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Higher Soil Respiration Rate Beneath Arbuscular Mycorrhizal Trees in a Northern Hardwood Forest is Driven by Associated Soil Properties

Ashley K. Lang,[1]* Fiona V. Jevon,[1] Matthew P. Ayres,[1] and Jaclyn Hatala Matthes[2]

[1]*Department of Biological Sciences, Dartmouth College, 78 College St., Hanover, New Hampshire, USA;* [2]*Department of Biological Sciences, Wellesley College, 106 Central St., Wellesley, Massachusetts, USA*

Abstract

Soil respiration is the dominant pathway by which terrestrial carbon enters the atmosphere. Many abiotic and biotic processes can influence soil respiration, including soil microbial community composition. Mycorrhizal fungi are a particularly important microbial group because they are known to influence soil chemistry and nutrient cycling, and, because the type of mycorrhizal fungi in an ecosystem can be assessed based on the plant species present, they may be easier than other soil microbes to incorporate into ecosystem models. We tested how the type of mycorrhizal fungi—arbuscular (AM) or ectomycorrhizal (ECM) fungi—associated with the dominant tree species in a mixed hardwood forest was related to soil respiration rate. We measured soil respiration, root biomass, and surface area, and soil chemical and physical characteristics during the growing season in plots dominated by ECM-associated trees, AM-associated trees, and mixtures with both. We found rates of soil respiration that were 29% and 32% higher in AM plots than in ECM and mixed plots, respectively. These differences are likely explained by the slightly higher nitrogen concentrations and deeper organic horizons in soil within AM plots compared with soil in ECM and mixed plots. Our results highlight the importance of considering mycorrhizal associations of dominant vegetation as predictors of carbon cycling processes.

Key words: Soil respiration; Mycorrhizal fungi; Carbon; Microbial activity; CO_2; Northern hardwood forest.

Highlights

- We found higher rates of soil respiration in AM-dominated forest plots
- Respiration was associated with temperature, soil %N, and organic horizon depth
- Mycorrhizal fungi may influence soil respiration via covarying soil properties

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**Corresponding author; e-mail:* akl.gr@dartmouth.edu

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Introduction

Soil respiration is the dominant pathway by which terrestrial carbon (C) enters the atmosphere, yet we lack a clear understanding of the factors that control this flux on local scales (Schlesinger and Andrews 2000; Stoyan and others 2000). In forests, soil respiration is comprised of carbon dioxide (CO_2) produced by roots and soil microbes, which vary in both biomass and metabolic rate. The metabolic activity of both roots and microbes is thought to be primarily influenced by soil microclimate. Indeed, mean annual temperature and precipitation account for much of the variability in soil respiration rates within and across biomes (Raich and others 2002; Huang and others 2014), yet spatial heterogeneity in this flux within ecosystems is often large (Maestre and Cortina 2003; Tang and Baldocchi 2005; Giasson and others 2013). This residual variability may be partly explained by differences in other conditions that influence root and microbial metabolism, including overall biomass of roots and microbes (Stoyan and others 2000; Wang and others 2017), microbial substrate quality and quantity (Maier and Kress 2000; Wang and others 2003; Wei and others 2015), and the composition of the microbial community in soil (Monson and others 2006). These factors are likely to vary with characteristics of the vegetation, including plant diversity and the quality of plant litter inputs (Carney and Matson 2005). Building on these ideas, we tested the hypothesis that the functional type of mycorrhizal fungi associated with dominant trees may influence patterns in soil respiration in temperate deciduous forests.

Mycorrhizal fungi are important drivers of soil C and nitrogen (N) dynamics in forests (Read and Perez-Moreno 2003; Courty and others 2010; van der Heijden and others 2015). Most temperate tree species associate with either arbuscular mycorrhizal (AM) or ectomycorrhizal (ECM) fungi, either of which facilitates plant uptake of soil nutrients in exchange for photosynthate (Smith and Read 2010). By providing plants with nutrients needed for plant growth and photosynthesis, mycorrhizal fungi contribute to plant C accumulation and also represent a belowground C sink of up to 15% of plant NPP (Smith and Read 2010).

Functional differences inherent to AM and ECM fungi may influence the soil respiration rate in a variety of ways. For example, ECM species typically produce extracellular enzymes, some of which stimulate organic matter decomposition and subsequent CO_2 efflux (Talbot and others 2008). AM fungi, in contrast, rely more on mineralization of organic matter by free-living microbes. By virtue of their extracellular enzyme production and extensive hyphal networks, ECM fungi may also influence rhizosphere biogeochemistry to a greater extent than AM fungi. ECM fungi stimulate C mineralization in soil near ECM roots (Phillips and Fahey 2006), whereas AM fungi may promote soil aggregation and slow mineralization by exuding glycoproteins (Rillig and others 2001). AM and ECM fungi may also influence soil biogeochemistry through decomposition. Both fungal groups have been variously reported to suppress or stimulate organic matter decay through (1) competitive interactions with soil decomposers (Gadgil and Gadgil 1971; Brzostek and others 2015; Fernandez and Kennedy 2015; Gui and others 2017), (2) altering the decomposition rate of plant roots (Langley and others 2006; Koide and others 2011), and (3) altering the composition and activity of neighboring soil microbial communities (Herman and others 2012; Nuccio and others 2013; Cheeke and others 2016; Paterson and others 2016).

Mycorrhizal associations of trees often correspond to plant traits and soil characteristics that affect and/or reflect biogeochemical processes. Leaf litter chemistry and root morphology vary with plant taxonomy and mycorrhizal associations (Cornelissen and others 2001; Valverde-Barrantes and others 2018), leading to differences in nutrient and C cycling in AM and ECM systems. These differences have led some to suggest that AM- and ECM-dominated ecosystems have distinct nutrient cycling syndromes and C cycle dynamics (Vargas and others 2010; Phillips and others 2013). For example, the soil beneath AM-associated trees tends to have higher N and phosphorus-acquiring enzyme activities as well as higher nitrification rates compared to ECM soils (Phillips and others 2013; Cheeke and others 2016), which may influence soil C sequestration. AM- and ECM-associated plants also tend to differ in root traits such as tissue density (Valverde-Barrantes and others 2018) and root architecture (Brundrett 2002), likely owing to their coevolutionary history with mycorrhizal fungi and the varying mechanisms of root colonization by AM versus ECM fungi. Furthermore, differences among tree species in their associations with environmental and soil conditions may be related to their mycorrhizal associations. For example, among the seven most abundant tree species at the Hubbard Brook Experimental Forest, trees that associate with AM fungi (for example, *Acer saccharum, A. rubrum*) tend to grow in deeper soil with high base cation concentrations and relatively high pH, whereas ECM tree species are

relatively more abundant in shallow soil and on rocky slopes (Schwarz and others 2003). These differences in soil conditions and plant traits that covary with mycorrhizal association likely also influence soil respiration rates.

Some recent studies provide evidence for lower soil respiration rates in ECM-dominated soils compared to AM-dominated soils, with suggested mechanisms including associated plant and microbial communities (Soudzilovskaia and others 2015) and differences in soil chemistry, root biomass, and environmental factors including soil temperature and moisture (Wang and Wang 2018). These observations lead to two central questions: (1) *Do mycorrhizal associations of dominant trees influence soil respiration rate?*, and (2) *Is the effect of the mycorrhizal type, if any, due to correlations between mycorrhizal type and soil characteristics that more directly influence respiration?*

We conducted this study within a north temperate deciduous forest to test whether the mycorrhizal associations of locally dominant trees explained within-site variation in soil respiration rates. We also measured soil temperature, moisture, root abundance, and other soil characteristics, and evaluated how well these measurements predicted soil respiration independent of canopy tree species and mycorrhizal type. Finally, we tested for remaining associations between respiration and mycorrhizal type after accounting for the effects of soil and fine root characteristics.

Methods

Site Description

We conducted this study at Hubbard Brook Experimental Forest in Woodstock, NH (43°56′N, 71°46′W). Soils in this region are well-drained spodosols derived from glacial till. The site has a humid continental climate with a mean annual temperature of 6 degrees Celsius and mean annual precipitation of 1434 mm, one-third of which generally falls as snow (USDA Forest Service 1996).

We established 21 forest plots (100 m^2) in May 2017. Plots were selected to include the full existing gradient of tree–mycorrhizal associations as determined by basal area representation of tree species associated with either AM or ECM fungi. The representation of tree species associated with ECM fungi ranged from 4 to 100% of the total basal area across our study plots (Figure S1). We classified plots as AM-dominated (n = 7) or ECM-dominated (n = 7) if trees associated with the mycorrhizal type of interest represented at least 70% of the basal area. In mixed plots (n = 7), AM trees constituted 40 to 60% of the basal area. The dominant ECM-associated tree species in the study area were American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula allegheniensis* Britton), with occasional paper birch (*B. papyrifera* Marsh.) and Eastern hemlock (*Tsuga canadensis* L. Carrière) (< 6% and < 9% total basal area, respectively). The dominant AM-associated tree species were sugar maple (*A. saccharum* Marsh.) and white ash (*Fraxinus americana* L.), with occasional red maple (*A. rubrum* L.; < 4% total basal area). The understory was composed mainly of hobblebush (*Viburnum lantanoides* Michx.) and beech saplings (< 3 cm in diameter at breast height). All study plots were contained within an area of 1.14 ha and were separated from the nearest plot by 10–30 m.

Soil Respiration

Within each plot, we installed two PVC soil respiration collars (10.1 cm diam.) to a depth of 7 cm in opposite corners of an internal subplot (5 × 5 m). Two weeks after collar installation, we began measuring soil respiration approximately monthly throughout the growing season with a greenhouse gas analyzer using cavity ring-down spectroscopy (Los Gatos Research, Los Gatos, CA). Briefly, measurements were conducted by placing a PVC cap on each soil respiration collar, with CO_2 concentrations measured every 5 s during a 2-min period. Soil respiration rate was calculated as the slope of the linear model fit to the rise in CO_2 concentrations in the closed chamber between 30 and 90 s of the chamber top deployment. At the time of each soil respiration measurement, we measured volumetric soil moisture in the top 5 cm of the soil with a portable soil moisture probe (Decagon Devices, Pullman, WA) and soil temperature approximately 8 cm below the soil surface with a thermometer.

Soil and Root Analyses

In May 2018, soil respiration collars were removed and the soil and roots within them were collected to a depth of 10 cm, with organic and mineral soils separated. These samples were passed through a sieve (2 mm) to remove rocks and coarse roots. All fine roots were removed, examined with a dissecting microscope, and visually classified as belonging to an ECM-associated or AM-associated plant species using morphological characteristics (Yanai and others 2008). The occasional roots belonging to herbaceous plants were discarded. We classified some roots as ‘‘unknown’’ when frag-

ments were too small or damaged to identify distinguishing characteristics. AM and ECM root lengths and surface area in each sample were determined with IJ_Rhizo (Pierret and others 2013) and roots were oven-dried at 40°C for 72 h and weighed to determine the biomass of AM and ECM roots within each collar. We measured soil chemistry in the organic horizon, which varied from 1 to 10.5 cm in depth. Subsamples of organic horizon soil were analyzed for pH, and for C and N concentrations using an elemental analyzer (Carlo-Erba Instruments, Wigan, UK).

Data Analysis

Soil respiration rate was calculated using functions in the R base package (version 3.5.2; R Core Team 2018) following the method described in Matthes and others (2018) for each measurement time at each respiration collar. We removed one anomalously large (> 10 standard deviations above mean) respiration measurement on one sampling date from the dataset. To test our central hypothesis that the dominant mycorrhizal type of the trees in our study plots influenced the rate of soil respiration, we first modeled soil respiration rate as a function of plot mycorrhizal type with a linear mixed-effects model using the nlme package (Pinheiro and others 2019) in R. We included individual soil respiration collars nested within the study plots as a random effect and used an AR1 autocorrelation structure to reflect the repeated measures design. Respiration rates were square-root-transformed prior to statistical analyses.

Next, we developed a second linear mixed-effects model for soil respiration rate based on physical and chemical characteristics of the soil and root abundance within the respiration collars. For this model, we selected predictors that we expected to influence both heterotrophic (microbial activity and organic matter availability) and autotrophic respiration fluxes (root abundance) from soil a priori. We included soil temperature, soil moisture, fine root surface area, soil %N, C/N, and organic horizon depth as fixed effects and respiration collars nested within each study plot as a random effect, as well as specifying an AR1 autocorrelation structure. Finally, we tested for remaining effects of mycorrhizal type on soil respiration by comparing the information content (AIC) of this model to one with the additional fixed effect of plot mycorrhizal type. By testing for additional explanatory power of mycorrhizal type, we can determine whether the dominant functional group of mycorrhizal fungi present in our plots influenced soil respiration by direct pathways beyond their associations with physical and chemical characteristics of the soil. Differences in soil and root characteristics in AM, ECM, and mixed plots were determined with ANOVA, using mean soil %N, organic horizon depth, pH, C/N, and fine root surface area from both soil respiration collars in each plot. To test for differences in the repeated measurements of soil moisture and temperature with plot mycorrhizal type, we constructed linear mixed-effects models of temperature and moisture with date as a random effect and plot type as a fixed effect.

Results

Soil Respiration

Soil respiration rate ranged from 1.47 to 11.36 μmol CO_2 m^{-2} s^{-1} across all plots and sampling dates. Throughout the growing season, soil respiration rate averaged 29–32% higher in AM-dominated plots compared to ECM and mixed plots (Figure 1; $F_{18,186} = 3.51$, $p = 0.052$). The soil conditions with a significant effect on respiration were soil temperature, %N, and organic horizon depth, while fine root surface area, moisture, and C/N did not influence respiration. From our model comparison procedure, we found that adding information about the mycorrhizal type of the study plots did not describe additional variation in soil respiration beyond that which was explained by the soil characteristics (Table 1).

All significant predictors in our respiration model were positively associated with soil respiration rate.

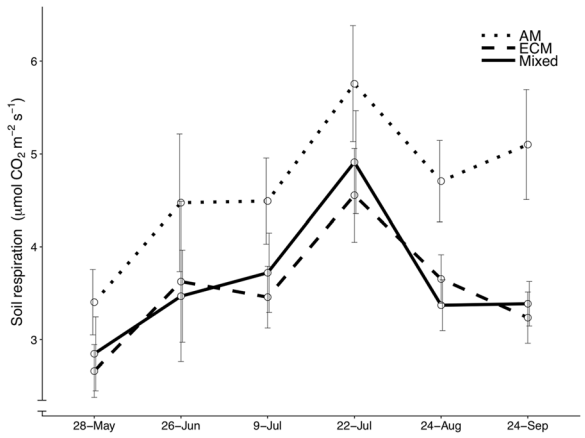

Figure 1. Soil respiration across the growing season in AM, ECM, and mixed forest plots. Each point represents the mean respiration rate (± SE) from seven plots of each plot type on each sampling date. Note axis break.

Table 1. Soil Respiration Model Parameters for (A) Model Without Plot Mycorrhizal Type as a Predictor, and (B) Model Including Plot Mycorrhizal Type

Model	Fixed effects	Estimate (standard error)	*p* value	Model AIC
(A)	*Intercept*	0.684 (0.409)		120.7
	Soil temperature (+)	**0.066 (0.008)**	**0.000**	
	Soil moisture (+)	0.388 (0.233)	0.098	
	Fine root surface area (0)	0.000 (0.000)	0.972	
	Soil %N (+)	**0.257 (0.100)**	**0.019**	
	Soil C/N (−)	− 0.019 (0.015)	0.224	
	O horizon depth (+)	**0.045 (0.021)**	**0.042**	
(B)	*Intercept*	0.742 (0.420)		128.7
	Soil temperature (+)	**0.066 (0.008)**	**0.000**	
	Soil moisture (+)	0.390 (0.233)	0.096	
	Fine root surface area (0)	0.000 (0.000)	0.908	
	Soil %N (+)	**0.233 (0.105)**	**0.039**	
	Soil C/N (−)	− 0.017 (0.016)	0.304	
	O horizon depth (+)	0.046 (0.024)	0.073	
	Plot mycorrhizal type—ECM (−)	− 0.048 (0.135)	0.726	
	Plot mycorrhizal type—Mixed (−)	− 0.112 (0.125)	0.382	

Signs indicate the direction of the effect on respiration for each parameter. Soil characteristics with a significant ($p < 0.05$) impact on respiration indicated in bold.

At peak respiration (late July), soil respiration rate increased by 154% (3.68–9.37 umol CO_2 m^{-2} s^{-1}) across the range of soil nitrogen concentrations and 157% (3.64–9.37 umol CO_2 m^{-2} s^{-1}) with increasing organic horizon depth in each plot.

Fine Root Characteristics

Fine root biomass collected from the top 10 cm of each soil respiration collar ranged from 92.4 to 312.0 g m^{-2}. We classified 97.7% of the root material as either AM- or ECM-associated. AM roots were overrepresented in 13 of the 21 plots, and the proportion of AM-associated roots corresponded poorly with the proportion of AM-associated tree species (Pearson's $r = 0.29$; Figure 2). AM roots represented 69.4% of the surface area of fine roots in AM plots, 60.4% in ECM plots, and 49.3% in mixed plots, though these differences were not as distinct as above-ground patterns in tree basal area (Table S1). Mean surface area of AM-associated roots was slightly higher in AM plots than in ECM plots and mixed plots ($F_{2,18} = 3.24$, $p = 0.06$). Overall, ECM tree species were underrepresented by our root metrics, comprising 51.2% of the total basal area in all plots, but only 45.6% of the fine root mass and 37.5% of the root surface area in the plots. AM plots contained, on average, slightly higher total root surface area compared to ECM and mixed plots ($F_{2,18} = 2.62$, $p = 0.10$).

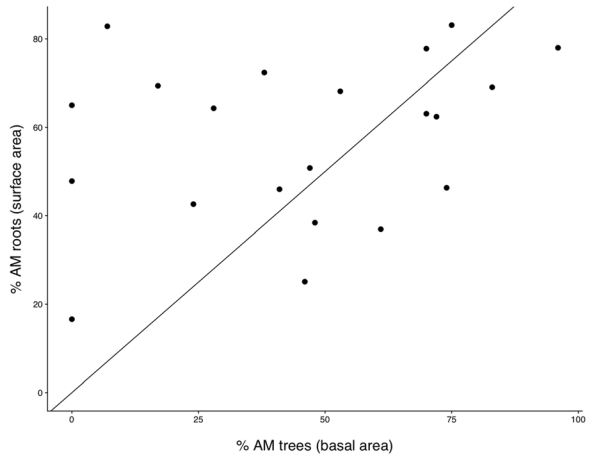

Figure 2. Percentage of fine root surface area from AM-associated trees in each sampling plot relative to the percentage of the tree basal area from AM-associated tree species. Solid line indicates 1:1 ratio of AM root and tree representation.

Soil Physical and Chemical Conditions

Within sampling dates, soil temperature tended to be about 0.3°C cooler in AM plots than in ECM and mixed plots ($p < 0.001$). Volumetric soil water content varied by mycorrhizal type, with the lowest average moisture in ECM plots (0.27 cm^3/cm^3) and the highest in AM plots (0.31 cm^3/cm^3; $p < 0.001$). Soil pH, %N, C/N, and fine root biomass did not vary significantly with plot mycorrhizal association (Figure 3). The average N

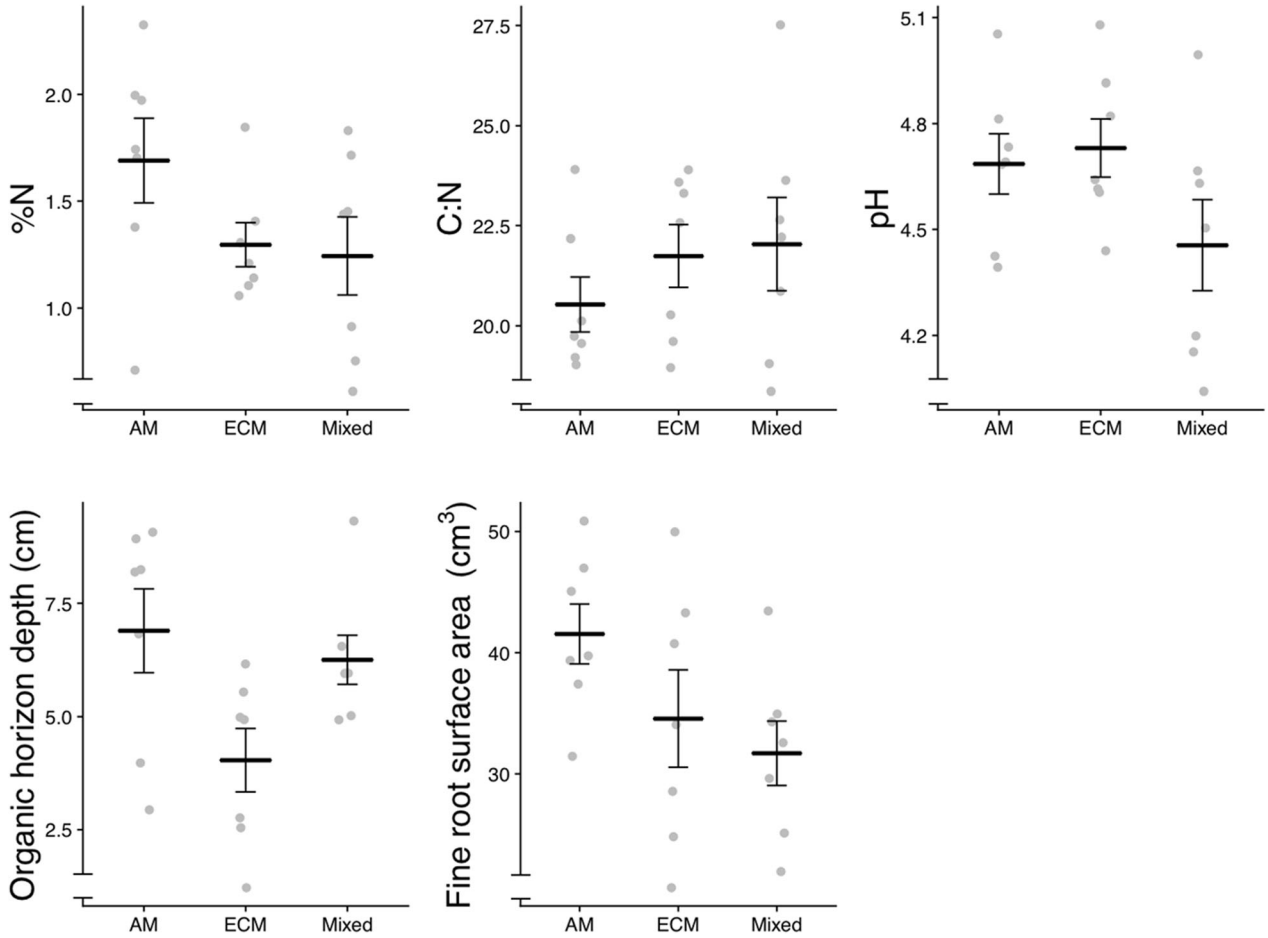

Figure 3. Soil physical and chemical conditions in AM, mixed, and ECM plots (n = 7). Values are averages from the two soil respiration collars in each plot. Significant differences among plot types are indicated by asterisks (*$p < 0.05$). Central bars represent mean values and error bars are standard error of the mean. Note axis breaks.

concentration in the organic horizon was 31% higher in AM plots (1.7% in AM compared to 1.3% in ECM and mixed plots), but the differences between plot types were not statistically significant ($F_{2,18}$ = 2.15, p = 0.146). Soil % C and % N were closely correlated (Pearson's r = 0.93, $p < 0.001$). The average depth of the organic horizon was 2–3 cm lower in ECM plots (4.04 ± 0.7 cm) than in AM (6.89 ± 0.9 cm) and mixed (6.25 ± 0.5 cm) plots ($F_{2,18}$ = 4.09, p = 0.034). Mean soil pH was between 4.5 and 4.7 in all three plot types.

Discussion

Soil Respiration

Our finding that soil respiration rate was significantly higher in AM plots than in mixed and ECM plots is consistent with other studies from tree monocultures in common gardens (Wang and Wang 2018) and in experimental mesocosms (Taylor and others 2016; Wurzburger and Brookshire 2017). Of the potential drivers we measured, we found that patterns in soil respiration in this site were described by soil temperature, N concentration, and organic horizon depth. This model of soil respiration was not improved by adding information about the dominant mycorrhizal association of the trees in our plots. Further, adding plot mycorrhizal type to our model reduced the strength of the influence of soil conditions on respiration, indicating that mycorrhizal fungi influenced soil respiration indirectly by their associations with soil conditions that ultimately affected microbial respiration (Table 1).

Soil moisture did not appear to be a significant predictor of soil respiration, likely because the range of soil moisture values we measured was small and fell above thresholds of moisture stress for microbial activity (Savage and Davidson 2001). Consistent with recent reports that fine root bio-

mass is not directly related to soil respiration rate (Bae and others 2015), the amount of root surface area in the respiration collars was also a poor predictor of soil respiration.

The strong, positive relationship between soil respiration and N concentration (Table 1) highlights the importance of substrate availability for local-scale CO_2 efflux. Because soil N and C concentrations were closely related in all plots, we used soil N rather than C in our soil respiration models to reflect the resource we considered more likely to limit microbial activity. Given the strength of the correlation between C and N concentrations, we consider N concentration to generally represent the availability of organic matter for microbial decomposition. Thus, a possible explanation for this strong trend in respiration rate with soil N concentration may be that soil with more organic matter supports more microbial biomass (Yang and others 2010), which contributes to higher soil respiration rates (Wei and others 2015). Interestingly, this pattern is in contrast to many studies showing declines in soil respiration rate with N additions to ecosystems (Bowden and others 2004; Burton and others 2004; Phillips and Fahey 2007; Janssens and others 2010; Zhou and others 2014). In response, we suggest that the values of soil N concentration observed in our study were too low (approximately 1–2% N) to reach levels that are thought to reduce microbial activity, and were likely much lower than soil N concentrations in N addition studies, which are often designed to increase N inputs by threefold or more (Bowden and others 2004; Burton and others 2004; Phillips and Fahey 2007). Further, decomposition in our system is likely limited by the availability of easily accessible nutrients, including simple forms of nitrogen. Indeed, low levels of N addition have been shown to stimulate decomposition by fungi isolated from another N-limited northern forest soil (Allison and others 2009), and it is logical to expect that microbial activity will be stimulated by greater nutrient availability if microbes become limited by other resources (that is, increasing cellulolytic (Frey and others 2004; Keeler and others 2009) or P-degrading (Sinsabaugh and others 2002) enzyme production with N addition). However, our soil C/N values were nearly all below the 25:1 threshold above which N is considered to be limiting for microbial growth and respiration (Martin and others 2009), which may indicate that soil N in these plots is bound in complex forms and not readily available for microbial uptake. Microbial activity may also be limited by soil phosphorus concentration, which is likely correlated with nitrogen concentrations in our plots. Thus, higher respiration rates from soil with higher N concentrations may reflect a response to greater P availability (Fisk and others 2015).

Alternatively, fine root proliferation and activity in soil patches with higher N concentrations may have led to increased soil respiration per unit root surface area. Because our respiration collars were installed to a depth of 7 cm, most of the fine roots sampled from the top 10 cm of soil in the collars at the end of the growing season grew into the soil during the course of the study. Though we did not see a pattern in soil respiration rate with fine root biomass or surface area as measured at the end of the growing season, *rates* of root growth into the soil respiration collars over the growing season may have been higher for collars with higher soil N concentrations (Hodge 2004), leading to a corresponding increase in soil respiration rate that may not necessarily be reflected by the static variables of root abundance we measured.

Root Characteristics of AM and ECM Trees

Though root abundance did not influence soil respiration in our study, we found patterns in fine root morphology with mycorrhizal associations that may influence other soil processes. AM roots were overrepresented in our study area relative to AM tree basal area, which could lead to significantly more root biomass beneath AM-dominated trees, and may increase the potential contribution of roots to soil respiration in AM-dominated forests. The pattern in AM root representation is supported by another recent study, which found that roots of American beech, one of the most common species in our plots, were underrepresented in a mixed temperate forest relative to above-ground biomass (Valverde-Barrantes and others 2018). However, the patterns we detected in AM and ECM fine roots should be considered with caution given the low species richness in each functional group (three AM and four ECM tree species) and high likelihood that individual species traits related to taxonomy also contribute to variation in AM and ECM root morphology in our study (Kong and others 2019; Liu and others 2019). Additionally, both AM and ECM roots were found in all plots, regardless of the dominant tree mycorrhizal type, and AM roots constituted up to 65% of the fine root surface area in plots where 100% of the tree basal area was ECM-associated species (Figure 2).

Soil Conditions Beneath AM and ECM Trees

The trends we noted in soil %C, %N, and C/N are consistent with other studies showing that higher C/N beneath ECM trees appears to be driven by a decline in soil N concentration rather than changes in C concentration (Lin and others 2017; Zhu and others 2018). However, the slightly higher C and N concentrations we measured in organic soil beneath AM tree species relative to ECM tree species are in contrast to theoretical expectations and several studies that found the opposite trend (Phillips and others 2013; Taylor and others 2016; Zhu and others 2018). Likewise, the negative relationship between ECM tree basal area and organic horizon depth in our plots is not supported by the larger body of literature, which suggests that ECM litter recalcitrance should lead to thicker organic soil horizons and greater forest floor C stocks in ECM-dominated forests compared to AM-dominated forests (Phillips and others 2013; Lin and others 2017). These discrepancies may be partly due to the traits of yellow and paper birch, which together account for 20% of the basal area in our plots. Birch leaf litter has a higher N content and decomposes faster than most of the other litter species in our study plots, which may limit the accumulation of organic matter on the forest floor (Melillo and others 1982; Sommerville and others 2004). Yellow birch also commonly grows on rocky outcrops and boulders in this landscape, leading to, on average, shallower and rockier soils beneath yellow birch trees as a correlated but not causal factor (Schwarz and others 2003). However, soil respiration rates in ECM plots were similar to mixed plots, despite organic horizons that were about 2 cm thicker in mixed plots. These relationships suggest that while organic horizon depth varies by plot mycorrhizal type, it is not the principal driver of differences in soil respiration rate with mycorrhizal type.

Limitations of Collar-Based Soil Respiration Measurements

We employed a standard method of measuring in situ soil respiration with the installation of PVC soil collars in our study plots. Though widespread, this procedure can lead to measurement artifacts and biases that must be considered with respect to the study question. We installed collars to a depth of 7 cm with the intention to isolate the organic horizon soil and reduce lateral diffusion of CO_2 from surrounding areas within this porous soil horizon (Creelman and others 2013). In many, but not all cases, this depth was sufficient to reach the bottom of the organic horizon, but the depth of the organic horizon varied systematically with plot mycorrhizal type, which may have influenced patterns in our data attributed to tree mycorrhizal associations. However, the patterns we observed do not reflect the expected trend if lateral diffusion was reducing respiratory fluxes from our soil; in fact, we found higher fluxes in soils with deeper organic horizons, despite their lower density than deeper mineral soils.

Further, in our measurements of soil respiration, we did not vent our chambers during the 2-min measurement period when the instrument was attached to the respiration collar, as is recommended (Davidson and others 2002). However, we took precautions to minimize the chance of measurement error including visual inspection the linear relationship of the CO_2 concentration in the chamber headspace in real time during each measurement period. Measurements with nonlinear patterns in CO_2 accumulation were immediately remeasured, and those with a coefficient of determination less than 0.998 were omitted from the analysis.

Relevance for Ecosystem Models

The functional group of mycorrhizal fungi associated with dominant vegetation may be an important secondary driver of soil respiration rate via correlated soil chemical and physical factors. The relationship between mycorrhizal type and soil respiration in our study matched other recent reports that AM fungi are associated with higher rates of soil respiration (Soudzilovskaia and others 2015; Taylor and others 2016; Wurzburger and Brookshire 2017; Wang and Wang 2018). Though our study plots were located close together within a small area of forest containing both AM and ECM trees, it is possible that individual tree species grew preferentially in patches of soil with particular chemical and physical characteristics, leading to the observed relationships between mycorrhizal type and soil chemistry. Regardless of the underlying drivers of these associations, the patterns described here indicate that mycorrhizal associations of dominant vegetation may be useful for predicting soil respiration at the within-site scale.

Additionally, our data suggest an additive effect of AM and ECM fungi on soil, given that soil measurements in plots with roughly equal parts AM and ECM tree basal area often fell between AM and ECM-dominated plots. This is consistent with

several recent studies of forest soil across gradients of ECM dominance in which soil and microbial properties tend to change linearly with increasing proportions of ECM trees (Cheeke and others 2016; Craig and others 2018). Studies in ecosystems with mixtures of AM and ECM-associated vegetation may be critical for biogeochemical models given that most ecosystems support both AM and ECM fungi (Phillips and others 2013), yet most studies about mycorrhizal effects on ecosystem processes compare AM and ECM-dominated systems.

For all soil characteristics related to mycorrhizal associations, relationships were stronger between soil and nearby tree mycorrhizal type rather than root mycorrhizal association within each respiration collar. These trends are likely due to high variability in fine root abundance over small spatial scales and seasonal timescales (Büttner and Leuschner 1994; Stoyan and others 2000). Thus, the roots we sampled did not necessarily represent the mycorrhizal functional group that has influenced that soil area over time. Indeed, our data show high variability both within and between plots in the mycorrhizal type of the roots we sampled that did not often reflect the plot-level tree mycorrhizal associations (Table S1). Based on these observations, we suggest that above-ground metrics of mycorrhizal dominance at plot scales (i.e., tree basal area) better represent the effect of mycorrhizal type on soil properties in forests than fine-scale root measurements within a single year.

Summary and Conclusions

Higher soil respiration rates in AM-dominated forest plots relative to ECM and mixed forest plots were at least partially explained by a trend toward higher soil N concentration and deeper organic horizons beneath AM trees. These results indicate that mycorrhizal associations of trees may influence soil respiration indirectly by affecting soil chemistry and physical structure. We also found poor correspondence between below and above-ground metrics of tree representation by mycorrhizal type, suggesting that measurements of fine root abundance at a single time point may not capture the long-term effects of AM and ECM tree species on soil processes. With incipient changes in forest composition that may shift the relative dominance of AM- and ECM-associated tree species, soil processes including respiration rate may change in predictable ways. Understanding the magnitude and direction of these differences in soil processes beneath AM and ECM trees is an important first step for modeling forest C dynamics into the future.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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