Mycorrhiza
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SHORT NOTE

Length and colonization rates of roots associated with arbuscular or ectomycorrhizal fungi decline differentially with depth in two northern hardwood forests

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Abstract
Ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) fungi are often studied independently, and thus little is known regarding differences in vertical distribution of these two groups in forests where they co-occur. We sampled roots at two soil depths in two northern hardwood stands in Bartlett, New Hampshire, co-dominated by tree species that associate with AM or EM fungi. Root length of both groups declined with depth. More importantly, root length of EM plant species exceeded that of AM plants at 0–10-cm depth, while AM exceeded EM root length at 30–50-cm depth. Colonization rates were similar between mineral and organic portions of the shallow (0–10 cm) samples for EM and AM fungi and declined dramatically with depth (30–50 cm). The ratio of EM to AM fungal colonization declined with depth, but not as much as the decline in root length with depth, resulting in greater dominance by EM fungi near the surface and by AM fungi at depth. The depth distribution of EM and AM roots may have implications for soil carbon accumulation as well as for the success of the associated tree species.

Keywords Arbuscular mycorrhiza · Ectomycorrhiza · MELNHE · Northern Hardwood · Roots · Soil depth

Introduction

Mycorrhizal fungi can improve the supply of mineral nutrients to plant hosts. The most widespread types are arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi. AM fungi, recorded from fossils over 400 million years old, associate with the majority of terrestrial plant species and have often been studied in environments limited by phosphorus (P) such as tropical forests (Smith and Read 2008). EM fungi, which appeared much later in the fossil record, about 50 million years ago, tend to dominate where nitrogen (N) is limiting, as is common in temperate and boreal ecosystems (Nicolás et al. 2019). Both N and P are supplied near the soil surface where leaf litter and roots turn over, whereas in young soils common in post-glacial landscapes inorganic P becomes available for biotic uptake following the weathering of minerals high in P, especially apatite, a process that occurs deeper in the soil (Schaller et al. 2009). The ability of AM fungi to acquire P, especially inorganic P (George et al. 1995) and EM fungi to acquire N (Hobbie and Horton 2007) might suggest an increased presence of each mycorrhizal group where the respective nutrient is in short supply (Read 1991). This paradigm predicts that EM fungi should dominate in surface soils where they can actively decompose organic matter to acquire N, and AM fungi could acquire weatherable P deeper in the soil profile. Recently, however, AM fungi have been found to colonize leaf litter in forests (Bunn et al. 2019) and to enhance microbial mineralization of N and P from organic matter (Herman et al. 2012).

A few studies have addressed vertical differentiation between AM and EM colonization of roots. In a boreal aspen (*Populus tremuloides* Michx.) stand, aspen roots in upper soil horizons were more thoroughly colonized by EM than AM fungi, while roots deeper in the soil were colonized mostly by AM fungi (Neville et al. 2002). Studies in tropical rain forests in Cameroon (Moyersoen et al. 1998) and tropical heath forests in Borneo (Moyersoen et al. 2001), however, failed to find differences between EM and AM colonization with soil depth. To our knowledge, this question has yet to be addressed in a mixed species temperate forest.

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We compared the length and colonization rate of roots associated with AM and EM fungi at two soil depths in two stands of northern hardwoods in the White Mountains of New Hampshire. We tested the hypotheses that EM root length and colonization rates would be more dominant near the soil surface compared to AM root length and colonization rates.

Methods

Site description

This study took place in two stands in the Bartlett Experimental Forest, NH (44° 4′ N, 71° 14′ W). The regional climate is cool-temperate humid continental, with a monthly mean temperature range from − 9℃ in January to 19℃ in July and an average annual precipitation of ~ 130 cm (Adams et al. 2004). Soils are well drained Spodosols that developed in glacial drift derived from granite and gneiss (Vadeboncoeur et al. 2014). Stand C5 was 35 years old at the time of sampling and was dominated by yellow birch (*Betula alleghaniensis* Britt.) and white birch (*B. papyrifera* Marsh.), followed by red maple (*Acer rubrum* L.), American beech (*Fagus grandifolia* Ehrh.), and sugar maple (*A. saccharum* Marsh.), with a total basal area of 109 m^2/ha (Supplementary information S1). Stand C7 was 110 years old at the time of sampling and was dominated by American beech and sugar maple, the climax species for this forest type, with a total basal area of 128 m^2/ha. Both stands had more basal area in tree species that associate with EM than AM fungi (Supplementary information S1). In C5, the proportion of basal area occupied by trees that form ectomycorrhizae was 78 ± 6% (standard error) and in C7 it was 63 ± 4%.

Root collection

Both stands, C5 and C7, had four replicate 30 m × 30 m sampling plots each divided into nine 10 m × 10 m subplots. Shallow and deep cores were collected at five systematic positions within each plot, in the central and four corner subplots.

Shallow cores were collected on September 22 and October 10, 2010, using a 2″ diameter core hammered 10 cm into the soil after removing the Oi (litter layer). Shallow cores were further separated into organic or mineral soil horizons, with an average organic layer (Oe and Oa horizons) depth of 3.2 ± 0.5 cm. Both parts were stored frozen until analysis. In C5, one core lacked an organic horizon ($n = 19$); in C7, all 20 cores included an organic sample. Mineral soil was present in all but two cores in C5 (i.e., the Oea was > 10 cm). One shallow core was lost after collection from stand C5.

Deep cores were collected in July 2010 using a gas-powered rotary corer with a 10-cm diameter diamond-tipped cylindrical drill bit (Levine et al. 2012). Deep cores were taken 30–50 cm from the top of the mineral soil for analysis of soil carbon and nitrogen (data not reported here), which provided an opportunity to characterize roots at depth. Intact root branches were separated from the soil and frozen for use in this study. Of the 20 deep cores collected in each stand, 7 root samples from C5 and 4 from C7 were lost and not used in this analysis. The number of deep cores per plot that provided roots for this analysis ranged from 2 to 5.

The total number of samples analyzed was 44 in C5: 14 mineral shallow, 17 organic shallow, and 13 mineral deep. In C7, the total number of samples was 50: 17 mineral shallow, 17 organic shallow, and 16 mineral deep. For each of these soil core portions, both EM and AM roots were processed, as described below, for a total of 188 root samples.

Root processing

Distinguishing AM and EM roots

Shallow cores were thawed and washed over a sieve to extract root branches at least 3 cm in length. Roots from the deep cores were thawed and washed. All roots were preserved in ethanol until analysis. Roots were sorted based on morphology and wood anatomy into AM or EM types viewed under a dissecting microscope (Yanai et al. 2008). Rarely, in later processing steps, a root initially typed as AM was observed to have a Hartig net and was reclassified as EM. The mycorrhizal status of AM roots was verified after clearing with potassium hydroxide and staining with Chlorazol black E, as described below.

Root length

To measure the length of AM and EM roots, each root sample was placed on a dissecting microscope dish and intersections with grid lines were counted (Newman 1966). Root length per unit soil volume was calculated by dividing the length of roots by the volume of the core.

Clearing and staining roots

Putative AM roots were cleared by autoclaving in 10% potassium hydroxide solution for 20 min at 15 ATM and 120 °C, soaked in 3% hydrogen peroxide for 10 min and washed in 1% nitric acid (Brundett et al. 1996). Roots were stained in 0.03% Chlorazol black E and autoclaved for 20 min at 15 ATM and 120 °C to reveal fungal hyphae (Cannon 1941; Brundett et al. 1996). Stained roots were viewed at 400× to assess the presence of AM features.

Arbuscular mycorrhizal colonization

Each sample of cleared and stained AM roots was cut into 2-cm-long segments. Root segments were floated in a Petri dish and one segment was picked from 25 sections of the dish (Brundett et al. 1996), except for 70 samples that had only 4–23 segments, all of which were examined. Root segments were placed on glass slides and examined at 400× magnification, and the presence or absence of the following mycorrhizal fungal structures was noted at up to 200 intersections of a micrometer in the eyepiece: coenocytic hyphae, vesicles, arbuscules, and hyphal coils (McGonigle et al. 1990; Brundett et al. 1996). Roots were classified as colonized by AM fungi based on the presence of AM structures, although many other fungal structures were commonly seen including septate hyphae (evidence of dark septate ascomycete endophytes) and clamp connections (evidence of basidiomycetes). Colonization was calculated as the number of intersections with AM fungal structures divided by the total number of intersections viewed.

Ectomycorrhizal colonization

To quantify colonization of roots by EM fungi, each root sample was examined under a dissecting microscope. Colonization was calculated as the number of root tips colonized by EM fungi divided by the total number of root tips (Brundett et al. 1996). If necessary, a cross-section of a root tip was taken for compound microscopy, whereby the presence of EM features such as a mantle could easily be distinguished.

Statistical analysis

To test whether root length density and colonization of roots by AM or EM fungi differed between mineral and organic portions of the shallow cores, we used four separate analyses of variance (ANOVAs) with soil type (mineral or organic) and stand (C5 or C7) as predictor variables. Subplot (nested within plot) and plot were random effects in all models. Because soil type was not a significant predictor of any of the response variables (as described in the Results), data from the mineral and organic portions of the shallow cores were numerically re-combined for further data analysis.

To test whether colonization differed with depth for AM fungi or EM fungi, the ratio of EM to AM colonization, and the ratio of EM to AM root length density, we used four ANOVAs with soil depth (shallow or deep), stand, and their interaction as predictor variables.

To test whether root length density differed with depth, we used ANOVA with soil depth, stand, mycorrhizal type (EM or AM), and all combinations of interactions as predictor variables.

All the response variables were log transformed to achieve normality of the residuals; for root length density, a constant was added to every value before log transformation to avoid taking the log of zero. The best model for each response variable was determined based on a comparison of Akaike's information criterion (AIC) for models that included all main effects but different combinations of interaction terms. ANOVA tables for the best models are provided in Supplementary Information. Statistical analyses were conducted in R with the packages dplyr, ggplot, nlme, and tidyr (R Core Team 2020).

Depth distribution of roots by mycorrhizal type

More root length (56% in C5 and 62% in C7) was identified as EM than AM, consistent with greater basal area of tree species associated with EM than AM fungi; this difference was not significant ($p = 0.10$ for the main effect of mycorrhizal type). EM and AM root length densities both declined from shallow to deep soils ($p < 0.001$ for the main effect of depth) (Fig. 1). Root length density of EM roots declined more than that of AM roots with depth ($p = 0.007$ for the interaction of depth and mycorrhizal type), and thus the ratio of EM to AM root length decreased with depth ($p = 0.03$; Fig. 1). The root length density of both types combined averaged 4.6 cm/cm^3 in surface soils (0–10 cm) and 0.25 cm/cm^3 in deep soils (30–50 cm). The decline of root length density from shallow to deep soil was similar between stands C5 and C7 ($p = 0.70$ for the interaction of depth and stand).

Colonization of roots by soil depth and mycorrhizal type

All cores included both roots colonized by AM fungi and roots colonized by EM fungi. Colonization ranged from 3 to 97% of root length for AM fungi and from 4 to 91% of root tips for EM fungi (Fig. 2).

We expected colonization rates to differ between the mineral and organic portions of the shallow cores (0–10-cm depth), but this was not the case for either EM fungi ($p = 0.68$) or AM fungi ($p = 0.96$). EM colonization rates were 61 ± 4% in the organic and 62 ± 4% in the mineral portions of the shallow cores. AM colonization was 64 ± 3% in the organic and 64 ± 4% in the mineral portions of the shallow cores. Therefore, we combined the results from organic and mineral portions of the shallow cores in subsequent analyses.

Colonization rates declined with depth from 0–10-cm to 30–50-cm depth for both EM ($p < 0.001$) and AM fungi ($p < 0.001$) (Fig. 2). EM colonization rates were 33 ± 3% in the deep cores, compared to 63 ± 3% for the whole of the shallow cores. AM colonization was 25 ± 2% in the deep cores, compared to 65 ± 3% in the whole of the shallow

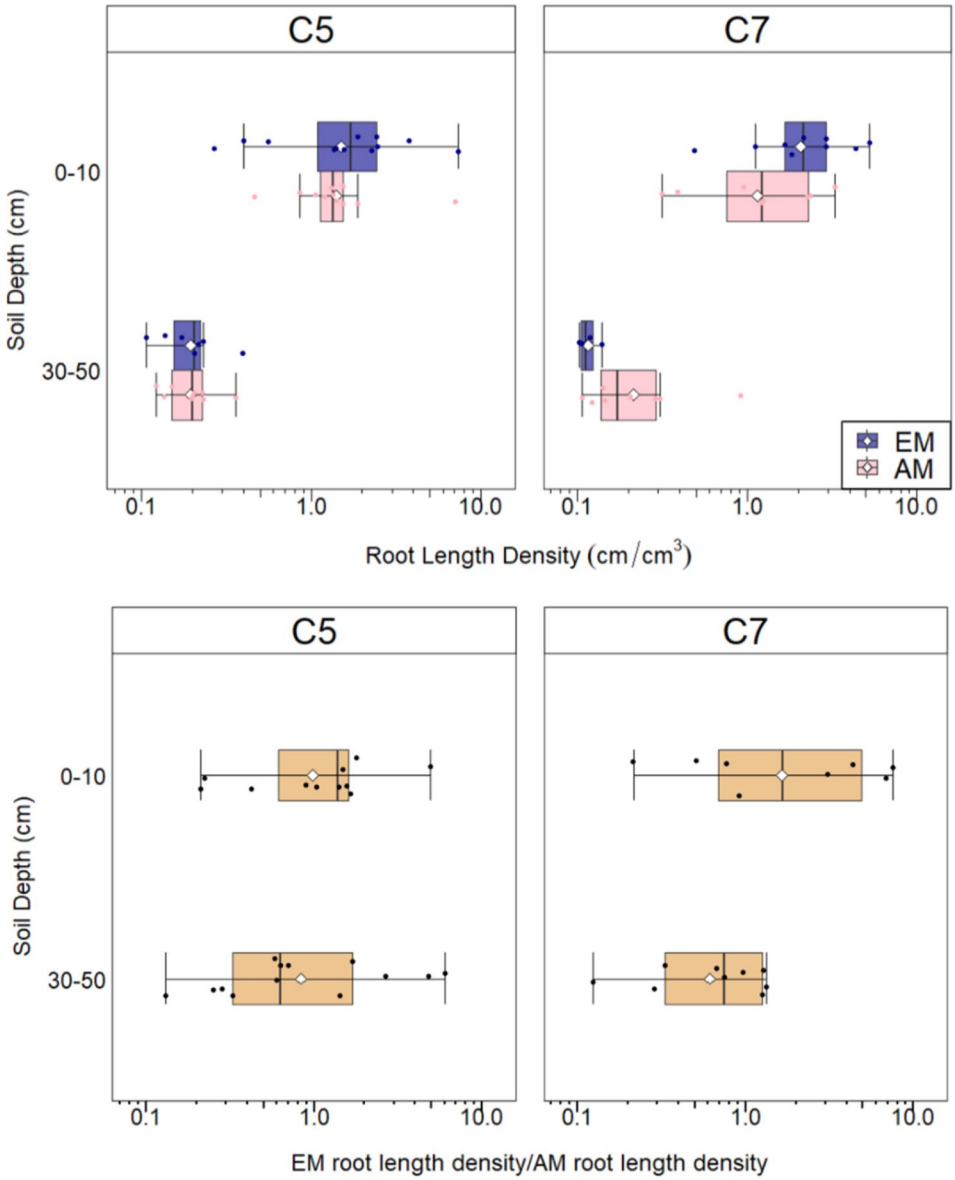

Fig. 1 Root length density versus depth for roots associated with EM and AM fungi in stands C5 and C7 (above) and the ratio of EM to AM host root length in shallow and deep cores (below). Each point represents a soil core. The lines in the boxes represent the medians; the means are shown as white diamonds. Boxes represent the interquartile range, and whiskers extend to extreme values within 1.5 times the interquartile range. Both variables are shown on a log scale

cores. Thus, the ratio of colonization by EM to AM fungi increased with depth ($p = 0.01$; Fig. 2). The increase in the ratio of EM to AM colonization rates was similar in C5 and in C7 ($p = 0.50$ for the interaction of depth and stand). With an outlier (high EM and low AM colonization in a C7 deep core) removed, the main effect of depth on the ratio of EM:AM colonization was even more significant ($p < 0.001$).

Discussion

The decline of root length density with depth is well known; differences in rooting depth by mycorrhizal association in mixed-species forests, however, have rarely been quantified. We hypothesized that EM roots would be favored near the soil surface and AM roots would predominate at depth, based on their roles in acquiring N and P, and we found this to be supported by our data (Fig. 1). Differential depth distribution of AM and EM root length may also reflect affinities with host plants with different rooting depths (Molina et al. 1992). The species in our study differ in rooting depth (Kessler 1966; Eshel and Beeckman 2013). In a previous study that included the Bartlett Experimental Forest, where our study took place, roots of yellow birch and beech, which are EM species, declined with depth more steeply than sugar maple, which is AM (Yanai et al. 2008). This is consistent with our findings that EM root length was greater near the soil surface and AM root length was greater at depth.

As expected, mycorrhizal colonization of both types was greatest near the soil surface, which receives inputs

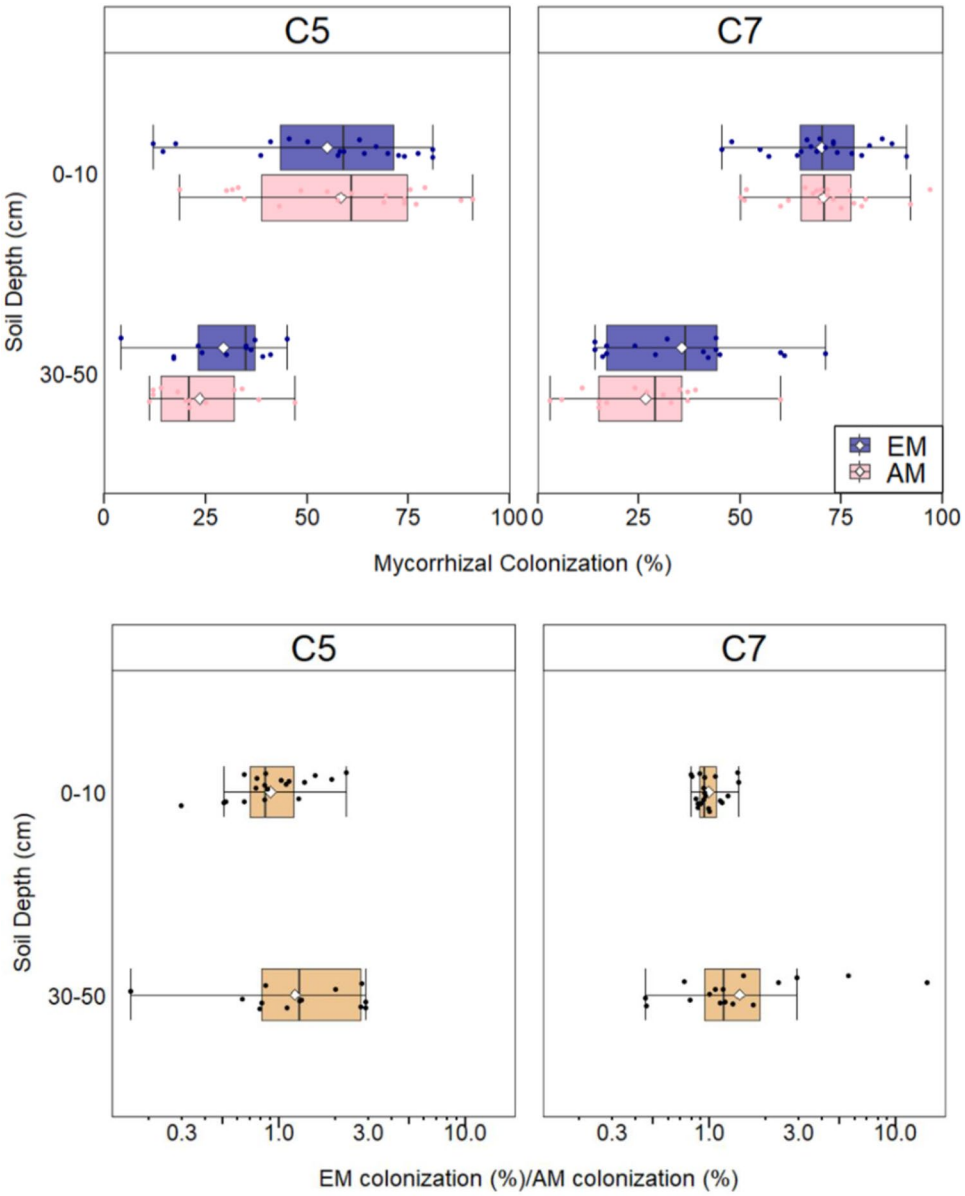

Fig. 2 Mycorrhizal colonization of EM root tips and AM root length in shallow and deep cores in stands C5 and C7 (above) and the ratio of these rates (below). Each point represents a soil core. The lines in the boxes represent the medians; the means are shown as white diamonds. Boxes represent the interquartile range, and whiskers extend to extreme values within 1.5 times the interquartile range. The ratio of colonization rates is shown on a log scale

of relatively labile nutrients from aboveground litter and fine root turnover. EM fungal colonization is commonly high on roots in surface soil where the EM fungi have access to organic matter for decomposition (Read 1991). Similarly, AM fungi may colonize leaf litter, stimulating organic matter decomposition by releasing labile carbon to soil microbes (Herman et al. 2012). Less favorable soil conditions for the fungi (pH, moisture, and oxygen availability) may also contribute to reduced rates of colonization with soil depth (Shukla et al. 2013). Because the pH of organic and mineral soil differed dramatically in our study sites (Oe pH = 4.51 ± 0.09 in C5, 4.15 ± 0.05 in C7; Oa pH = 4.28 ± 0.13 in C5, 3.87 ± 0.14 in C7; versus surface mineral soil pH = 4.68 ± 0.04 in C5 and 5.25 ± 0.07 in C7), the finding that EM and AM fungal colonization did not differ between the organic and mineral portions of the 0–10-cm depth cores suggests that pH is not responsible for the difference we observed in colonization rates with depth.

Contrary to our expectations, we found a greater decline in colonization from 0–10-cm to 30–50-cm soil depth for AM fungi relative to EM fungi. The only other report of differential depth distribution was from an aspen stand, where EM fungal colonization of roots was greater in surface soil and AM fungal colonization was greater at depth (Neville et al. 2002), the opposite of the pattern we observed. Because aspen associates with both AM and EM fungi, the differences in colonization by soil depth in that study reflect factors affecting the mycorrhizal fungi, not dominance by roots of different tree species at different depths.

Although colonization rates declined with depth more rapidly for AM roots than for EM roots (Fig. 2), this effect was more than compensated by the decline in EM root length density with depth (Fig. 2). In this sense, our hypothesis was supported: EM root tips were relatively more dominant in the shallower samples and AM colonized root length was more dominant at depth. For EM roots, the length times the proportion of colonized root tips was 38 and 80 times greater in the surface than at depth for C5 and C7, respectively, whereas the colonized length of AM roots was only 31 and 18 times greater near the surface than at depth for C5 and C7.

EM fungal species have multiple methods of hyphal exploration (Agerer 2001). *Suillus* is an example of an EM fungus with hyphae that travel great distances through the soil. Hyphae from *Russula*, another EM fungus, do not produce an extensive mycelial network (Rosling et al. 2003). Different types of hyphal exploration may result in dissimilar distributions of mycorrhizal colonization of roots throughout the soil profile. Differences in movement of spores may also affect patterns of colonization with depth: the hydrophobicity of spores affects which species are carried downwards in the soil profile, and some EM species such as *Rhizopogon* and *Suillus* have spores that may remain dormant and viable within the soil for many years (Horton 2017). In black spruce forests in Alaska, deep and shallow soil were often colonized by different EM species (Taylor et al. 2014). EM fungal species were also found to vertically differentiate in a red pine (*Pinus resinosa* Sol.) plantation in Pennsylvania (Dickie et al. 2002) and a mixed coniferous forest in Sweden (Rosling et al. 2003). It is possible that the differences we observed in colonization rates with depth are associated with differences in fungal life history traits; elucidation of these relationships may be advanced by molecular genetic techniques.

Competition between EM and saprotrophic fungi may drive EM fungi deeper into the soil (Carteron et al. 2021). Some EM fungi have the ability to decompose organic matter, particularly for the acquisition of nitrogen (Lindhal and Tunlid 2015), but EM fungi obtain carbon from their host plant, while saprotrophs acquire carbon from decomposing organic matter, limiting saprotrophic communities to shallow soils with high-carbon substrates (Lindahl et al. 2007; Carteron et al. 2021). The potential dependence of AM fungi on the release of mineral nutrients from organic matter by saprotrophs might help explain high root colonization by AM fungi in shallow soils.

Another factor that may contribute to the differential depth distribution we observed between AM and EM fungal colonization is the difference in the times that roots were collected. If AM fungi were less active in July than September, or if AM colonization rates were slower relative to root growth rates in July than September, this might explain why fewer AM structures were observed in the roots collected at depth (in July) than those collected near the surface (in September). Seasonal variation in EM colonization is less likely to explain the pattern we observed, because the root tips would be classified as colonized even after senescence of the fungi. If the phenology of root growth differs by species—specifically, if beech and birch, which are EM associated, produced more fine roots between July and September than maple, which is AM, and they are distributed higher in the soil profile, as discussed above—this could contribute to our finding of greater EM root length near the soil surface and greater AM root length at depth.

Forests dominated by trees that associate with EM fungi have been reported to have high soil organic matter contents in upper soil horizons, while forests dominated by AM fungi accumulate carbon in deeper soil horizons (Craig et al. 2018), and our findings are consistent with this generalization. The translocation of plant-derived carbon by AM fungi, as well as by EM fungi, may stimulate decomposition of soil organic matter by microbes (Averill et al. 2014; Herman et al. 2012). Consequently, the depth distributions of EM and AM roots may have implications for soil carbon accounting as well as for the success of associated tree species.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s00572-022-01071-8.

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Author contribution RDY designed the study and obtained the funding. FMD analyzed the samples. JMN analyzed the data and made the figures. FMD drafted the first report, and JMN picked it up again, years later, under the direction of RDY.

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Declarations

Conflict of interest The authors declare no competing interests.

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