Viewpoints

Re-examining the evidence for the mother tree hypothesis – resource sharing among trees via ectomycorrhizal networks

Summary

Seminal scientific papers positing that mycorrhizal fungal networks can distribute carbon (C) among plants have stimulated a popular narrative that overstory trees, or 'mother trees', support the growth of seedlings in this way. This narrative has far-reaching implications for our understanding of forest ecology and has been controversial in the scientific community. We review the current understanding of ectomycorrhizal C metabolism and observations on forest regeneration that make the mother tree narrative debatable. We then re-examine data and conclusions from publications that underlie the mother tree hypothesis. Isotopic labeling methods are uniquely suited for studying element fluxes through ecosystems, but the complexity of mycorrhizal symbiosis, low detection limits, and small carbon discrimination in biological processes can cause researchers to make important inferences based on miniscule shifts in isotopic abundance, which can be misleading. We conclude that evidence of a significant net C transfer via common mycorrhizal networks that benefits the recipients is still lacking. Furthermore, a role for fungi as a C pipeline between trees is difficult to reconcile with any adaptive advantages for the fungi. Finally, the hypothesis is neither supported by boreal forest regeneration patterns nor consistent with the understanding of physiological mechanisms controlling mycorrhizal symbiosis.

Introduction

In forest ecosystems, the extramatrical fungal mycelia extending from mycorrhizas play a key role in tree nutrient acquisition. The classical view of the symbiosis is that the mycelia act as microbial extensions of tree root systems and improve access to water and nutrients while the fungi in return receive carbon (C) from tree photosynthesis. This view has been complemented by the recognition of a continuum of outcomes of the symbiosis ranging from the mutualistic to parasitic, even in a single type of mycorrhiza (Johnson *et al.*, 1997; Smith & Read, 2008). This, and the fact that plants can have multiple mycorrhizal fungal partners and vice versa, stimulated the formulation of biological market models for

mycorrhizal fungi (Schwartz & Hoeksema, 1998; Kiers *et al.*, 2011; Näsholm *et al.*, 2013; Franklin *et al.*, 2014).

Several highly recognized papers have suggested that trees may share common mycorrhizal networks (CMNs) to allow redistribution of resources such as C from one plant, tree, or seedling to another (e.g. Simard *et al.*, 1997a,b; Teste *et al.*, 2009; Bingham & Simard, 2012; Klein *et al.*, 2016; Cahanovitc *et al.*, 2022). One suggested implication of this has been that overstory trees use the mycorrhizal mycelium to transfer C from their own photosynthesis to struggling and shaded seedlings to facilitate their growth and survival. This idea has been termed the *mother tree* hypothesis, and in addition to the growing body of scientific literature it has also gained a strong popular following.

However, a recent meta-analysis (Karst *et al.*, 2023) showed a growing tendency toward unsupported citations in the scientific literature in favor of a beneficial view of CMNs in forest ecosystems. Claims in favor of the mother tree concept have been controversial in the scientific community (Robinson & Fitter, 1999; Booth & Hoeksema, 2010; Högberg & Högberg, 2022). The controversy arises partly because mycorrhizal fungi are not extensions of roots but are organisms with their own strategies. Net transfer of C among plants via mycorrhizal mycelia would contradict the current understanding of the evolutionary rationale of mycorrhizal symbioses between trees and fungi: that fungi acquire C from trees in exchange for water and nutrients. Carbon transfer from fungus to plant undoubtedly occurs in orchid mycorrhiza at early developmental stages and in all mycoheterotrophic associations, and is especially important in plants with microscopic seeds containing minimal C reserves (Leake, 2005; Cameron *et al.*, 2008). Although this has not been shown for trees, it is an interesting hypothesis for C transfer through mycorrhizal fungi to tree seedlings.

The objectives of the current work are to first provide perspective by comparing predicted implications of the hypothesized resource sharing among trees with field observations of forest regeneration and seedling growth, mainly in boreal forests, which represent around a third of the forests in the world; and second, to review the current understanding of ectomycorrhizal (ECM) fungal C metabolism as it relates to the physiological potential for C export to host plants. Third, we scrutinize the most prominent published experimental evidence for such sharing. We evaluate and discuss the conclusions made in several of the most influential articles presenting evidence for C sharing via CMNs.

In these studies, two C isotopes (the stable ^{13}C and the unstable radioisotope ^{14}C) were used. Hence, our analysis focuses on the extent to which such isotopic data conclusively demonstrate net C transfer between plants. To determine that CMNs mediate C transfer among plants, it must be irrefutably shown that: (1) C from a donor plant enters the tissue of a receiver plant; (2) transfer occurs through CMNs; and (3) the mycorrhizal hyphal connections do increase the magnitude of transfer as compared with
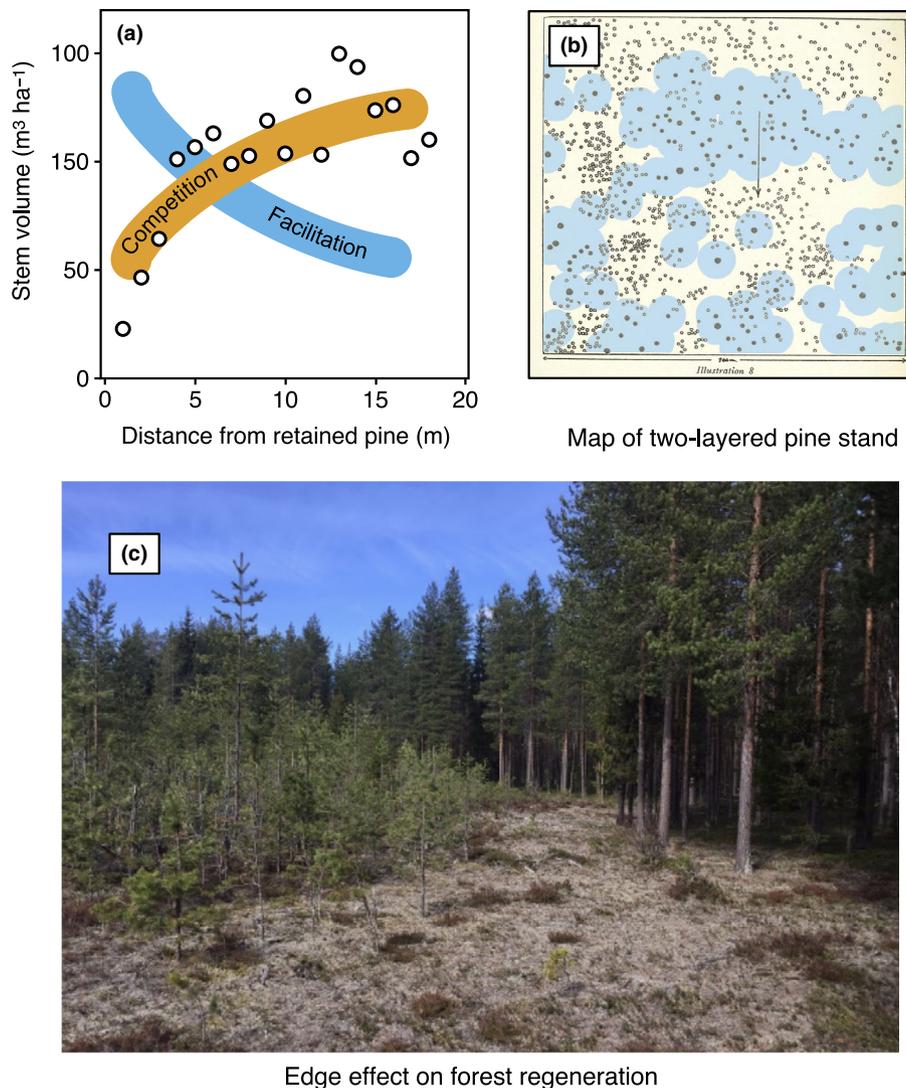
Fig. 1 Panel (a) shows stem volume of *Pinus sylvestris* stands around trees that were retained at harvest from the previous stands. Data were extracted from Jakobsson (2005) describing Swedish stands between 55°N and 68°N 20 yr or more after the liberation of the large trees. The authors found that trees closer than 5 m from the retained trees exhibited 24% reduced growth, compared with trees farther away. The orange and blue brush strokes indicate the hypothetical growth pattern of the younger stand in the case of competition or facilitation by the large tree, respectively. Panel (b) is a figure from Aaltonen (1926) mapping the locations of *Pinus sylvestris* trees in a two-layered stand in southern Finland (100 × 100 m). The older trees are denoted by closed circles (sizes correspond to stem diameter classes), and the younger trees are denoted by open circles. The area within 5–6 m radius around the older trees has been shaded in blue, to highlight the low density of younger trees there, compared with the areas without old trees. The figure is reprinted with permission from Oxford Academic Press. Panel (c) shows the southwest-facing edge of a boreal Scots pine stand, and the naturally regenerated stand adjacent to it (Sweden, 64°N). Note the poor growth near the larger trees. Photo: Peter Högberg.

other processes such as turnover of litter by soil biota and the subsequent redistribution of its C, and transport in soil water by diffusion and mass flow. The mother tree hypothesis also requires that there is a net transfer in the direction from overstory trees to young seedlings.

The mother tree hypothesis and field observations from boreal forests

If overstory trees do facilitate seedling survival and/or growth via CMNs, then it should be reflected in forest regeneration patterns. These are directly observable in the field and do not require isotopic methods to quantify (Högberg & Högberg, 2022). The mother tree

hypothesis predicts that seedling abundance and growth should be higher within the zone of active roots and associated mycorrhizal fungi of large trees than outside this zone. Observations of seedling development near pine trees in boreal forests contradict this prediction (Fig. 1a). As early as 1926, a Finnish field study showed that belowground competition hampered seedling establishment in extremely nutrient-poor Scandinavian pine heaths (Aaltonen, 1926) (Fig. 1b). In fact, poor regeneration near overstory pines was a widespread concern among Scandinavian foresters at the time, and remains well known today (Ruuska *et al.*, 2008).

Axelsson *et al.* (2014) used a previous stem-girdling experiment (Högberg *et al.*, 2001) to demonstrate that massive pine regeneration occurred after liberation from belowground

competition by parent-stand trees and their associated ECM mycelia. Importantly, belowground competition was a more important constraint for regeneration than light competition with the canopy trees. The earlier mentioned examples of field observations in boreal forests show that natural regeneration is poor around larger trees and the zone of negative impact is similar to the zone of overstory root systems and associated ECM activity (Göttlicher *et al.*, 2008; Henriksson *et al.*, 2021b). Indeed, in the study by Axelsson *et al.* (2014), regeneration was especially poor in a zone within 5 m of alleged mother trees and coincided with the distribution of ECM sporocarps and tree uptake of ^{15}N tracer in the same experimental site (Göttlicher *et al.*, 2008).

In British Columbia, seedling foliar N concentration was shown to decline from open areas in forest gaps to forest understories (Walters *et al.*, 2006). Soil moisture content and N mineralization rates were also lower in the presence of overstory trees (Walters *et al.*, 2006), indicating higher competition for these resources, rather than facilitation. Similarly, advance regeneration of *Abies amabilis* on Vancouver Island displayed improved N uptake and shoot N concentration after overstory removal (Hawkins & Moran, 2003). Trenching, or root exclusion experiments, reduced belowground competition with overstory trees, increasing height and diameter growth of naturally regenerated Douglas-fir saplings, as well as foliar N concentrations (Devine & Harrington, 2008). Evidently, resource competition between trees and seedlings is a common phenomenon (Coomes & Grubb, 2000).

By contrast, natural regeneration in a Douglas-fir-dominated forest in British Columbia was shown to benefit from retention of forest patches after harvest (Simard *et al.*, 2021). After three growing seasons, stem density of emerged seedlings was greatest near retained seed trees. Seedlings were reported to be significantly taller where 30% of the stand area had been retained in forest patches, but no mention was made of seedling height growth as a function of distance to seed trees. In the Hubbard Brook Experimental Forest in the north-eastern United States, regeneration was quantified along transects stretching from intact spruce and fir forests into 10-yr-old clearcuts. It was found that seedling germination was abundant beneath intact canopies, but the root collar diameter of nearly all established seedlings was < 1 cm, whereas *c.* 50% of seedlings in the clearcuts had a root collar diameter of 1–5 cm (Hughes & Bechtel, 1997). Seedling age was not reported, so seedlings growing under canopy may have had very low growth rates, or had high mortality and turnover rates (Hughes & Bechtel, 1997). High seedling mortality could be related to the presence of compatible pathogens in the soil near the tree's roots (Connell, 1970; Janzen, 1970). In temperate forests of North America, Bennett *et al.* (2017) observed greater seedling density under conspecific trees, but only for ECM species, and attributed this to protection against root pathogens by ECM colonization. However, these studies indicate that although the density of germinating seeds is highest near the seed source, seedling survival and growth does not necessarily follow the same pattern, and in boreal forests poor regeneration near overstory trees is most common.

In volcanic soils lacking native ECM mycelium, Nara (2006) found growth enhancement of current-year *Salix* germinants when grown together with a *Salix* 'mother plant' infected by ECM fungi. This effect was not found when the germinants were growing together with a non-infected *Salix* plant. However, it cannot be ruled out that this growth benefit indicated successful mycorrhization of the germinants rather than establishment of CMN connections between them and the larger plants. The study was conducted in the early successional volcanic desert on the slopes of Mt Fuji, specifically because the lack of mycorrhizal inoculum in the soil was a limiting factor for germinating *Salix*. Therefore, the role of CMN for the observed growth enhancement is unclear.

For seedlings growing under a dense overstory canopy, light is a decisive resource for regeneration growth (Wagner *et al.*, 2010; Petritan *et al.*, 2011). Still, relief from root competition by trenching increased regeneration growth for both beech and Douglas fir (Wagner *et al.*, 2010; Petritan *et al.*, 2011) at a given light availability (Fig. 2a, based on Wagner *et al.*, 2010; Fig. 2b, based on Petritan *et al.*, 2011). This indicates that seedling growth was in fact hampered by belowground competition, whereas facilitation by a mother tree should have improved seedling growth at a specific light intensity, which was not observed (Fig. 2a,b). It has been suggested that simultaneous competition and facilitation may contribute to the net outcome for seedlings, and that CMNs should rarely occur in nature without concurrent root interactions (Booth & Hoeksema, 2010). But separating these component processes is not trivial, and methods involving buried physical barriers around seedlings may affect root and mycelial distributions in ways that do not mimic natural conditions and is beyond the scope of the current review.

ECM C metabolism

The evolutionary incentive for a mycorrhizal fungus to redistribute C toward the seedlings has not been addressed, nor has any physiological process been indicated by which such redistribution could occur. Although this does not disprove the occurrence of C transfer via CMNs, a physiological mechanism is lacking that could describe the molecular process underpinning the mother tree hypothesis, which should be acknowledged when interpreting data from field experiments. This might, for example, include which plant and ECM fungal enzymes are involved. Several physiological adaptations in both symbiotic partners have evolved to facilitate nutrient exchange. In ECMs, fungi colonize plant root tips and grow between the cortical cells and the plant–fungus interface forms. Plant photosynthate arrives at the interface mainly in the form of sucrose, which ECM fungi cannot take up and use as a C source (Nehls *et al.*, 2016). In the apoplastic space, wall-bound plant invertases cleave sucrose into hexoses, which can be imported by root and fungal cells. Hence, the plant exerts direct control over C transmission to the fungus.

Ectomycorrhizal fungi can be strong C sinks. It has been estimated that between 10% and 20% of the plant photosynthate is transferred toward the fungal partner (Smith & Read, 2008). The imported hexoses are immediately metabolized by the fungus, converting them to fungal trehalose and polyols like mannitol and
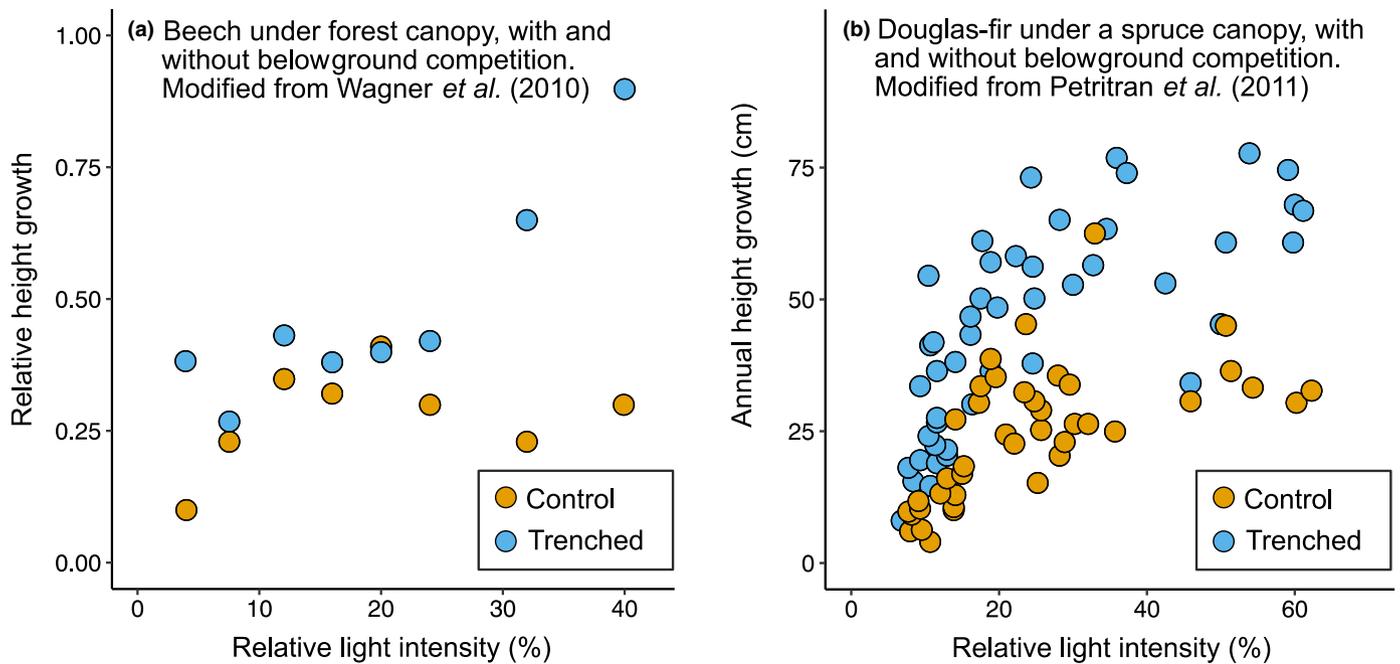
Fig. 2 (a) Relative height growth of beech seedlings, growing under a beech canopy, as a function of relative light intensity (% of above-canopy light); data extracted from Wagner *et al.* (2010). Blue markers represent seedling growth rate after 2 yr of belowground isolation via trenching treatments. Orange markers show relative growth rate in the same plots before trenching was performed (control). (b) Annual height increment of Douglas-fir saplings growing under a Norway spruce canopy, as a function of relative light intensity (% of above-canopy light); data extracted from Petritan *et al.* (2011). Blue markers show seedlings growing within trenched plots, and orange markers show growth in untreated control plots.

arabitol, which cannot be exported back to the plant–fungus interface (Smith & Read, 2008), thereby maintaining the concentration gradient of hexoses between apoplast and fungus (Nehls *et al.*, 2016). Fungi regulate their cytosolic glucose concentration by trehalose production for short-term storage and trehalose cycling (Nehls *et al.*, 2016), which also prevents C export back to the plant. Studies using auto-radiography (Finlay & Read, 1986; Wu *et al.*, 2001) have shown that labeled C can move from a donor plant to the ECM fungal sheath of another plant. This does not show transfer of C to the other plant. Finlay & Read (1986) found ^{14}C in shoots of non-labeled seedlings in some cases, but Wu *et al.* (2001) did not. Carbon transfer to the fungal sheaths of another plant may represent a subsidy of the fungal C cost for that plant, but could also negatively affect the transfer of N, a limiting nutrient, to the other plant if the C supply drives N immobilization by the ECM mycelium (Näsholm *et al.*, 2013).

A significant transfer of C between plants via a fungal partner would necessitate an upregulation of the fungal degradation of trehalose to hexoses to satisfy the increasing demand of energy and C. Such upregulation does occur in fungi when cells are C limited, but importantly, hexose transfer back to the plant–fungal interface of seedling mycorrhizas would aggravate such a fungal C limitation.

Carbon transfer from ECM fungi to achlorophyllous mycoheterotrophs (plants parasitizing on mycorrhizal fungi) and partial mycoheterotrophic plants has been shown but the physiological mechanisms remain elusive (Selosse *et al.*, 2016). Full and partial mycoheterotrophs are not common in boreal forests. When they do occur, they only constitute a minute fraction of total plant biomass.

What is the evidence for plant–plant carbon transfer?

Isotopic labeling methods allow CO_2 assimilated by a plant to be traced and detected in neighbor plants (Simard *et al.*, 1997a,b; Wu *et al.*, 2001). The power of isotopic labeling techniques stems from the very low detection limits of mass spectrometers, which allow detection of minute shifts in isotopic abundance. However, this also represents a deceptive pitfall when interpreting the data, as miniscule differences can result from several naturally occurring processes that discriminate against the heavier isotopes (Offermann *et al.*, 2011). Extrapolation from small shifts in isotopic abundance may lead to overestimation of actual rates of transfer. Moreover, even if statistically significant transfer through CMNs can be shown, these need not represent biologically significant transfer rates. Therefore, the quantitative contribution to the receiver plant's total C provision should also be examined, to assess the benefit from transferred C. In addition, care must be taken to ensure that the magnitude of transferred C is greater than what may be expected from transport processes in the soil matrix; diffusion and mass flow or refixation of CO_2 from respiration. It is therefore important that experiments either contain rigorous controls to exclude alternative transfer pathways, or (if such controls are not available) explicitly acknowledge that the test is not conclusive. Both analyses are greatly facilitated by a high label intensity, as conclusions based on higher isotope ratios are more reliable than those near background variation in natural abundance.

Because hyphal links are fragile and cannot with current techniques be analyzed directly in the soil, transfer of elements is analyzed indirectly in fine roots colonized by mycorrhizal fungi.

Since the ECM root contains significant amounts of fungal tissue (Smith & Read, 2008), it is difficult to determine if labeled C in the roots of the recipient plant was actually transferred to the plant, or still remains in the fungal tissues around the root and root cortex cells. If the C remains within the fungal tissue, it might not provide any benefit to the host plant. Fungal use of stored C could possibly reduce the C sink strength and need of additional C, but it has also been suggested that ECM distribute nitrogen (N) among their hosts in proportion to the C contribution by each plant, so the potential benefit of such a reduced sink strength is unclear (Henriksson *et al.*, 2021a). Therefore, the labeled C must be detected in host tissue *per se* before conclusions of interplant C transfer can be claimed (Robinson & Fitter, 1999). A further complication to the interpretation is that bacteria thriving in the mycorrhizosphere assimilate labeled C compounds exuded by the fungi (Högberg *et al.*, 2010; Gorka *et al.*, 2019), and that soil invertebrates feed on ECM fungal hyphae (Högberg *et al.*, 2010; Bluhm *et al.*, 2019), which also affects the distribution of label in the soil.

Klein *et al.* (2016) reported that 40-m tall trees exhibited bidirectional exchange of photosynthate among species with overlapping root systems; they concluded that 40% of fine-root C had been obtained from other trees via CMNs. Together with figures reported by Avital *et al.* (2022), this is by far the highest reported contribution of C to a receiving plant from a donor plant, as most other studies have suggested contributions 10–20 times lower than this estimate (see Cahanovitc *et al.*, 2022). As Klein *et al.* (2016) note, these findings deviate markedly from our frequent assumption that adjacent trees interact primarily via competition. However, there are several open questions related to this study.

First of all, this is not a straightforward labeling experiment, as the labeled (donor) trees were exposed for 5 yr to elevated CO_2, which needs be considered a treatment, to which the recipient trees were not exposed. This treatment makes it possible that the donor trees had enhanced capacity to fix C and export photosynthates to their mycorrhizal mycelium, and hence potentially to other trees.

Second, Klein *et al.* (2016) and Avital *et al.* (2022) used the $\delta^{13}C$ of roots to infer the amount of label transfer. As mentioned earlier, the detected ^{13}C may thus remain in mycorrhizal tissues rather than having been transported into the root cells of potentially receiving trees (Wu *et al.*, 2001). The authors employed a linear mixing model based on the root $\delta^{13}C$ of labeled and control trees, resulting in an estimated 40% contribution from donor trees to C in the roots of adjacent trees. A similar mixing model approach was used by Avital *et al.* (2022), to estimate C transfer among potted seedlings of different species, concluding that seedlings received 4–118% of their C from a labeled donor plant. The authors note that the anomalous 118% result was likely due to very uneven label intensity in different roots of donor plants, confounding the end members of the mixing model (Avital *et al.*, 2022). Neither Klein *et al.* (2016) nor Avital *et al.* (2022) include a control treatment where mycorrhizal connections are absent, leaving the transfer mechanism uncertain. There is no suggested physiological mechanism to support such a high C export from fungal symbionts to plant hosts, and the issues described earlier call the mixing model

approach or at least the accuracy of the end-members into question. Also, Avital *et al.* (2022) reported C transfer between tree species which form incompatible mycorrhizal types (from ECM *Quercus* to arbuscular *Cupressus*), effectively demonstrating that C transfer of similar magnitude occurred via non-mycorrhizal pathways.

Have alternative pathways for carbon transfer between plants been excluded?

If uptake of labeled C by the recipient plant was conclusively shown, it must also be determined whether the C was transferred through the CMN. Alternative pathways must be excluded. These include respiratory CO_2 efflux from the labeled plant roots, or its mycorrhizal fungi, which may subsequently be fixed by the foliage of the receiving plant or by roots via anapleurotic CO_2 assimilation through PEP-carboxylase activity (Jackson & Coleman, 1959), circumventing inter-plant hyphal connections. Another alternative pathway occurs via exudation of labeled C compounds from the labeled roots and hyphae, such as carbohydrates and organic acids. These exudates could move through diffusion or mass flow to the receiving plant and be assimilated without transport through the CMN. Furthermore, labeled C can spread in the soil via root and hyphal litter turnover and subsequent redistribution by soil biota (Fig. 3).

Leaf refixation of respired label has been excluded in experiments using the so-called aerial controls, which consist of a potted plant placed in the experimental area, without any belowground connection to the labeling experiment (Teste *et al.*, 2009; Cahanovitc *et al.*, 2022). Experimental controls for root C-fixation, diffusion and mass flow through the soil, and uptake of exuded compounds are more technically challenging.

To test for transfer of C that is independent of mycorrhizal hyphal connections, hypothetical donor and receiver plants have often been separated by mesh barriers with pore sizes designed to exclude both roots and hyphae (< 1 μm), but which allow diffusive and convective transport (Simard *et al.*, 1997a; Teste *et al.*, 2009). It should be noted, however, that the placement of such barriers in the soil represents a disturbance which can leave millimeter-wide pore spaces that affect the hydraulic conductivity of the soil, potentially reducing both diffusion and mass flow which would lead to underestimation of non-CMN transfer. In addition, the open area of the mesh material varies greatly depending on its pore size – ranging from 40–50% (for 200–300 μm mesh) down to 1% (for 1 μm mesh), but this is generally not addressed when interpreting data from such mesh-barrier treatments.

Based on a dual isotopic-labeling approach (^{13}C and ^{14}C), Simard *et al.* (1997a) demonstrated inter-plant C transfer between seedlings of Douglas fir (*Pseudotsuga menziesii*) and paper birch (*Betula papyrifera*). The experiment used mesh barriers that excluded roots, but not fungal hyphae, and estimated that 5% of photosynthetically assimilated C was transferred to the neighbor plant. However, disrupting the hyphal connections between the seedlings did not significantly reduce the transfer between plants, suggesting that C was transferred by non-CMN pathways (Simard *et al.*, 1997a).

In a 2-yr-long field experiment employing a similar setup (Simard *et al.*, 1997b), a third species was introduced, western red-
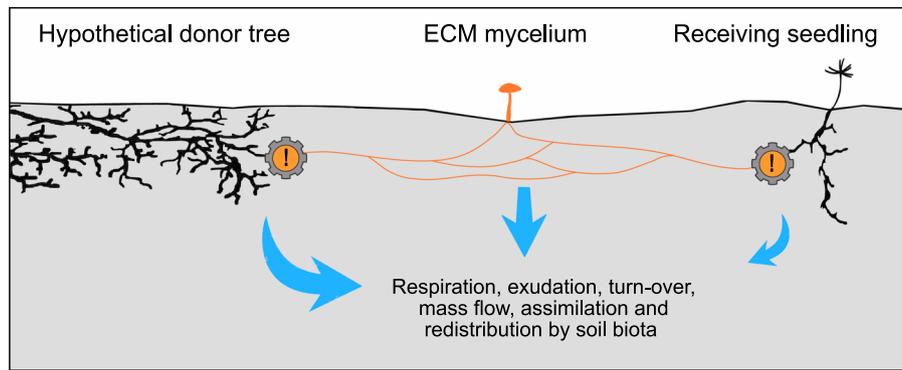
Fig. 3 Illustration of alternative C transfer pathways from a hypothetical donor tree to a receiving seedling. Blue arrows represent mechanisms for potential distribution of donor tree C into the soil which do not require common mycorrhizal network (CMN) connections between plants. Cellular respiration by the donor tree and its mycorrhizal fungi both release donor C into the soil, as CO_2 which can either be fixed by PEP-carboxylase in the receiving seedling's roots, or via photosynthesis. Root exudation by donor tree fine roots and mycorrhizal mycelium release organic compounds such as carbohydrates, organic acids, and secondary metabolites into the soil. Turnover of donor tree C in roots and mycorrhizal mycelia, assimilation and turnover of donor C by saprotrophic fungi, bacteria, archaea, and redistribution by these and other soil biota can also make C available to the mycorrhizal mycelium of the receiving seedling. Sprocket symbols illustrate the critical checkpoints of C transfer via CMN connections. At the first checkpoint, root cells of the donor tree export sucrose into the symbiotic interface and produce invertases that cleave the sugar into hexoses. The hexoses can be imported into the fungal cell, where they are immediately converted to trehalose and polyols, to maintain the hexose gradient. These compounds can be transported to different parts of the mycelium. At the second checkpoint, CMN transfer between plants would require that the fungal trehalose and polyols be converted back to hexoses and then be exported from the fungal cell into the symbiotic interface, from where the receiving root cell could import it. No such mechanism has been identified to date.

cedar (*Thuja plicata*), which forms arbuscular mycorrhiza (AM), an association which is incompatible with an ECM network. The innovative use of an AM species as a control enabled identification of effects of the CMN connections alone by providing a mycorrhizal plant that was unable to connect to the CMN (but see Avital *et al.*, 2022). By shading the plants, the effect of light intensity on the C transfer between seedlings was tested. Lacking hyphal connections between the labeled seedlings, C transfer to cedar was reduced relative to the networked Douglas fir (Simard *et al.*, 1997b). This seminal paper followed on the laboratory studies of Finlay & Read (1986), demonstrating interplant C transfer between tree seedlings in the field. Still, and as argued by Robinson & Fitter (1999), the AM red-cedar acquired significant amounts of labeled C, possibly via uptake by roots or AM hyphae of exudates or leaked labeled C from roots or hyphae. They also point to the possibility that higher label intensity in ECM plants could be due to more effective scavenging of labeled compounds because of greater hyphal density compared with the AM plant. Inferring a role of CMN in mediating C transport between seedlings from the difference in label intensity between ECM and AM plants may thus be complicated.

Teste *et al.* (2009) similarly addressed these questions using Douglas-fir seedlings. In their field study, the receiver plants grew 0.5 m from donor saplings and the donors were planted in 15 cm diameter and 35 cm deep mesh-bags of different mesh pore size. The bags were filled with ambient soil with corresponding forest floor and mineral soil material (A and B horizons), placed in this order. The donor saplings were exposed to isotopically labeled $^{13}CO_2$. After 1 wk, the receiver seedlings were harvested and the $^{13}C:^{12}C$ ratio of roots and shoots analyzed (Fig. 4). In this experiment, ECM hyphae and rhizomorphs should have freely passed through the 250-μm mesh, and individual hyphae should have passed through the 35-μm mesh, but the 0.5-μm mesh should be considered as a negative

control preventing any direct mycorrhizal connection between donor and receiver plants, while still allowing diffusion and mass flow of C dissolved in the soil solution.

Some seedlings did indeed display enriched ^{13}C levels in shoots, indicating C transfer. The critical question is whether the transfer occurred via mycorrhizal connections between plants. The hypothesis is that permitting hyphal connections will result in significantly greater ^{13}C transfer between plants than when connections are prevented. This was not the case (Fig. 4), and two-way analysis of variance (with mesh size and tissue type as factors) shows only that root $\delta^{13}C$ was higher than shoots ($P < 0.0001$) and that 'no mesh' seedlings were more enriched than the seedlings subjected to various mesh treatments ($P < 0.03$). No significant difference among mesh sizes was detected ($P > 0.78$). Because the 250-μm mesh also blocked ^{13}C transfer from the donor sapling, the hypothesis of mycorrhizal hyphal C transfer should have been rejected. The authors concluded that CMNs and mycorrhizal roots of trees may be important for regeneration, but that the role of resource transfer (by whatever pathway) remains uncertain.

In Deslippe & Simard (2011), dwarf birch (*Betula nana*) seedlings in an arctic tundra were isotopically labeled and transfer pathways were separated using mesh barriers (35-μm mesh), hyphal excision, and aerial controls. The study was well replicated ($n = 34–39$) and results showed that donor plants transferred 1.4% of the absorbed label via non-mycorrhizal soil pathways, 4.1% via mycorrhizal connections, and 5.2% via rhizomes and root grafts. However, variations within treatments were large and according to Tukey's *post-hoc* test, transfer of C attributed to CMN was not statistically different from either of the other treatments; see fig. 3 in Deslippe & Simard (2011).

The soil and hyphal systems are fragile and complex, and formation of mycelial connections between plants may be
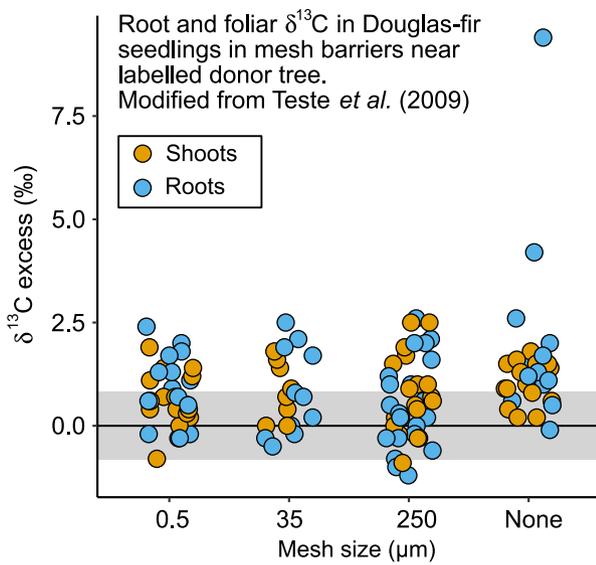
Fig. 4 Data extracted from Teste *et al*. (2009; figs 2, 3). Root (blue) and foliar (orange) ^{13}C in Douglas-fir seedlings grown in mesh barriers with various pore sizes, located 0.5 m from labeled donor trees in the field. The x-axis shows the pore size of the mesh barriers, and below it is specified if the barrier is permeable to roots and/or ectomycorrhizal (ECM) fungal hyphae. The 35-μm mesh is designated as allowing 'limited ECM' connectivity, because the pores permit entry of individual hyphae, but not of rhizomorphs. The 250-μm mesh is completely permeable to all ECM fungal hyphae and rhizomorphs but prevents root ingrowth/outgrowth. No significant differences among shoots of different mesh treatments were detected ($P > 0.5$, analysis of variance). A two-way analysis of variance (with mesh size and tissue type as factors) shows only that root δ^{13}C was higher than shoots ($P < 0.0001$) and that 'no mesh' seedlings were more enriched than the seedlings subjected to various mesh treatments ($P < 0.03$). No significant difference among mesh sizes was detected ($P > 0.78$). The hypothesis that common mycorrhizal networks (CMNs) enhance C transfer between plants predicts that the 0.5-μm mesh treatment (and possibly also the 35-μm treatment) should receive significantly less ^{13}C than the other treatments. This was not shown, and so the hypothesis should be rejected in this case.

disrupted by even the most careful experimental design. Mycorrhizal fungi are often considered merely as conduits for potential plant resource movement, but they do not grow equally well or form connections under all conditions, and fungal species differ in the amount of extramatrical hyphae produced (Agerer, 2001). This further highlights the importance of careful control treatments when drawing conclusions about the role of mycelial connections.

Can donors preferentially direct carbon transfer to kin plants?

Inter-plant resource sharing via mycorrhiza is sometimes used to infer that forest ecosystems are not characterized by competitive interactions, but instead form a system of mutual aid or facilitation (Van Der Heijden & Horton, 2009), although the potential presence of CMNs has also been shown to reduce or has

no effect on seedling growth (Van Der Heijden & Horton, 2009). In order for such resource sharing to conform to the theory of evolution by natural selection, C transfer from a donor tree must preferentially benefit its own progeny. Because mycorrhizal fungi are symbiotic, preferential transfer must also improve the fitness of the fungus.

Pickles *et al*. (2017) studied the transfer of C between seedlings of Douglas fir and asked whether such transfer would be preferentially directed to closely related seedlings. They were using a similar mesh approach as described earlier (Teste *et al*., 2009) but used kin and non-kin seedlings for the experiment. The authors report a higher occurrence of labeled C (^{13}C) in kin vs non-kin seedlings. However, this transfer occurred irrespectively of whether the mesh size used was 0.5 or 35 μm. Nonetheless, the authors used the isotopic data to infer preferential transfer to kin plants. They speculated that C could be transferred from donor to kin seedlings via a conduit involving donor plant root or ECM exudation followed by uptake by hyphae of receiver plants. Notably, such enhanced transfer of ^{13}C to kin plants was only found for half of the 'families' tested, suggesting such specific transfer, if real, would only occur in certain plant families. Also, and as noted by the authors, the absolute quantities transferred were small, and would not have a significant nutritional value for receiving plants. The possibility was then suggested that the C transfer could imply transfer of micronutrients or signaling compounds (Pickles *et al*., 2017), but there were no data to support this speculation.

What is the evidence for plant–plant nitrogen transfer?

The methodological challenges of tracing N movements between plants through CMNs are even greater than for tracing movements of C. A major problem is that there is only one suitable isotope at hand to be used as tracer, ^{15}N, because the radioactive N isotopes are so short-lived that they cannot be used in the experiments needed. A prerequisite for conclusive results in studies of N transfer is, just as was discussed earlier with respect to C transfer, sufficient label intensity. Conclusive evidence for N transfer between plants, and whether via CMN or not, can only be achieved if the ^{15}N abundance of the receiving plant is well above the variation in natural abundance. Furthermore, to demonstrate net transfer, the experimental setup should also be replicated with the roles of label donor and receiver being reversed among the plant species. A range of studies have investigated the potential role of CMNs for N transfer (see review by He *et al*., 2009) concluding that ecologically significant amounts of transfer have still not been reported.

Teste *et al*. (2009) studied transfer of ^{15}N from labeled donor plants to seedlings, with and without mesh barriers that prevent CMN connections. They reported ^{15}N transfer to three out of eight seedlings that were not enclosed by a mesh barrier, but no transfer to seedlings isolated by a 0.5-μm mesh. However, a Student's t-test performed on the data (from fig. 4 in Teste *et al*., 2009) cannot detect any significant difference between the two treatments (Fig. 5, $P = 0.65$ and $P = 0.47$ for shoots and roots, respectively). Despite this, Teste *et al*. (2009) concluded that seedlings do receive N from nearby donor trees, via CMN connections.
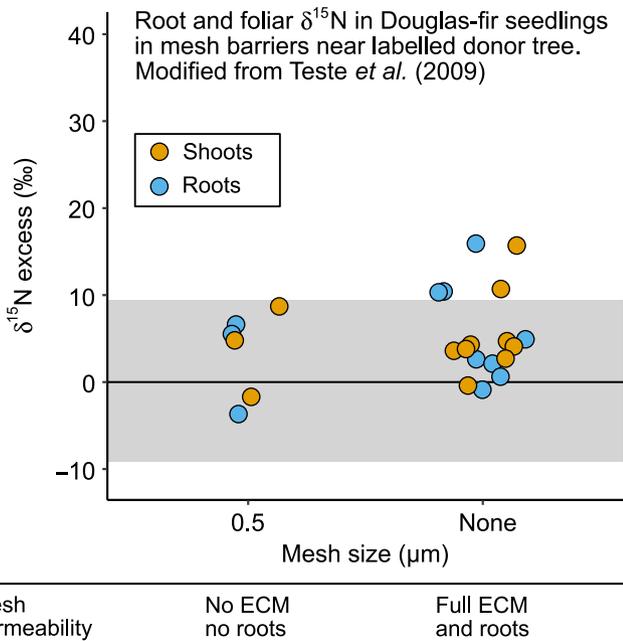
Fig. 5 Data extracted from Teste *et al.* (2009; fig. 4). Root (blue) and foliar (orange) ^{15}N in Douglas-fir seedlings in the field, with or without mesh barriers that prevent common mycorrhizal network (CMN) connections to labeled donor trees, 0.5 m away. The *x*-axis shows the pore size of the mesh barriers, and below it is specified if the barrier is permeable to roots and/or ectomycorrhizal (ECM) fungal hyphae. Student's *t*-tests performed on the extracted data revealed that the 0.5-μm mesh did not significantly affect seedling ^{15}N concentration in shoots ($P = 0.65$) or roots ($P = 0.47$).

Theoretical considerations and alternative hypotheses

Although it is difficult to quantify resource transfer in support of the mother tree hypothesis, it seems evident that some C transfer occurs. Thus, the question remains: how plausible is the mother tree hypothesis in comparison to alternative explanations? The role of the mycorrhizal fungi for such transfer is problematic from an evolutionary perspective. Why should a mycorrhizal fungi export C to suit the interest of a mother tree? Why should mycorrhizal fungi export C at all when the evolutionary stability of the symbiosis is based on fungal import of plant C in exchange for nutrients such as N? As mentioned earlier, fungal C export to the plant during the juvenile phase of orchids and other myco-heterotrophs does occur. These plants have small 'dust' seeds containing minute amounts of reserve C and early colonization of the plant cells by an appropriate fungus is a prerequisite for embryo development and survival (Smith & Read, 2008).

The only proven mechanism for direct C transfer from ECM to trees is when fungi take up and export organic N, hence providing organic C to host plants as part of the N export (Abuzinadah & Read, 1989). It was noted by Simard *et al.* (2012) that C transfer between plants could make evolutionary sense if transport between plants connected through a CMN occurred in the form of amino acids such as glycine and glutamine so that these compounds would not only be occurring within hyphae and rhizomorphs but also be transferred to the receiver plant. This argument is further elaborated by Simard (2018). Uptake of amino acids from soil by

mycorrhizal and non-mycorrhizal plants is well documented (Näsholm *et al.*, 2009). In the current context, however, a pathway involving a donor plant exporting organic N compounds to the CMN followed by the uptake of this organic N by the receiver plant is implied (Simard, 2018). An alternative scenario would be that inorganic N is acquired by a mycorrhizal fungus from soil and this N is subsequently assimilated by the fungus using C from a donor plant and the synthesized amino acid is subsequently exchanged for C from a receiver plant. The net C gain to the receiver plant, would, in this scenario, not necessarily be positive, as it would depend on the exchange rate of C contained in the organic N to the C delivered by the receiver plant to the fungus.

Furthermore, there is no evidence that a mother tree has any control of C once it has been exported to the fungus, and the fungus should control the rate of organic N export to a particular plant. Fungal control is also consistent with the findings that the C transfer between plants can be similar with and without hyphal connections between the plants (Simard *et al.*, 1997a; Teste *et al.*, 2009), which implies that soil organic C has been taken up by the fungi and then used according to its own need. In our view, these indirect transfer mechanisms provide more parsimonious and evolutionarily reasonable explanations of the observations than the direct transfers implied by the mother tree hypothesis. However, mature trees could interact with seedlings indirectly by providing inoculum of mycorrhizal fungi beneficial to the seedlings (Nara, 2006). Such provision of mycorrhizal inoculum could be considered a type of 'mother-tree' phenomenon but does not entail C-sharing.

Conclusions

We conclude that there is evidence for C movement among plants, but the importance of CMNs remains unclear, and evidence for a potential growth benefit from such movement is lacking. Similarly, nitrogen may move between plants at low magnitude, but there is no conclusive evidence that CMN connections are required.

Although no candidate for a physiological mechanism allowing large C flux from ECM fungi into the plant–fungal interface is known, mycoheterotrophic plants do receive some or all of their C from other plants, thereby demonstrating the capacity for CMNs to (re)distribute resources between plants. Thus, the only cases in which resource transfer has been shown to be of key importance for receiving plants are those of plants parasitizing mycorrhizal fungi and indirectly taking resources from neighboring plants.

The possibility of overstory trees facilitating seedling growth via CMNs would have far-reaching consequences within and beyond the realm of scientific research. The field is attracting a wide and diverse readership and scientific claims are being further disseminated by non-peer-reviewed media (Karst *et al.*, 2023). Based on the methodological caveats of studies on CMN-mediated resource sharing between trees, we argue that interpretations of the isotopic evidence should be revised. Directed C transfer from mother trees to seedlings via CMNs would imply a remarkably collaborative fungal behavior, with questionable adaptive benefits, especially to the fungus. Alternative indirect mechanisms for C sharing as a result of fungal strategies provide more parsimonious hypotheses for belowground C uptake by seedlings. Furthermore, the current formulation

of the mother tree hypothesis is incongruent with patterns of forest regeneration in boreal forests. Publications cited in this Viewpoint article have opened up a field of scientific research focusing on resource (in particular C) fluxes between forest plants. At the time of writing, however, the extent to which such fluxes are mediated by CMNs has not been conclusively shown.

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Competing interests

Author Torgny Näsholm declares a competing interest as he owns shares in, and works part time for, the company Arevo AB that develops, produces, and markets organic fertilizers.

Author contributions

NH, TN and JM initiated the work and NH drafted the manuscript. All authors (NH, JM, MNH, PH, AP, OF and TN) reviewed the literature and contributed significantly to the manuscript.

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