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Mycorrhizal associations of trees have different indirect effects on organic matter decomposition

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Summary

1. Organic matter decomposition is the main process by which carbon (C) is lost from terrestrial ecosystems, and mycorrhizal associations of plants (i.e. arbuscular mycorrhizas (AM) and ectomycorrhizas (ECM)) may have different indirect effects on this loss pathway. AM and ECM plants differ in the soil decomposers they promote and the quality of litter they produce, which may result in different patterns of organic matter decomposition, and hence, soil C loss.

2. To determine how mycorrhizal associations indirectly affect decomposer activity, we collected soils and litters from four AM and four ECM tree species from a mixed-deciduous temperate forest for a field and laboratory study. We first characterized *in situ* patterns in soil chemistry and soil microbial biomass among these eight tree species. We then conducted a microcosm experiment with mineral soils, leaf litter and fine roots originating from these tree species, where we reciprocally crossed litters and soils, and quantified the rate of heterotrophic respiration over a 140-day laboratory incubation.

3. In natural forest conditions, AM tree soils contained lower total C and microbial biomass C:N relative to ECM tree soils. In our microcosm experiment, AM soils supported greater heterotrophic respiration than did ECM soils. The addition of AM litter stimulated respiration more than did ECM litter, owing to the lower C:N of AM litter. Matching the mycorrhizal identity of litter and soil resulted in a difference in total respiration, such that combinations of AM litters with AM soils lost more C than did combinations of ECM litters with ECM soils.

4. *Synthesis.* Our findings demonstrate that AM and ECM trees have differing indirect effects on soil decomposer activity through the decomposers they cultivate and/or the quality of organic matter they produce. Mycorrhizal differences in litter quality accentuate these effects on soil C loss and may explain patterns in soil C dynamics in terrestrial ecosystems.

Key-words: arbuscular mycorrhizas, biogeochemistry, carbon, decomposition, ectomycorrhizas, nitrogen, plant–soil relationship, soil organic matter

Introduction

Soils represent the largest reservoir of terrestrial carbon (C; Jobbagy & Jackson 2000), and decomposition is the main process that depletes this C pool (Chapin *et al.* 2009). Mycorrhizal symbioses (i.e. AM vs. ECM) of plants indirectly affect decomposition, but they do so in distinct ways, and this may result in divergent patterns of C loss. AM and ECM plants promote soil microbial communities with distinct functional attributes (van der Heijden, Bardgett & van Straalen 2008), and they tend to generate litter of differential quality (Read, Leake & Perez-Moreno 2004). However, it is unknown whether these factors individually, or together, result in mycorrhizal-specific patterns in organic matter decomposition. Such knowledge is critical for resolving why AM-dominated biomes and ecosystems tend to contain lower stocks of soil C (or lower soil C:N) relative to their ECM counterparts (Read 1984; De Deyn, Cornelissen & Bardgett 2008; Averill, Turner & Finzi 2014).

Mycorrhizal symbioses of plants differ in the activity and composition of the decomposers they promote, and this may relate to their distinct strategies for nutrient acquisition. AM fungi 'scavenge' mineral forms of N and phosphorus (P; Lambers *et al.* 2008) and may stimulate decomposers to increase both C and N mineralization (Hodge & Fitter 2010; Nuccio *et al.* 2013). In contrast, ECM fungi can 'mine' N directly from organic matter via secretion of extracellular

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enzymes (Bending & Read 1997; Lambers *et al.* 2008), which creates a competitive context between mycorrhizal fungi and decomposers for organic N (Lindahl, de Boer & Finlay 2010). These mycorrhizal strategies may lead to different assemblages of saprotrophs in AM and ECM-dominated ecosystems (van der Heijden, Bardgett & van Straalen 2008; McGuire *et al.* 2010) and could explain why leaf-litter decay rates are often greater in AM-dominated versus ECM-dominated forests (McGuire *et al.* 2010; Midgley, Brzostek & Phillips 2015).

The quality of plant litter may also promote distinct mycorrhizal effects on decomposition. Arbuscular mycorrhizal plants tend to produce leaf litter with a higher quality (i.e. lower C:N) and greater decomposability relative to ECM plants in temperate ecosystems (Cornelissen *et al.* 2001; Vesterdal *et al.* 2012; Phillips, Brzostek & Midgley 2013), although it remains unclear if this pattern holds across all ecosystems and plant lineages (Koele *et al.* 2012; Dickie *et al.* 2014). Root litter is more poorly studied, but the available evidence suggests that ECM roots and fungi are recalcitrant (Langley & Hungate 2003; Langley, Chapman & Hungate 2006; Fernandez & Koide 2014; but see Koide, Fernandez & Peoples 2011) and may decompose more slowly than their AM counterparts (Langley & Hungate 2003).

The mycorrhizal identity of a plant may affect how its litter interacts with existing decomposers and soil organic matter pools. Litters can decompose more rapidly in 'home' soils relative to 'away' soils (Keiser *et al.* 2014), but this can depend on the ecosystem type (Freschet, Aerts & Cornelissen 2012) and its mycorrhizal composition (Midgley, Brzostek & Phillips 2015). For example, decomposition can be faster in AM- versus ECM-dominated forests (McGuire *et al.* 2010), and AM litter decay can be amplified in AM soils (Midgley, Brzostek & Phillips 2015). However, it is unclear how these patterns reflect how new litter C interacts with decomposers and organic matter, and specifically, whether new C adds to, or accentuates loss of, existing organic matter in the soil profile (Cotrufo *et al.* 2013). This issue may be most relevant for fine roots, which turn over directly in mineral soils and are a major source of soil C (Kramer *et al.* 2010; Clemmensen *et al.* 2013). If the relationships among litter, decomposers and organic matter differ by plant mycorrhizal identity, they may contribute to patterns in soil C balance across terrestrial ecosystems (Read 1984; De Deyn, Cornelissen & Bardgett 2008; Averill, Turner & Finzi 2014).

In this research, we sought to understand how the mycorrhizal identity of trees affect interactions among fresh litter, decomposers and soil organic matter, with a specific focus on C loss via heterotrophic respiration. To isolate effects of mycorrhizal fungi from those of climate and soil type, we conducted an experiment in a temperate forest ecosystem where AM and ECM trees naturally co-dominate. We first characterized soil biogeochemical patterns (total soil C and N, soil microbial biomass C, N and P, and the availability of N and P of individual species of AM and ECM trees *in situ*. We also characterized differences in soil pH between AM and ECM trees, as pH can be a determinant of soil chemistry and tends to be lower in ecosystems dominated by ECM versus AM plants (Cornelissen *et al.* 2001; Phillips, Brzostek & Midgley 2013). We then tested the importance of the mycorrhizal identity of mineral soil (including its natural organic matter and decomposers) and litter on soil C loss through respiration. To this end, we collected mineral soils and litters from species of AM and ECM trees in the field and conducted a microcosm experiment in the laboratory. We quantified heterotrophic respiration of soils and determined the response of respiration to additions of leaf and root litter. By isolating soils from plants and mycorrhizal fungi, we specifically determined how indirect effects of mycorrhizal identity contribute to organic matter decomposition.

We hypothesized that AM trees would demonstrate lower soil total C, N and C:N, lower microbial biomass C:N, but greater soil pH, and available N and P relative to ECM trees, as a reflection of their nutrient acquisition strategies and subsequent effects on soil chemistry (Phillips, Brzostek & Midgley 2013). For the microcosm experiment, we hypothesized that heterotrophic respiration would be greater in AM soils vs. ECM soils, and that the addition of AM litter would stimulate respiration more than ECM litter. These expectations were based on the idea that AM-dominated ecosystems promote litter decomposition relative to their ECM counterparts and that AM plants tend to produce more labile litter than ECM plants (McGuire *et al.* 2010; Midgley, Brzostek & Phillips 2015).

Materials and methods

STUDY DESIGN AND SITE DESCRIPTION

To understand how the mycorrhizal identity of soils and litters affect decomposer activity and soil C loss, we selected eight focal tree species in a mixed-deciduous temperate forest. First, we determined underlying patterns in biogeochemistry among these eight tree species in the field, by measuring soil C and N, pH, available N, P and microbial biomass C, N and P. Secondly, we collected mineral soils and litters from these trees and conducted a microcosm experiment in the laboratory. We quantified heterotrophic respiration from soils derived from these AM and ECM tree species and determined soil responses to litter addition, where we reciprocally crossed each species' soil by each species' litter, separately for both leaf and root litter.

Soil and litter samples were collected from two mature (~70 years old) upland areas of Whitehall Forest, a mixed pine-hardwood forest in Athens, Georgia, USA (33°53′ 35.78″ N, 83° 21′ 30.94″ W, altitude 230 m) (Bauweraerts *et al.* 2014). The climate is warm temperate (mean annual temperature 16.5 °C and mean annual precipitation of 127 cm (Dyer & Brook 1991; Teskey 1998)), and soils are classified as acidic Ultisols (Soil Survey Staff Web Soil Survey). The land was previously used for cotton production, abandoned in the early 20th century, and has since reforested naturally (Daniels 1987).

We selected eight tree species, including four AM species: tulip poplar (*Liriodendron tulipifera* L.), sweetgum (*Liquidambar styraciflua* L.), American holly (*Ilex opaca* Ait.) and Eastern red cedar (*Juniperus virginiana* L.) and four ECM species: mockernut hickory (*Carya tomentosa* Poir. Nutt.), American beech (*Fagus grandifolia* Ehrh.), white oak (*Quercus alba* L.) and loblolly pine (*Pinus taeda* L.).

Each species is hereafter referred to as LITU, LIST, ILOP, JUVI, CATO, FAGR, QUAL and PITA. We selected species that were abundant enough to encounter 10–12 mature individuals (at least 20 cm dbh) in our two ~5-ha study areas. Further, we sought to select species as phylogenetically distinct as possible (e.g. we included one gymnosperm in each group), to better represent the phylogenetic breadth of each mycorrhizal type. All trees sampled in our study were well intermixed between two upland areas (i.e. there were no patterns of local monodominance), and QUAL, LITU, FAGR and CATO are among the five most abundant species in a nearby sampling plot (J. Mohan, pers comm). LIST is more common in areas of former disturbance, such as recovering treefall gaps. All trees in our study were mature, canopy-height specimens, with the exception of ILOP, which is an understorey tree.

SOIL AVAILABLE N AND MICROBIAL BIOMASS

Tree soils were sampled during the growing season (July–August) to determine nutrient availability and soil microbial biomass. From each tree, we collected 12 soil samples (10 cm deep, 2.5 cm diameter) of the A horizon, where six samples were taken from random locations ~50 cm from the tree stem and six from ~1 m from the stem. We excluded the O horizon from our soil samples because the fragmented and humic layers (Oe and Oa) in our forest are heterogeneous (typically < 1 cm, but vary from ~0 to 3 cm depending on species and individual tree), and thus, indiscriminant sampling by soil depth would introduce horizon-specific variability to our study. Soil samples were homogenized and sieved (2 mm) of roots and rocks. A subsample of soil was immediately extracted for dissolved inorganic N (DIN) in the field. We combined 40 g of soil with 50 mL of 2M KCl. Samples were placed on a shaker (150 rpm) for 3–4 h and then filtered through paper (Whatman 41) and glass fibre (1 μm). Samples were frozen until analysis of NO_3^- and NH_4^+ using colorimetry on a continuous flow autoanalyser (Autoanalyzer 301, Alpkem Corporation, Clackamas, OR, USA).

Remaining soils from each tree were prepared for microbial biomass extractions within 1–3 h after collection. Using the method described by Fierer & Schimel (2003), two 7 g subsamples of each tree soil sample were combined with either 40 mL 0.5 M K_2SO_4 (unfumigated) or a mixture of 40 mL 0.5 M K_2SO_4 and 0.5 mL ethanol-free $CHCl_3$ (fumigated) and placed on a shaker for 3 h (150 rpm). Fumigated samples were bubbled vigorously with air using a fumigation manifold for 30 min to remove $CHCl_3$, and all samples were filtered as above. Samples were frozen until analysis of total C (TOC-5000A; Shimadzu, Kyoto, Japan). Total dissolved N (TDN) and P (TDP) was determined after a persulfate digestion (Cabrera & Beare 1993) and then analysed via colorimetry (Autoanalyzer 301, Alpkem Corporation). Microbial biomass C, N and P values were calculated from the difference between unfumigated and fumigated samples, and no correction factor was used.

SOIL AND LITTER MICROCOSM EXPERIMENT

In the fall, we collected leaf and fine root litter from 5 to 7 individuals of each species using traps to capture falling senesced leaves and by tracing fine roots (< 2 mm diameter, which represent 1st- to 3rd-order roots) from the stem of target trees. These individuals were different from those selected for soil sampling (to prevent disturbance effects of root tracing on our sampled soils). Roots were cleaned with DI H_2O, surface sterilized in a 30% hydrogen peroxide (H_2O_2) solution for 1 min, then triple rinsed in DI H_2O. A subsample of fresh root tissue was preserved in a 70% ethanol solution for subsequent mycorrhizal quantification. Leaf and root litters were dried (40 °C) for 48 h and fragmented to ~1 cm^2 pieces.

In the winter, we collected soil samples from five individuals of each tree species for our microcosm experiment. From each tree, we collected 12 soil samples (10 cm deep, 2.5 cm diameter) of the A horizon, where six samples were taken from random locations ~50 cm from the tree stem and six from ~1 m from the stem. Soil samples were homogenized, sieved (2 mm) of roots and rocks and homogenized at the level of tree species, where equal masses of soils from all five individuals were combined. Soils were stored at 5 °C for 48–72 h before the experiment.

Representative subsamples of each species' soil were analysed for pH and total C and N. To determine soil pH, ~10 g fresh soil was combined with 10 mL DI H_2O to form a slurry (4 replicates per species) and placed on a shaker (150 rpm) for 30 min prior to measurement. Subsamples of soil and litter samples were ground to a fine powder and analysed for total C and N (3 replicates per species; Carlo Erba Strumentazione, Milan, Italy).

To initiate the microcosm experiment, fresh soil samples from each tree species (10 g dry weight equivalent) were placed in 50 cm^3 centrifuge tubes, which then received 300 mg of fragmented leaf litter, root litter or no litter (soil-only control). Soils of each species were crossed with leaf litter from each species in a fully factorial design (with the same design for root litter) with three replicates of each combination to create 192 leaf–soil, 192 root–soil, and 24 soil-only microcosms. Litter was mixed into the upper soil volume (~1 cm) of each microcosm by placing the litter on top, covering the container and gently shaking. Shaking was also performed on soil-only controls. Microcosms were covered with perforated film, maintained at 25 °C in an incubator and monitored weekly to maintain 18% gravimetric moisture content with additions of DI H_2O.

We quantified soil respiration five times over the 140-day experiment (days 1, 26, 46, 73 and 140). During a sampling event, microcosms were flushed with N_2 and capped with a gas-tight lid outfitted with a septum. Headspace was mixed vigorously, sampled (2 cm^3) and analysed for CO_2 concentration using an infrared-gas analyser (LiCor 6252, LiCor, Lincoln, NE, USA). During each sampling event, headspace was sampled at three consecutive time points over 1.5 h to determine the respiration rate (mmol $CO_2 \cdot g\ C^{-1}\ h^{-1}$). Total respiration (or cumulative CO_2 production over the 140-day experiment) was estimated by interpolating these measured rates between the sampling points (mmol $CO_2 \cdot g\ C^{-1}$). For litter additions only, we also calculated the response of respiration relative to the soil-only controls.

MYCORRHIZAL COLONIZATION

Mycorrhizal colonization was quantified from preserved samples collected for root litter (< 2 mm diameter). For ECM trees, colonization was quantified using the grid intercept method to determine the percentage of root length with a fungal mantle. For AM trees, roots were cleared and stained and quantified following the procedures of Collins, Wright & Wurzburger (2016). Roots were analysed for mycorrhizal structures using a modified version of the method described by McGonigle *et al.* (1990) using random intercepts to quantify presence or absence of arbuscules, vesicles and hyphae.

STATISTICAL ANALYSES

We analysed the soil and litter chemistry response variables (soil total C, N, C:N, pH; litter C, N and C:N) from species-level mixtures,

where we used two sample *t*-tests (one-tail and unequal variance) to test for differences between AM and ECM trees. Soil extractable N (NO_3^- and NH_4^+), P (resin extractable) and total microbial biomass C, N and P were analysed across individual tree replicates ($n = 5$) of each species with linear mixed-effect models in R (version 3.2.1, package: LME4; R Development Core Team, 2008; Bates *et al.* 2014), where tree species was treated as a random effect. We used the confint.merMod function in the LME4 package to calculate 95% confidence intervals on parameter estimates using a parametric bootstrap procedure (Bates & Sarkar 2007). Two values of microbial biomass C:N and 4 values of C:P were missing because there was insufficient extractant to perform the analysis, or they were removed because the value was an outlier (> 2 standard deviations from the mean).

To test the effect of soil mycorrhizal identity in our microcosm experiment, we analysed heterotrophic respiration on the soil-only controls over time and on a cumulative basis. We constructed linear mixed-effect models (as above) where soil species identities were treated as random effects. In our time-series model, we nested individual microcosms within soil species as a random effect and allowed day to interact with soil mycorrhizal identity. In our cumulative flux models (for soil-only microcosms and those with litter, see below), we included soil chemical factors (i.e. pH, soil C:N), individually to avoid issues of collinearity, and these were retained in our final models only if significant.

We then analysed the heterotrophic respiration of soil with litter addition and determined the importance of soil mycorrhizal identity (AM vs. ECM), litter type (root or leaf) and litter mycorrhizal identity (AM vs. ECM litter) where soil species and litter species identities were treated as random effects. We analysed the effects of these factors on respiration over time and on cumulative respiration. In our time-series model, we nested individual microcosms within soil species as a random effect, allowed day to interact with the above factors and only retained significant interactions in the model. We used the glht function in the MULTCOMP package (Hothorn, Bretz & Westfall 2008) to conduct *a priori* contrasts between AM and ECM soils when litter identity either matched or mismatched the mycorrhizal identity of soils.

We then analysed the response of heterotrophic respiration to litter, as the difference between litter and soils and the soil-only control. We constructed this model for cumulative respiration only and included fixed and random effects as above. For both cumulative respiration and the response to respiration, we included litter C:N as an explanatory variable, which we allowed to interact with soil mycorrhizal identity. Last, to determine whether the abundance of mycorrhizal fungi was important in determining the response of respiration to root litter addition, we included mycorrhizal colonization (per cent root length) as an explanatory variable.

Results

From our study site, soils from AM trees generally contained lower C relative to those from ECM trees ($P = 0.059$; Fig. 1a,b), but other soil chemical variables were less affected by mycorrhizal identity (Tables 1 and 2). Soil pH tended to be greater in AM versus ECM soils ($P = 0.07$; Table 1). Although total microbial biomass C was not different between soils of AM and ECM trees, microbial biomass C:N was higher in ECM versus AM soils (LMM estimate = 2.36 units of C:N, lower 95% CI = 0.48, upper 95% CI = 4.26; Tables 2 and S1 in Supporting Information). To normalize for the difference in soil C between AM and ECM soils, we analysed soil respiration data on a per g C basis.

Over the 140-day incubation, soil respiration declined rapidly and then gradually stabilized over time (LMM estimate = −3.70e-04 mmol CO_2 g C^{-1} day^{-1}, lower 95% CI = −4.5e-04 upper 95% CI = −2.7e-04), but respiration remained higher in AM soils than ECM soils (LMM estimate = −1.16e-02 mmol CO_2 g C^{-1} day^{-1}, lower 95% CI = −2.08e-02 upper 95% CI = −2.31e-02; Fig. S1, Table S2). Because of the lack of treatment interactions with day, we subsequently focus on patterns in cumulative respiration. AM soils supported ~40% greater cumulative respiration than those from ECM trees, despite wide variation among tree species within a mycorrhizal guild (LMM estimate = −1.459 mmol CO_2 g C^{-1}, lower 95% CI = −2.619, upper 95% CI = −0.315; Fig. 1c,d, Table S2). Soil C:N and soil pH did not explain variance in soil respiration and were excluded from our final model.

In the case of litter addition, our time-series model demonstrated that the effects of soil mycorrhizal identity, litter mycorrhizal identity and litter type were all significantly different from zero early in the experiment, but all also significantly interacted with day (Fig. S2, Table S2). However, the interaction effects were quantitatively weak relative to the main effects and largely resulted from the overall decline in respiration over time leading to reduced absolute differences in respiration between groups. Importantly, the relative ranking of treatments (e.g. litter mycorrhizal identity and litter type) did not change over time, and thus, we subsequently focus on analyses of cumulative respiration.

Cumulative respiration was lower for soils that received roots versus leaves (LMM estimate = −2.39 mmol CO_2 g C^{-1}, lower 95% CI = −2.59, upper 95% CI = −2.17) and lower for ECM litter versus AM litter (LMM estimate = −0.79 mmol CO_2 g C^{-1}, lower 95% CI = −1.55, upper 95% CI = −0.01), but did not differ by soil mycorrhizal identity (Table S2, Fig. 2a–c). However, matching the mycorrhizal identity of soils and litter resulted in a difference in the absolute rate of respiration (*a priori* contrast; $P < 0.05$), while mismatching did not ($P > 0.05$) (Fig. 2a).

The respiration response to litter (i.e. the difference between respiration with and without litter) was similar as above, where the response was lower for roots versus leaves (LMM estimate = −2.39 mmol CO_2 g C^{-1}, lower 95% CI = −2.26, upper 95% CI = −1.77), and lower for ECM versus AM litters (LMM estimate = −0.79 mmol CO_2 g C^{-1}, lower 95% CI = −1.52, upper 95% CI = −0.13; Table S2, Fig. 2d–f). Neither soil C:N nor pH explained the observed variance in models of total respiration or response to litter.

We further explored the possibility that litter C:N explained the effect of litter mycorrhizal identity in our models. Total respiration and the response of respiration declined with increasing litter C:N (LMM estimate = −0.03 mmol CO_2 g C^{-1} per unit C:N, lower 95% CI = −0.04, upper 95% CI = −0.02; Table S2, Fig. 3), but the effect of litter C:N did not differ by soil mycorrhizal identity (i.e. no soil by litter C:N interaction). The addition of the litter C:N term made litter mycorrhizal identity no longer significant, suggesting that the mycorrhizal effect derived in part from differences in litter C:

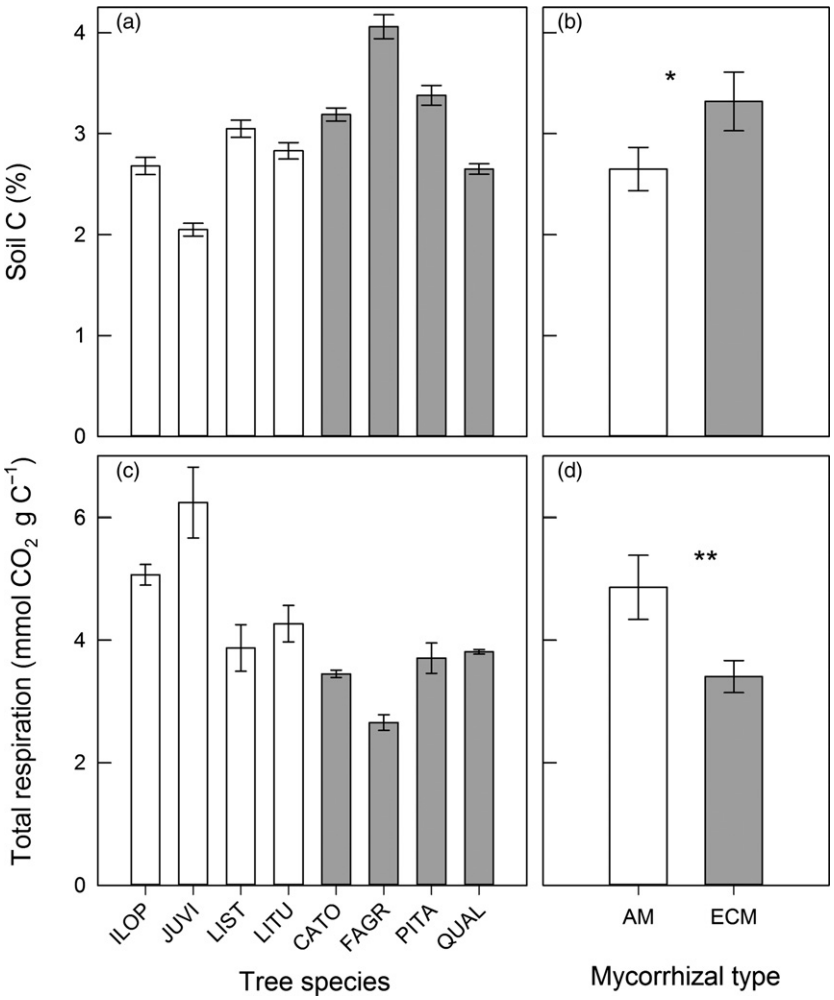

Fig. 1. Carbon content and heterotrophic respiration of soils originating from arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) tree species at Whitehall Forest, with (a) soil C content from eight tree species, (b) soil C grouped by mycorrhizal identity, (c) cumulative respiration over the 140-day laboratory incubation, where soils originated from eight tree species and (d) cumulative respiration grouped by mycorrhizal identity. Values are means ± SE. Species were included as random effects in our model, and significant differences between mycorrhizal types denoted by *($P < 0.1$) and **($P < 0.05$). Species codes: LITU, *Liriodendron tulipifera*; LIST, *Liquidambar styraciflua*; ILOP, *Ilex opaca*; JUVI, *Juniperus virginiana*; CATO, *Carya tomentosa*; FAGR, *Fagus grandifolia*; QUAL, *Quercus alba*; PITA, *Pinus taeda*.

Table 1. Soil chemistry variables from arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) tree species at Whitehall Forest

Species	pH	Total N (%)	C: N	NO_3^- (ppb)	NH_4^+ (ppm)	PO_4^{3-} (ppm)
AM	6.05 (0.18)a	0.16 (0.02)	17.69 (1.32)	27.57 (8.15)	1.10 (0.22)	0.26 (0.05)
LITU	6.10 (0.02)	0.19 (0.002)	15.08 (0.34)	42.44 (23.07)	1.42 (0.55)	0.32 (0.16)
LIST	6.52 (0.05)	0.19 (0.0004)	16.09 (0.26)	22.08 (10.38)	0.85 (0.16)	0.22 (0.09)
ILOP	5.84 (0.02)	0.14 (0.005)	18.64 (0.75)	28.48 (22.34)	0.52 (0.12)	0.18 (0.09)
JUVI	5.73 (0.01)	0.19 (0.002)	20.93 (0.09)	17.27 (5.88)	1.61 (0.60)	0.22 (0.03)
ECM	5.63 (0.17)b	0.18 (0.02)	19.04 (1.53)	13.25 (3.64)	0.86 (0.16)	0.23 (0.04)
CATO	6.02 (0.03)	0.20 (0.002)	15.80 (0.06)	17.09 (10.50)	1.22 (0.35)	0.35 (0.10)
FAGR	5.33 (0.06)	0.21 (0.004)	19.35 (0.17)	14.03 (6.57)	0.59 (0.08)	0.21 (0.07)
QUAL	5.83 (0.03)	0.15 (0.002)	17.92 (0.10)	14.23 (9.15)	1.06 (0.18)	0.18 (0.05)
PITA	5.36 (0.05)	0.15 (0.001)	23.06 (0.24)	9.18 (6.01)	1.42 (0.53)	0.20 (0.05)

Values are means and (SE), with $n = 5$ for each species. Significant differences ($P < 0.1$) between mycorrhizal types, denoted by different letters. Species codes: LITU, *Liriodendron tulipifera*; LIST, *Liquidambar styraciflua*; ILOP, *Ilex opaca*; JUVI, *Juniperus virginiana*; CATO, *Carya tomentosa*; FAGR, *Fagus grandifolia*; QUAL, *Quercus alba*; PITA, *Pinus taeda*.

N. Total % N was higher ($P = 0.046$), and C:N was lower ($P = 0.06$), in AM versus ECM leaf litter, but there were no differences in root litter C, N and C:N (Table 3).

To determine whether the abundance of fungal biomass on roots (i.e. mycorrhizal colonization, Table S3) affected the response of respiration to root litter addition, we added mycorrhizal colonization to a model of root litter only. There was no effect of colonization, nor an interaction between litter mycorrhizal identity and colonization, on the response of respiration (Tables S2 and S3). However, ECM roots resulted in lower respiration relative to AM roots (absolute rate: LMM estimate = −1.5 μmol CO_2 g $soil^{-1}$, lower 95% CI = −2.91, upper 95% CI = −0.15), and this was not explained by differences in litter C:N.

Table 2. Soil microbial biomass (MB) C, N, P and ratios for arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) tree species at Whitehall Forest

Species	MB C (ppm)	MB N (ppm)	MB P (ppm)	MB C:N	MB N:P	MB C:P
AM	218.51 (29.72)	20.34 (2.74)	1.49 (0.39)	10.42 (0.69)b	31.31 (14.6)	201.36 (10.25)
LITU	241.93 (35.72)	25.48 (3.55)	1.22 (0.25)	9.48 (0.51)	23.24 (4.34)	212.37 (35.63)
LIST	291.40 (19.58)	24.63 (1.76)	1.88 (0.49)	12.11(1.23)	16.87 (3.77	216.97 (61.37)
ILOP	163.32 (50.25)	16.11 (2.62)	0.55 (0.19)	9.57 (1.98)	74.47 (54.5)	204.52 (63.38)
JUVI	177.37 (12.10)	15.14 (2.27)	2.31 (0.75)	10.57 (1.17)	10.66 (3.35)	171.59 (36.24)
ECM	212.57 (19.78)	17.13 (1.30)	0.97 (0.25)	12.78 (0.65)a	50.25 (31.4)	227.72 (32.35)
CATO	212.97 (29.18)	18.35 (3.38)	0.92 (0.08)	12.68 (2.39)	20.50 (3.97)	231.87 (18.78)
FAGR	217.72 (18.17)	17.37 (2.14)	1.68 (0.36)	13.08 (1.60)	12.55 (3.45)	161.88 (40.07)
QUAL	161.55 (20.25)	13.43 (1.29)	0.47 (0.26)	11.98 (0.67)	144.22 (73.7)	202.42 (60.89)
PITA	258.03 (42.34)	19.36 (3.11)	0.83 (0.14)	13.36 (0.75)	23.75 (1.59)	314.72 (21.14)

Significant differences ($P < 0.05$) between mycorrhizal types, denoted by different letters. Species codes: LITU, *Liriodendron tulipifera*; LIST, *Liquidambar styraciflua*; ILOP, *Ilex opaca*; JUVI, *Juniperus virginiana*; CATO, *Carya tomentosa*; FAGR, *Fagus grandifolia*; QUAL, *Quercus alba*; PITA, *Pinus taeda*.

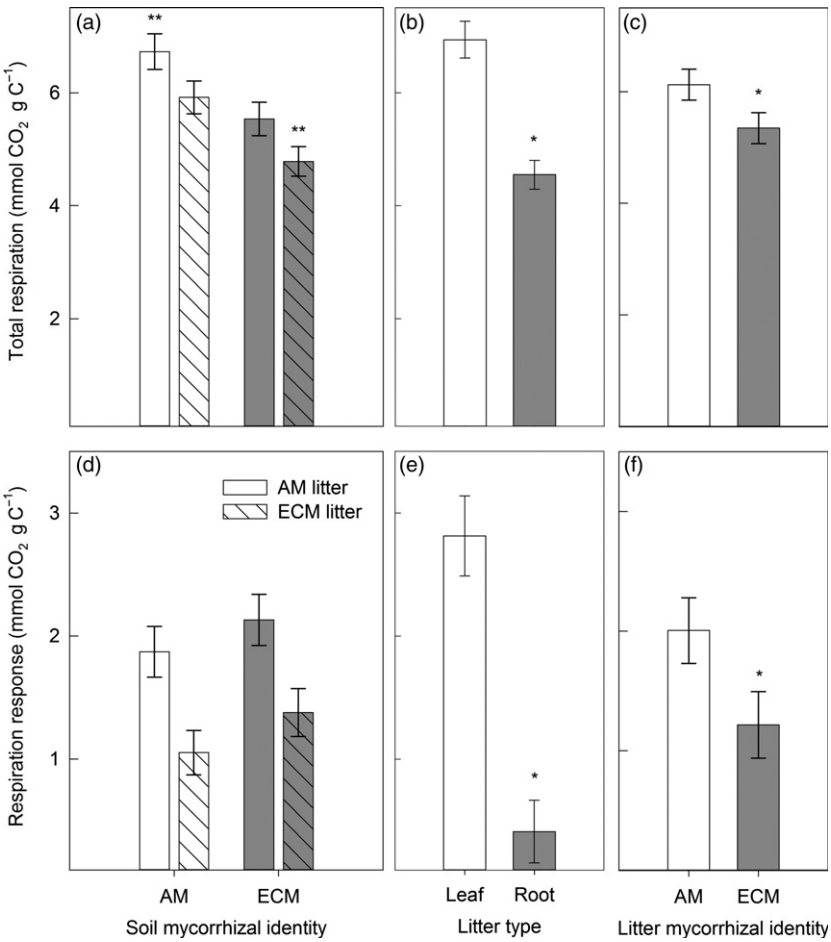

Fig. 2. Cumulative heterotrophic respiration of soil + litter microcosms over the 140-day incubation, where litter and soil originated from arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) tree species at Whitehall Forest. Cumulative respiration by (a) soil and litter mycorrhizal identity, (b) litter type and (c) litter mycorrhizal identity. The response of respiration to litter addition by (d) soils and litter mycorrhizal identity, (e) litter type and (f) litter mycorrhizal identity. Values are means ± SE. In panel (a), double asterisks denote a significant difference ($P < 0.05$) between matches of mycorrhizal soil and litter identity, from *a priori* contrasts. In panels b, c, e and f, single asterisks denote significant effects ($P < 0.05$) of litter type and litter mycorrhizal identity.

Discussion

Our study demonstrates that AM and ECM trees have different indirect effects on organic matter decomposition and soil C loss. In the absence of litter, decomposition triggered 45% more C loss in AM relative to ECM soils (i.e. 5.8 vs. 4% of the total C pool was lost over the 140-day incubation). With the addition of litter, the difference between AM and ECM soil C loss was maintained, but only when soils and litters were matched by mycorrhizal identity. This finding results from the combination of higher respiration in AM soils and greater lability of AM litter, relative to those of ECM trees. In our study, soils were isolated from living plants and mycorrhizal fungi, which prevented direct biotic interactions with decomposers that are important in nature. Our findings suggest, however, that AM trees promote decomposer

communities that are more active, or generate organic matter pools that are more accessible to decomposers, than do ECM trees.

In our study, patterns in soil C loss may result from differences in soil microbial activity or composition. Decomposer communities can differ between AM and ECM-dominated ecosystems (McGuire *et al.* 2010), and while the composition of decomposers in our study system is unknown, we observed lower microbial biomass C:N in AM relative to ECM soils. This suggests that ECM soils contain a higher ratio of fungi to bacteria than AM soils, which tend to possess bacterial-based food webs (Bardgett *et al.* 2005) perhaps due to higher soil pH (Fierer *et al.* 2009). These stoichiometric differences also suggest contrasting rates of respiration (Six *et al.* 2006) and turnover, where the higher C:N of microbial biomass in ECM soils may explain lower C loss relative to AM soils (cf, Rousk & Frey 2015). In addition, we cannot rule out the possibility that the elevated microbial biomass C:N in ECM soils was due to greater abundance of mycorrhizal hyphae relative to AM soils (Finlay & Söderström 1992).

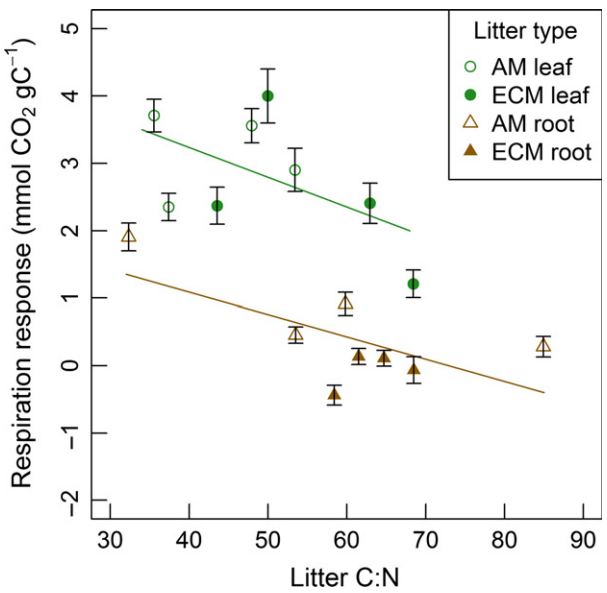

Fig. 3. The negative relationship between the response of heterotrophic respiration to litter over the 140-day incubation and litter C:N among eight tree species. Litter and soils originated from arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) tree species at Whitehall Forest. Values are means ± SE for each tree species. Litter C:N and litter type were both significant explanatory variables in our model, r^2 = 0.08 (leaves) and 0.19 (roots).

The stability of organic matter pools may also explain differences in soil respiration in our study. Although we detected no difference in the soil C:N ratio of AM and ECM soils, these organic matter pools may be chemically or physically protected in different ways, which may affect the accessibility of organic matter C for microbes. Sieving and homogenizing soils in our study may have preferentially released protected forms of soil organic C from AM versus ECM soils, since AM fungi tend to produce stable organic matter through the formation of aggregates (Rillig *et al.* 2001), whereas ECM fungi increase soil C stabilization through the addition of recalcitrant root and fungal-derived organic matter (e.g. Clemmensen *et al.* 2013).

The addition of litter maintained the difference in C loss between AM and ECM soils only when the litter matched the mycorrhizal identity of soil. This pattern results from the high rate of soil respiration in AM soils and the stimulation of respiration from AM litter, suggesting that litters and soils had additive effects on decomposition. This finding contributes to the growing recognition that AM soils and ecosystems support greater rates of decomposition than do ECM soils and ecosystems (McGuire *et al.* 2010; Midgley, Brzostek & Phillips 2015). For example, leaf-litter decay is faster in AM- versus ECM-dominated forests (McGuire *et al.* 2010) and this difference can be amplified when AM litter is more labile than ECM litter (Midgley, Brzostek & Phillips 2015).

Our findings suggest that matching or mismatching the mycorrhizal identity of litter and soils has consequences on the biogeochemistry of plant–soil relationships. Litter C can incorporate into soils (Cotrufo *et al.* 2013), be lost to respiration, or even stimulate loss of existing organic matter C (i.e. priming effects; Fontaine, Mariotti & Abbadie 2003).

Table 3. Leaf and root litter chemistry from arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) tree species at Whitehall Forest

Species	Leaf C (%)	Leaf N (%)	Leaf C:N	Root C (%)	Root N (%)	Root C:N
AM	50.01 (0.37)	1.18 (0.12)a	43.57 (4.26)a	50.57 (1.37)	0.98 (0.19)	57.64 (10.82)
LITU	49.82 (0.18)	1.04 (0.01)	47.92 (0.45)	48.95 (0.21)	1.51 (0.01)	32.33 (0.34)
LIST	49.45 (0.07)	0.93 (0.01)	53.41 (0.52)	48.83 (0.26)	0.82 (0.01)	59.82 (0.31)
ILOP	51.09 (0.17)	1.44 (0.03)	35.55 (0.55)	54.62 (0.27)	0.64 (0.01)	84.91 (0.70)
JUVI	49.69 (0.11)	1.33 (0.02)	37.40 (0.54)	49.86 (0.06)	0.93 (0.01)	53.51 (0.41)
ECM	49.16 (1.85)	0.90 (0.07)b	56.21 (5.73)b	51.74 (0.34)	0.82 (0.03)	63.26 (2.16)
CATO	46.00 (0.02)	1.08 (0.02)	49.96 (1.06)	50.87 (0.07)	0.74 (0.01)	68.47 (0.41)
FAGR	46.83 (0.18)	0.92 (0.01)	43.55 (0.67)	52.48 (0.03)	0.90 (0.01)	58.40 (0.28)
QUAL	49.60 (0.08)	0.79 (0.01)	62.94 (0.65)	51.95 (0.20)	0.80 (0.02)	64.69 (1.57)
PITA	54.21 (0.04)	0.79 (0.01)	68.41 (1.01)	51.68 (0.09)	0.84 (0.03)	61.48 (2.38)

Values are means and (SE), where n = 5 for each species. Significant differences ($P < 0.05$) between mycorrhizal types, denoted by different letters Species codes: LITU, *Liriodendron tulipifera*; LIST, *Liquidambar styraciflua*; ILOP, *Ilex opaca*; JUVI, *Juniperus virginiana*; CATO, *Carya tomentosa*; FAGR, *Fagus grandifolia*; QUAL, *Quercus alba*; PITA, *Pinus taeda*.

Although we did not partition these individual processes, our findings indicate that mycorrhizal identity of litter and soils determined the extent of C loss. Matching litters and soils accentuated differences between mycorrhizal types, which may benefit the respective mycorrhizal strategies for N acquisition and tighten biogeochemical feedbacks between plants and soils (Wurzburger & Hendrick 2009). For instance, the N-mining capabilities of ECM fungal symbionts may be especially beneficial to hosts when litter inputs and soil organic matter are recalcitrant to decomposers. And in contrast, the N scavenging strategy of AM fungi may benefit hosts whose litter stimulates decomposition in soils. However, mismatching litter and soils may occur in mixed-mycorrhizal ecosystems, over succession or during species invasions, and may weaken these biogeochemical feedbacks.

In our study, AM litter stimulated respiration more so than ECM litter. While foliar chemistry can vary widely within mycorrhizal guilds globally (Koele *et al.* 2012), in temperate forests, dominant ECM tree species tend to produce more recalcitrant leaf litter than dominant AM tree species (e.g. Cornelissen *et al.* 2001; Phillips, Brzostek & Midgley 2013). Litter C:N explained the effect of litter mycorrhizal identity on soil respiration in our models, despite the fact we selected species as phylogenetically diverse as possible within our study system. The AM species of our study possessed lower leaf litter C:N than did the ECM species, but we did not observe a clear C:N pattern among root litters. In response to litter, respiration declined with increasing litter C:N, regardless of soil mycorrhizal identity and litter type. While root and leaf tissues clearly differed in their effect on respiration, our findings suggest that when new litter is added to existing soil organic matter, its C:N has a consistent negative effect on soil C loss.

The addition of leaf litter substantially increased heterotrophic respiration relative to root litter, despite the fact both increased the microcosm C pool by ~50%. This litter-type effect was not explained by differences in C:N and therefore must reflect compositional differences in leaves versus roots that promote, or suppress, microbial respiration. Indeed, previous work demonstrates that leaf and root litter decomposition are controlled by distinct chemical constituents (Hobbie *et al.* 2010). The diversity in morphological traits and chemistry of fine roots (Comas & Eissenstat 2009) and the abundance and type of mycorrhizal fungal biomass (Langley & Hungate 2003) may contribute to differences in root litter decomposition. In our study, the extent of mycorrhizal colonization did not explain the response of respiration to root litter addition; however, ECM roots produced lower respiration relative to AM roots, even after accounting for litter C:N. These findings suggest a chemical difference in AM and ECM roots that affects decomposition (e.g. Langley, Chapman & Hungate 2006; Fernandez & Koide 2014).

Our study demonstrates that AM and ECM trees differ in their indirect effects on organic matter decomposition. AM soils lost more C than ECM soils, and this difference was maintained with litter additions by matching the mycorrhizal identity of litter and soils. These findings suggest that mycorrhizal symbioses give rise to soil microbial communities that differ in composition (i.e. fungal versus bacterial biomass) or function (i.e. respiratory cost and N demand; Fierer *et al.* 2009). Our findings also raise the possibility that patterns of C loss result from differences in organic matter quality – a potential legacy of litter quality, decomposers and mycorrhizal fungi over the life span of a tree. While the balance of soil C ultimately depends on long-term patterns of inputs and losses, our study demonstrates key differences between mycorrhizal associations in decomposer behaviour and soil C loss, which may contribute to patterns in soil C among terrestrial ecosystems.

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Data accessibility

All data used are present in the manuscript and its supporting information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Microbial biomass (MB) and soil nutrient linear mixed-effects model estimates, and 95% confidence intervals (CI).

Table S2. Mixed-effect model estimates and 95% confidence intervals (CI) for soil respiration.

Table S3. Mycorrhizal colonization (% of root length) for arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) tree species at Whitehall Forest.

Figure S1. Heterotrophic respiration rate over the course of the 140 day lab incubation by soil mycorrhizal identity.

Figure S2. Heterotrophic respiration rate over the course of the 140 day lab incubation by soil and litter combinations.