that the resource can be reused later. There is evidence that in a wide range of plants that, while starch levels in tissues vary seasonally, pools are never completely depleted [10], even in extreme circumstances (such as starch remaining in the roots of girdled trees after their death, or being unaffected by severe defoliation [90]). Measuring NSC pools cannot be used to quantify C storage and a proportion of NSCs might in fact be physiologically **sequestered**, rather than stored. This implies surplus C being allocated to a metabolic dead end, where it can accumulate without any other physiological consequences [91]. This would make starch an ideal candidate as there are no osmotic consequences and might explain the accumulation of starch in leaves, stems, and roots of many species across a wide range of biomes, from boreal to tropical [10]. This would also imply that active storage actually reflects metabolic disposal of surplus C.

nutrients (for forest trees, see [47]), and when new sinks continue to be available [48]. In natural forests with a steady-state microbial nutrient cycle, elevated CO_2 concentrations have so far never been found to stimulate tree growth [49–51]. Instead, higher concentrations of C-based secondary metabolites and NSCs [52–54], increased C exudation [55], and enhanced growth of mycorrhizal fungi [27] and soil microbes (especially *r* strategists [56]) are often reported, with an associated rise in respiratory metabolism along the C dissipation pathway [12,57]. Increased exudation has been interpreted as a means through which nutrient-deficient plants increase nutrient mineralisation or uptake from soil [55,58]. Alternatively, we may view elevated rates of root exudation of C compounds under conditions of elevated CO_2 as the disposal of surplus photosynthates induced by nutrient limitation. Likewise, increased exudation of trehalose from arbuscular mycorrhizal hyphae under elevated CO_2, concentrations, and associated stimulation of hyphal-associated bacteria such as *Burkholderia* and *Pseudomonas* [59] indicate that surplus C is also released via mycorrhizal fungi.

The striking commonality in plant responses and below-ground consequences to limitation by nutrients, water or low temperatures, or by elevated CO_2 suggests a common cause: the production, distribution and release of surplus C under conditions that are not conducive to growth.

Consequences of Surplus C

Given the evidence that most plants in a current atmosphere fix C in surplus to their requirement [15], it is curious that fixed C is commonly implicitly considered a limiting resource in discourses about C allocation by plants and below-ground interactions of plant roots and soil organisms. Rather than strategies through which plants invest, trade, or share C in order to receive some benefit from other organisms, the stimulation of root growth and proliferation of heterotrophic root-associated microorganisms under conditions that limit above-ground plant growth can be seen as metabolic consequences of one organism's waste being another organism's resource.

Surplus C provides an alternative explanation for many phenomena that may otherwise require less parsimonious explanations. For example, the less efficient production of above-ground biomass and large fluxes of recently fixed C to below-ground organisms [60] on nutrient-poor sites are both predictable consequences of the generation and disposal of surplus photosynthate when above-ground growth is constrained by low availability of N or P. Likewise, the greater concentration of recently fixed C in below-ground organisms in boreal forests in August compared with June [28] is a predictable consequence of the movement and removal of surplus C (i.e., that not required for leaf growth or maintenance) following full leaf expansion.

Greater consideration of the metabolic and ecological consequences of surplus fixed C in plants has the potential to improve our understanding of factors that influence the amount and nature of secondary metabolites, root exudates and root-associated microorganisms such as mycorrhizal fungi. The greater abundance of mycorrhizal fungi on infertile versus fertile sites is often explained as plants adjusting their root: shoot ratio or investing more photosynthates in roots and root symbionts [4] in order to increase nutrient acquisition [5,24]; that is, trade C for nutrients [3]. This assumption is contradicted by recent evidence that investment in mycorrhizal associations does not increase the tree's access to limiting nutrients [12,61], and may actually perpetuate the nutrient limitation [62]. These findings are not counterintuitive if mycorrhizal associations are viewed as an outcome of plants discharging surplus C. Viewing plant C allocation and plant–soil interactions through the lens of surplus C could enable better prediction and modelling of the consequences of global-change factors such as N deposition, intensified drought and increased atmospheric CO_2 concentrations. For example, 4-year exposure of a P-limited mature *Eucalyptus* forest to elevated CO_2 concentrations did not result in downregulation

of photosynthesis, additional biomass accumulation, or enhanced aboveground respiration; instead it increased belowground C allocation and soil respiration [12]. Furthermore, an initial enhancement in N and P mineralisation rates did not persist, such that the increased belowground C flux was not effective in increasing P availability to the plants. These findings are inconsistent with existing terrestrial vegetation models and C cycle models [12], but are entirely consistent with expectations based on surplus C.

Concluding Remarks

We review evidence that plants often have surplus fixed C, as a consequence of growth limitations imposed by insufficient nutrients or water or low temperature (or elevated atmospheric CO_2). The consistency of the responses to these limitations indicates that surplus C may be a trigger for plant responses, and consequent effects on other organisms. To alleviate the oversupply, surplus C is converted into sugars and secondary metabolites and a considerable portion may be transported to roots and metabolised or exuded or transferred to mycorrhizal fungi. Plant secondary metabolites and root exudates affect other organisms in myriad ways, but this is not evidence that these compounds are produced and excreted for this purpose. These metabolites may instead indicate resources that the organism has in surplus to requirements. We propose considering the production and disposal of surplus C under growth-limiting conditions prior to invoking arguments about adaptive strategies, investments or trade-offs to explain relationships between environmental conditions, plant growth, and below-ground components of ecosystems. Only phenomena that cannot be explained as consequences of surplus C require further explanation. Focusing scientific efforts on improving our understanding of the conditions under which plants produce and discharge surplus photosynthates could advance our comprehension of relationships between plants and soil organisms (see Outstanding Questions).

Outstanding Questions

How well do current plant and ecosystem C models perform using assumptions based on known effects of nutrient and water limitations on surplus C supplies?

How does the abundance of sugars and secondary metabolites in the phloem and roots of plants, whose growth is limited by N, P, or water compare with plants under optimal growing conditions?

Is the proportion of surplus C in roots in the form of secondary metabolites sufficient to promote the abundance of mycorrhizal fungi capable of catabolising these compounds?

Given that extreme water or nutrient shortage can interfere with export of sugars and reduce abundance of mycorrhizal fungi, at what level of deficiency is there maximum export of surplus C and consequent below-ground effects?

Why has evolution not selected against production of surplus C by plants?

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