



TAMM review: Continuous root forestry—Living roots sustain the belowground ecosystem and soil carbon in managed forests

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ABSTRACT

An estimated half of the carbon fixed by trees is transported belowground, a portion of which is exuded into the soil where it fuels a complex belowground food web. The biological transformation of exudates into microbial metabolites and necromass is a major source of soil organic matter (SOM), including persistent mineral-associated organic matter (MAOM). Recent recognition of the fundamental importance of these inputs from living roots for sustaining life belowground and replenishing SOM demands a rethinking of how we harvest forests. By severing the lifeline of living roots, clearcut harvesting devastates much of the belowground biodiversity in forests, and prohibits a principal pathway through which SOM and C stocks are replenished. Retention harvesting retains the influence of living roots within retention patches and potentially throughout the harvested area, but only if inter-tree distances are 15 m or less. Retention trees sustain and support the re-establishment of belowground life and function following forest harvest and may mitigate post-harvest soil C losses. Sustaining the belowground ecosystem via inputs from living roots is an underappreciated benefit of continuous-cover and retention forestry.

1. Introduction

Sustainable forest management is rooted in evidence, and forestry policies and practices must be continuously adapted in response to developments in forest science. Although soil is recognized as the foundation of the forest ecosystem (Kimmins, 2003), forestry policies for soil protection in many jurisdictions are still limited to preventing erosion and compaction of soil, and retaining some woody debris on the surface. Soil organic matter (SOM) content is a key property of soils, influencing fertility, water retention and site productivity. SOM is also a critical store of C containing more C than the atmosphere and vegetation combined (Scharlemann et al., 2014). Forest soils contain more than 40 % of the total organic C in terrestrial ecosystems (IPCC, 2007; Wei et al., 2014). Soil C stocks comprise about 70 % of the ecosystem C stock in the boreal forest, 60 % in temperate forests and 30 % in tropical forests (Pan et al., 2011). Soils also harbour an estimated one quarter of the earth's biodiversity (Wagg et al., 2019), with millions of species and billions of individual organisms living belowground within a single ecosystem (Bardgett and van der Putten, 2014; Table 1). The taxonomic diversity of soil organisms in terrestrial ecosystems is several orders of magnitude greater than that of aboveground organisms on a per-area basis (Bardgett 2005; Parker 2010). This complex and diverse belowground ecosystem is responsible for the many ecosystem functions and services delivered by healthy soils (de Graaff et al., 2015; de Vries et al., 2013; Bardgett and van der Putten, 2014; Crowther et al 2019). Soil

communities include plant roots and associated mycorrhizal fungi, microorganisms such as bacteria, archaea, and fungi, and fauna across a wide range of sizes and trophic groups, linked together in complex food webs (Nielsen et al., 2015). This belowground ecosystem is fueled by plant residues from both above- and belowground and from recent plant photosynthate delivered from living root systems (Wardle et al., 2004; Pollierer et al., 2007; Fig. 1).

Recognition of the key role of soil in the global C cycle and the potential to increase C sequestration in soil—and prevent its release—has fueled a great scientific effort to understand the processes leading to the formation and retention of SOM, and the roles of the soil biota in these processes. Numerous new insights have been made through innovative techniques for determining the nature of SOM (e.g. pyrolysis GC-MS; ¹³C NMR spectroscopy; near-edge X-ray fine-structure spectroscopy), fluxes of C from plants into the soil food web (e.g. stable isotope (¹³C) natural abundance, ¹³CO₂ pulse-labelling and probing), and the composition and activity of the soil microbial community (e.g. phospholipid fatty acid analysis; qPCR; metagenomics; meta-transcriptomics, proteomics). These studies have illuminated the central role of the soil biota in generating SOM and influencing soil C stocks.

In this paper we present the current scientific evidence for the importance of living roots in sustaining the biodiversity and functioning of the belowground ecosystem and for the production and preservation of soil C in forests. We then recommend forest harvesting practices that foster life belowground and facilitate the formation and retention of

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Table 1

Estimates of abundance and diversity of several types of soil organisms.

Taxon	Abundance	Diversity
bacteria & archaea	4–20 billion /cm ³	100–9,000 /cm ³
AM hyphae	20–111 m /cm ³	10–20 /m ²
ECM hyphae	1.75 km /cm ³	100–400 /ha
protists	10,000–10 million /m ²	600–4800 /g
nematodes	2–90 million /m ²	10–100 /m ²
enchytraeids	12,000–311,000 /m ²	1–15 /ha
collembola	100,000–500,000 /m ²	20 /m ²
oribatid mites	100,000–1 million /m ²	100–150 /m ²
isopods	10 /m ²	10–100 /m ²
diplopods	110 /m ²	10–2500 /m ²
earthworms	300 /m ²	10–15 /ha

Diversity may be based morphology, genome equivalents, operational taxonomic units or genome sequences. Numbers are approximate as most soil species have not yet been described, and most estimates are based on a single ecosystem or region. Sources: Richard et al., (2005); Bardgett and van der Putten, (2014); Brabcova et al., (2016); Kranabetter et al., (2018); Almeida et al. (2019); See et al., (2022). Anders Dahlberg, personal communication 10/19/2022; Marty Kranabetter, personal communication 10/19/2022; Petr Baldrian personal communication 10/23/2022.

SOM.

Living roots and soil biodiversity.

Organic compounds exuded from living roots and associated mycorrhizal fungi are essential for soil biodiversity. Although leaf litter was long assumed to be the principal fuel for the belowground ecosystem, it is now evident that a substantial fraction of soil biota are directly dependent on recent photosynthate from the tree canopy (Högberg et al., 2010; Chomel et al., 2019). Carbon-labeling trees has demonstrated that within days, much of the C fixed in leaves is transported to roots, exuded from living roots and/or mycorrhizal fungi, and processed through the belowground food web. For example, in a mature temperate forest in Switzerland in which trees were labelled with ¹³C-depleted CO₂, the label was found in most soil invertebrates (earthworms, chilopods, gastropods, diplurans, collembolans, mites and

isopods), indicating that most soil invertebrates obtain carbon from living roots, probably via mycorrhizal fungi (Pollierer et al., 2007). In contrast, only juvenile millipedes obtained most of their C from leaf litter. In a boreal pine forest, Högberg et al., (2010) found that C from tree photosynthesis was transferred through roots within a few days and then rapidly distributed through the mycorrhizal fungal mycelium to the soil food web. Even fungal feeders such as Collembola became labelled within days, suggesting they preferentially feed on live mycorrhizal fungal mycelium and consume recent photosynthate (Johnson et al., 2005; Högberg et al., 2010; Kanters et al., 2015). Similarly, significant ¹³C enrichment in mites and enchytraeids were detected 4–6 days after injecting ¹³C-labeled aspartic acid into the stems of Sitka spruce trees, indicating an association of these organisms with recent photosynthate (Churchland et al., 2012).

Rhizosphere and hyphosphere bacteria also take up organic compounds exuded from roots and fungal mycelium (Treonis et al., 2004; Kaštovská and Santruckova, 2007). These bacteria are grazed by various protists (Gao et al., 2019; Ceja-Navarro et al., 2021) which may then be consumed by other invertebrates and further transformed through the food web. Several studies have detected recent (C-labeled) plant photosynthate in predators (Ruf et al., 2006; Eissfeller et al., 2013); within 72 h, glucose-C propagated through the food web to the highest trophic level - predatory mesostigmatid mites (Strickland et al., 2012). Microarthropods derive a substantial proportion of their C from recently photosynthetically fixed C and are themselves an important food source for aboveground predators. Thus, recent photosynthate exuded from roots or mycorrhizal fungi supports both belowground and aboveground food webs (Strickland et al., 2012; Fig. 1).

Living roots also promote soil porosity and aggregation. Pores, especially those in the 30–150 µm radius size range, are especially important in converting new C inputs from fine plant roots into microbial necromass and decomposition products that are transported and protected within the soil matrix surrounding pores (Kravchenko et al., 2019; Buckeridge et al., 2022). Mucilage and exudates from living roots and associated mycorrhizal hyphae also facilitate formation of

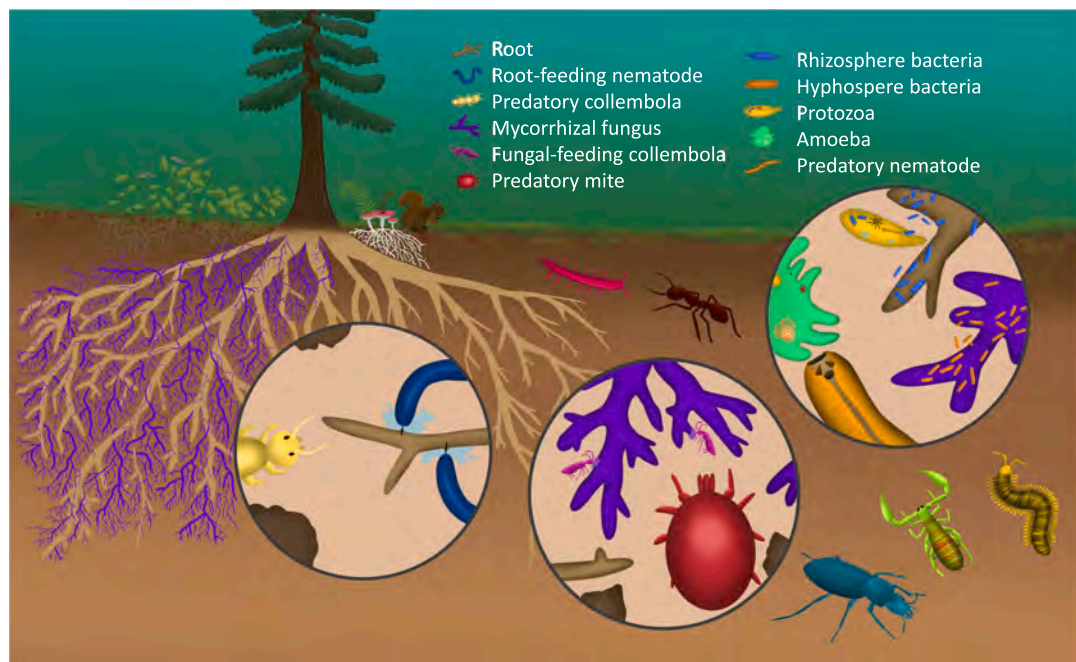


Fig. 1. Living roots and associated mycorrhizal fungal hyphae support a complex belowground food web. (A) Root-feeding nematodes pierce roots and extract photosynthate. (B) Mycorrhizal fungal hyphae are grazed by micro-arthropods such as collembola. (C) Root and fungal exudates are absorbed by bacteria which are consumed by protozoa. These organisms are in turn consumed by predatory microarthropods (mites, collembola, nematodes), which are consumed by predatory arthropods such as pseudoscorpions, centipedes and beetles. Clearcut harvesting eliminates the belowground fluxes of carbohydrates that sustain this web of life. ©Lewis K. Fausak (MSc.).

microaggregates (Six et al., 2004), and entangle soil particles thereby contributing to the formation of macroaggregates and preventing soil loss through water or wind erosion (Jastrow et al., 1998; Six et al., 2004; Stokes et al., 2009).

2. Living roots and soil organic matter

Soil organic matter includes (1) particulate organic matter (POM) which is dominated by plant litter in various stages of decomposition and fragmentation, (2) mineral-associated organic matter (MAOM) which is smaller organic molecules of plant and microbial origin that are chemically or physically bound to surfaces of silt- and clay-sized soil minerals, and (3) dissolved organic matter (DOM), a small and dynamic pool of simple organic compounds exuded from roots or mycorrhizal fungi or leached from litter. MAOM is slow-cycling relative to other SOM pools, while DOM turns over quickly and is the major precursor of MAOM (Haddix et al., 2016, 2020; Cotrufo et al., 2015). Maintenance of SOM stocks requires continuous replenishment with organic materials (Lajtha et al., 2014). Although some MAOM can be centuries old, all SOM exists in a dynamic state in which losses through decomposition and mineralization must be continuously replenished by inputs (Dynarski et al., 2020). Therefore, maintaining SOM stocks requires continuous input of organic compounds that are transformed into SOM, in addition to reducing losses by minimizing disturbance.

Aboveground litter, particularly leaf litter, has long been considered the main source of organic matter in forest soils, but roots contribute similar amounts of litter. Average rates of fine-root production in forests range from 3.1 to 6.0 t ha⁻¹ y⁻¹ (Finér et al., 2011) which is similar to average rates of leaf litter production (1–9 t ha⁻¹ y⁻¹; Bray and Gorham 1964; 4.62 t ha⁻¹ y⁻¹, Jevon et al., 2022). Likewise, the range of annual C inputs from root turnover in forests (80 to 839 g C/m² y⁻¹) is similar to that of leaves plus stems (90–860 g C/m² y⁻¹, Cotrufo and Lavalée 2022). In a global meta-analysis, root litter accounted for 48 % of annual plant-litter inputs in forests, compared to 41 % for leaf litter (Freschet et al., 2013). Fine roots also tend to decompose more slowly than leaf litters (Taylor et al., 1991; Freschet et al., 2013; Hicks Pries et al., 2017; Sun et al., 2018), further increasing the proportion of SOM derived from roots.

Mycorrhizal fungal mycelia are another substantial source of SOM in forest soils (Godbold et al., 2006; Clemmenen et al., 2013; Brabcová et al., 2016). Annual C inputs from mycorrhizal hyphae in forests range from 1228 to 6890 g C/m² y⁻¹ (Cotrufo and Lavalée 2022). Estimates of mycelial biomass for ectomycorrhizal (ECM) fungi typically range from 100 to 600 kg ha⁻¹ (Brabcová et al., 2016) and estimated turnover rates of mycorrhizal mycelia are 0.3–1.1 month⁻¹ (See et al., 2022), so input rates of residues of mycorrhizal external mycelia may be in the order of 1 t ha⁻¹ y⁻¹. In a poplar plantation, 62 % of C entered the SOM pool via arbuscular mycorrhizal (AM) mycorrhizal mycelia, which exceeded inputs via leaf litter and fine-root turnover (Godbold et al., 2006).

Living roots release a variety of organic materials that are important precursors of SOM (Sokol et al., 2019), including mucilage, sloughed cells, volatiles, lysates and exudates—collectively known as rhizodeposits (Dennis et al., 2010). Rhizodeposition has been estimated to account for 11 % of net fixed C and 27 % of the C allocated to roots (Jones et al., 2009). Polysaccharide-rich mucilage is secreted by the root cap and represents 2–12 % of total rhizodeposition. Exudates are released from meristemic regions just behind the root cap and consist of a vast array of organic compounds, including primary metabolites (sugars, amino acids, and organic acids; Grayston et al., 1997; Dennis et al., 2010).

Considerable amounts of fixed C are transferred to the mycorrhizal fungi associated with living roots. Mycorrhizae develop in the zone of elongation, just behind the meristemic region (Dennis et al., 2010). An estimated 10–44 % of photosynthetically fixed carbon is released by roots or transferred to mycorrhizal fungi (Bais et al., 2006; Pausch and Kuzyakov, 2018). Like roots, mycorrhizal fungi exude a wide range of

compounds into the hyphosphere surrounding their mycelia, including polysaccharides and glycoprotein such as glomalin (Ritz and Young 2004). The hyphosphere covers a much larger portion of the soil than the rhizosphere; compared to average root length density of 6.8 cm cm⁻³, hyphal length densities average 20 m cm⁻³ for AM hyphae and 1.75 km cm⁻³ in ECM-dominated soils (See et al., 2022). Release from living roots and mycorrhizal fungi may therefore be a major conduit for C flow throughout the upper soil. Högborg et al., (2008) estimated that half or more of the soil activity in boreal forests is driven by photosynthate that is transported to mycorrhizal fungi and root-associated microbes within a few days of being fixed.

The simple organic compounds exuded from roots and mycorrhizal fungi are rapidly taken up by abundant bacteria in the rhizosphere (Treonis et al., 2004; Kaštovská and Santruckova 2007) and hyphosphere (Kaiser et al., 2015; Guennoc et al., 2018; Gorka et al., 2019), and converted into microbial biomass, necromass and extracellular metabolites. Microbial metabolites and necromass are an important source of MAOM in many soils (Miltner et al., 2012; Kallenbach et al., 2016; Buckeridge et al., 2020). Microbial necromass has been estimated to account for 30 % of the SOC in temperate forest soils (Liang et al., 2019) and 15 % of the MAOM in silt- and clay-sized fractions in forests soils (Angst et al., 2021). Annual inputs of C from microbial biomass in forests range from 70 to 2508 g C/m² y⁻¹ (Cotrufo and Lavalée 2022). Bacteria produce extracellular polymeric substances composed mainly of polysaccharides, proteins, and DNA, that generate the biofilm in which they live (Costa et al., 2018; Cai et al., 2019). These substances stick to mineral or organic particles, roots and fungal hyphae, and glue materials together in aggregates, which can increase the persistence of the organic matter. A considerable amount of SOM, including the more persistent MAOM, is derived from C released by living plant roots or associated mycorrhizal fungi and processed by microbial communities on or near their surfaces. Inputs from living roots were 2–13 times more efficient than litter inputs in forming both slow-cycling, mineral-associated SOM and fast-cycling, particulate SOM (Sokol et al., 2019). The contribution of rhizodeposits and associated microbial-derived compounds to C stocks in forest soils, although less than that in grassland soils, may be considerable (Angst et al., 2018; Liu et al., 2019). Inputs from living roots can also stimulate decomposition of SOM, particularly under conditions of low soil N availability (Kaiser et al., 2010; Fontaine et al., 2004). Therefore, the net effects of this “labile-microbial” pathway from plant to SOM need to be considered in managing soil C stocks in forests (Sokol et al., 2022).

3. Managing forests to sequester C and promote life belowground

Envisioning forest management through a lens that recognizes the importance of belowground C fluxes from living root systems (both residues and labile inputs) for belowground biodiversity and C sequestration allows us to more fully understand the ecosystem-level consequences of forestry practices. Forest harvesting, particularly clear-cut harvesting, has sudden and profound effects as inputs of labile C from living roots cease, as do turnover of fine roots and aboveground litterfall. Instead, there is an immediate pulse of detritus in the form of logging slash aboveground, followed by a pulse of dead roots and mycorrhizal hyphae belowground. This pulse sustains soil organisms in the litter-detritivore web as the residues decompose. However, soil organisms in the labile-microbial web are very much diminished until root systems and mycorrhizal networks are re-established. Following clear-cut harvesting, ectomycorrhizal fungal biomass, diversity and species composition are greatly reduced (Hagerman et al., 1999; Jones et al., 2003; Grebenc et al., 2009). Soil fungal communities shift from ectomycorrhizal to saprotrophic-dominated assemblages (Byrd et al., 2000; Jones et al., 2003; Busse et al., 2006; Kohout et al., 2018), and this shift can persist for decades after harvest (Kranabetter et al., 2005; Twieg et al., 2007; Spake et al., 2015; Kyaschenko et al., 2017). Disrupting C flow to

roots through stem girdling (Yarwood et al., 2009) or root severing (Lindahl et al., 2010) has similar effects, confirming that these changes are a consequence of interrupted belowground C flux to roots and mycorrhizae following clear-cut harvesting. Clear-cut harvesting also reduces microbial biomass and fungal biomass (*meta-analysis* by Holden and Treseder, 2013) and abundances of mites, spiders and earthworms (Abbott et al., 1980; Bird and Chatarpaul, 1986; Blair and Crossley, 1988; Marra and Edmonds, 1998).

Decomposition of residual SOM without replenishment of newly generated SOM following clearcut harvesting leads to a gradual reduction in SOM and SOC stocks over 1 to 3 decades, which may require several decades to recover (James and Harrison, 2016; Achat et al., 2015). Long-term declines in SOM can occur in forests managed on a rotation basis (Harmon et al., 1990; Harmon and Marks, 2002; Seely et al., 2002; Dean et al., 2017) if stands are harvested before SOM stocks return to pre-harvest levels. Globally, managed forests have about 50 % lower C stocks than unmanaged forests (Noormets et al., 2015). This may be partly attributable to smaller belowground fluxes in young managed stands relative to mature forests (Litton et al., 2004). If belowground inputs do not keep pace with stem growth in managed forests, rotation lengths based on stem growth may lead to long-term declines in soil C. Greater depletion of the more persistent MAOM pool compared to the POM pool (Lacroix et al., 2016) and reductions in macroaggregates in clear-cut forests (Siebers and Kruse, 2019) are also probable consequences of the cessation of belowground C fluxes from living roots. More research is needed to distinguish the effects of reduced belowground fluxes on SOM stocks from the effects of post-harvest changes in aboveground litter flux, temperature and availabilities of water and nutrients.

3.1 Maintaining living roots through partial harvesting

Can the negative effects of forest harvesting on soil C stores and belowground biodiversity be ameliorated through harvesting systems that retain a significant number of living trees? There is some evidence that soil C losses are smaller following partial harvesting than clear-cut harvesting. In a *meta-analysis* of 81 studies of partial harvesting (Zhou et al., 2013), the average reduction in forest floor C stock in harvested plots was 10 % (not significantly different from uncut forests), compared to the average reduction of ~ 30 % in forest-floor C stock following clear-cut harvesting in the *meta-analysis* by Nave et al., (2010). The average loss in mineral soil C stock relative to uncut controls was 5 % and the difference was not significant (Zhou et al., 2013). In Douglas-fir forests Simard et al., (2020) found smaller reductions in forest-floor C one year after harvest in areas where living trees were retained either as single trees (25 large stems ha⁻¹) or in 30-m-diameter patches, compared to clearcut areas.

Retention of living trees is also effective in retaining soil biodiversity following forest harvest, particularly if a large number or proportion of live trees are retained. In the *meta-analysis* of Holden and Treseder (2013), clear-cutting significantly lowered soil bacterial, fungal and total microbial abundance, but there were no significant effects of partial harvest. Several studies have indicated that belowground communities are not adversely affected if at least two-thirds of the living trees are retained. For example, in a boreal forest, fungal communities in a harvested area in which 70 % of living trees were retained were similar to those in unmanaged forests (Kim et al., 2021). In a coastal Douglas-fir forest, numbers of ECM fungal sporocarps were reduced by only 18 % in areas with 75 % tree retention, compared with 50 % reduction where 40 % of trees were retained, and 80 % reduction where only 15 % of trees were retained (Luoma et al., 2004). In a Scots pine forest three years after harvest, ECM species richness declined to 70 %, 50 % and 25 % of that in the unharvested plots where 60 %, 30 % and 0 % of the trees had been retained in a dispersed pattern (Sterkenburg et al., 2019). The abundance of ECM fungi in the O-horizon declined proportionally to the harvest intensity (Sterkenburg et al., 2019). In Norway spruce forests in

Finland, abundance of soil macro-arthropods was largely unaffected in areas in which 70 % of the trees were retained, but declined where 50 % or fewer of the trees were retained) (Siira-Pietikäinen et al., 2003; Siira-Pietikäinen and Haimi 2009). Spider assemblages in black spruce forests across a range of retention levels (0–100) were linearly related to residual stand basal area (Paradis and Work 2011).

Soil biodiversity is sustained within patches of living trees, even as small as 5 m in diameter, following forest harvest. At the STEMS experiment in coastal BC, soil microbial communities (Churchland et al., 2021) and fungal communities in soil (Churchland et al., 2013) and on decomposing fine roots (Philpott et al., 2018) were retained in retention patches, but not in clear-cut, dispersed retention or in the harvested areas surrounding retention patches. Abundance and diversity of mycorrhizal fungal species was largely maintained in retention patches of living trees at least 0.2 ha (Kranabetter et al., 2013). At STEMS, ECM communities were indistinguishable between uncut forest and the retention patches, even in patches as small as 5 m in diameter (Jones et al., 2008). Collembolan and pauropod communities within retention patches were similar to pre-harvest communities at the same locations; whereas those in the clear-cut areas differed after harvest (Addison, 2007).

The beneficial effect of retention patches on soil biodiversity extends a few meters into the harvested area, but becomes minimal within 10 m of the stem. This distance does not differ depending on the size of the retention patch (Hagerman et al., 1999; Jones et al., 2008), although the total area of the zone of influence increases with patch size. For example, species richness and diversity of ECM declined by about 50 % 2 m from the forest edge (Hagerman et al., 1999), by 75 % 4.5 m from the forest edge (Luoma et al., 2006). These distances are closely related to the distribution of root and mycorrhizal systems of the living trees. Numbers of live fine roots of lodgepole pine dropped substantially further than 5 m into clear-cuts (Parsons et al., 1994), and isotope signatures in mycorrhizal fungi were elevated within 6 m of mature spruce trees labeled with ¹³C₂O₂ relative to samples 12 and 18 m from the tree (Mildner et al., 2014). Likewise, at STEMS, stable isotope $\delta^{13}\text{C}_{\text{PDB}}$ values of soil-respired CO₂ were depleted in the retention patch, indicating that recently photosynthesized C from living trees was the major source of C being respired, but decreased rapidly into the clear-cut (Churchland et al., 2013; Fig. 2a). Within about 3 m of the patch edge, respiration rates were 50 % of those measured in the retention patch. The $\delta^{13}\text{C}$ values of fungal biomarker PLFA were low within 3 m of the patch edge indicating that fungi within this area obtain much of their C from living trees, and reached clear-cut values between 6 and 10 m from the retention patch (Churchland et al., 2013; Fig. 2b). Following stem injection of Sitka spruce trees with ¹³C-enriched aspartic acid, fungal PLFA biomarkers were enriched 5 and 10 m from the base of the trees (Churchland et al., 2012). Given this evidence that the influence of living trees becomes minimal within 10 m of the stem, an inter-tree spacing of no more than 15 m would be necessary to sustain belowground life throughout the harvested area.

The steep decline in belowground influence of trees with distance from patch edges indicates that dispersed retention (i.e. leaving living trees uniformly dispersed across the harvested area) could be more effective at sustaining soil biodiversity in harvested forests. For the same level of retention, Luoma et al. (2004) found smaller reductions in fall mushroom and truffle biomass in dispersed compared to aggregated retention blocks. In a Scots pine forest, Varenus et al., (2017) concluded that dispersed single retention trees do not ‘life-boat’ EMF mycelia and maintain EMF diversity throughout the harvested area, but this conclusion may be related to the low level of retention in these plots, which was similar to the Swedish average of 8 % of the stand basal area (Varenus et al., 2017; Anders Dahlberg, personal communication 9/15/2022). Applying this level of retention to the stand density of the Scots pine forest studied by Sterkenburg et al. (2019) would give an inter-tree distance of about 25 m. The limited efficacy of the very low retention levels in Fennoscandian forestry noted for other forest values

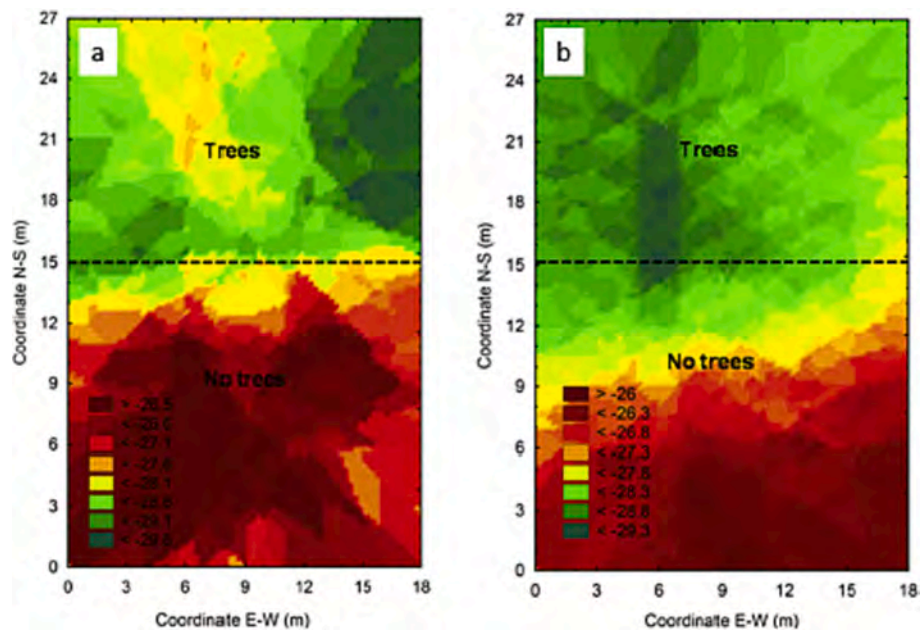


Fig. 2. $\delta^{13}\text{C}_{\text{PDB}}$ value of (a) CO_2 and (b) fungal biomarker PLFA 18:2u6,9 in a 27×18 m experimental plot extending from the retention patch (Trees) into the clear-cut (No Trees) at the STEMS Installation. The dashed line represents the border between the retention patch and the clear-cut area. From Churchland et al., (2013).

(Gustafsson et al., 2012; Kuuluvainen et al., 2019;) therefore applies to its efficacy for sustaining belowground life.

3.2 Conclusions and implications for forest management

For forestry to be fit for purpose in the 21st century, it must aim to steward biodiverse and resilient ecosystems, rather than just maximize stem growth of crop trees. Evidence of the critical importance of living roots for sustaining the exceptionally diverse belowground biota that support the critical ecosystem processes provided by forest soils behooves us to consider this hidden half of forest biodiversity in forest management—especially decisions about harvesting systems.

Clear-cut harvesting has profound negative effects on soil

biodiversity, which can be minimized by retaining at least half of the living trees during. Retaining about 50 % of pre-harvest basal area also maintains pre-harvest levels of other organisms, including plants, lichens, bryophytes, mushrooms, arthropods, birds and small mammals (Fenton et al., 2013; de Groot et al., 2016; Fedrowitz et al., 2014).

Retaining patches of mature living trees during harvest (i.e. aggregated retention) sustains soil biodiversity within the patch and for a few meters into the opening around each patch. The influence of living roots declines with distance from the stem and is generally negligible by 10 m from the stem. Therefore, to sustain life belowground, living trees also need to be dispersed throughout the cutblock, with inter-tree distances no greater than about 15 m. This requires a minimum of 40 retention trees per hectare dispersed throughout the cutblock. This is consistent



Fig. 3a. Dispersed Retention block at STEMS Installation 5 years after harvest. 40 mature living trees retained per ha in a cutblock of 18.2 ha. More than half the total area of the cutblock is within one tree-height from the base of a tree or the cutblock boundary.

with assertions that leaving 5–10 retention trees per hectare—as is common practice in Fennoscandia—still means that most of the harvested area is biologically and functionally a clearcut (Kuuluvainen et al., 2019). An example of a dispersed retention block containing 40 live trees per ha is shown in Fig. 3a.

In British Columbia, regulations for retention forestry systems require individual trees or groups of trees to be distributed over the cutblock, with edge influence covering at least 50 % of the opening (B.C. Ministry of Forests 2003). Edge influence is defined as being within one tree height of a live tree, which in coastal Douglas-fir forests could be 30 m (Mah and Nigh, 2015). The current minimum requirement for retention forestry in coastal Douglas-fir forests could therefore be met with 9 trees per hectare, which would render about 75 % of the soil in the cutblock devoid of living roots, mycorrhizal fungi, and the soil organisms that depend on them. This problem points to the need to revisit the outdated definition of ‘edge influence’. Equating tree influence with tree height assumes that the major effects of a tree are casting shade and wind. While forest influence on wind and light can be detected 25 to 50 m (one to two tree lengths) into the harvested area, forest influence on other values such as plant species, soil nutrients and soil organisms extend less than 10 m from the forest edge (Mitchell et al., 2004). Replacing ‘tree height’ with either ‘10 m from stem’, or ‘distance from stem to drip line’, as the estimate of tree influence would make retention forestry more conducive to sustaining the belowground ecosystem.

Despite investments in numerous silvicultural trials demonstrating the benefits of retention forestry, the most common harvesting system in B.C. currently is Clearcut with Reserves (Beese et al., 2019). This system is not retention forestry as it is not bound by a 50 % edge influence requirement, nor do the trees need to be distributed over the block (B.C. Ministry of Forests, 2003). An example of a Clearcut with Reserves which retains a single patch of trees on 3 % of the harvested area is shown in Fig. 3b. Almost all of the soil in this cutblock is devoid of the influence of living roots, so the negative effects of this harvesting system on the belowground ecosystem can be added to mounting evidence that such low levels of retention are inadequate to provide ecological benefits possible with retention forestry (Fedrowitz et al., 2014; Gustafsson et al., 2012; Kuuluvainen et al., 2019).

4. Research needs

The vital role of inputs from living roots for sustaining soil organic matter and belowground life has been recognized in agriculture and is a central principle of regenerative agriculture (Moyer et al. 2020; Prescott et al., 2021). Evidence presented in this review indicate that inputs from living roots may also be critical for sustaining belowground ecosystems in forests, but several knowledge gaps need to be addressed, including:

1. What proportion of net primary productivity is released from living roots and mycorrhizal fungi, and what are the diurnal and seasonal patterns of release?
2. Which components of soil biodiversity are sustained by exudates from living roots and mycorrhizal fungi (i.e. either consume exudates or consume other organisms which consume exudates)
3. How does exudation vary according to forest type, tree species, mycorrhizal symbiont, stand age, site fertility and site productivity?
4. How do soil biological communities change after forest harvesting, what are the spatial and temporal patterns of recovery, and are all members of the soil community equally capable of recovery?
5. What level and pattern of retention is optimal to sustain soil life throughout a cutblock and how does this vary among forest types?
6. How important is the production of MAOM through the labile-microbial pathway compared with that through other pathways, and how does this vary among forest types and tree species?

CRedit authorship contribution statement

Cindy E. Prescott: Writing – original draft. **Sue J. Grayston:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.



Fig. 3b. Clearcut with Reserve block at STEMS Installation 5 years after harvest. A 0.33-ha reserve of living trees is retained within a 10.9 ha cutblock. <https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/silviculture/silviculture-research/silvicultural-systems-research/stems/>.

Data availability

No data was used for the research described in the article.

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