ECOLOGY LETTERS

Ecology Letters, (2021) **24**: 626–635 doi: 10.1111/ele.13651

LETTER

Root-derived inputs are major contributors to soil carbon in temperate forests, but vary by mycorrhizal type

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Abstract

Roots promote the formation of slow-cycling soil carbon (C), yet we have a limited understanding of the magnitude and controls on this flux. We hypothesised arbuscular mycorrhizal (AM)- and ectomycorrhizal (ECM)-associated trees would exhibit differences in root-derived C accumulation in the soil, and that much of this C would be transferred into mineral-associated pools. We installed δ^{13}C-enriched ingrowth cores across mycorrhizal gradients in six Eastern U.S. forests (n = 54 plots). Overall, root-derived C was 54% greater in AM versus ECM-dominated plots. This resulted in nearly twice as much root-derived C in putatively slow-cycling mineral-associated pools in AM compared to ECM plots. Given that our estimates of root-derived inputs were often equal to or greater than leaf litter inputs, our results suggest that variation in root-derived soil C accumulation due to tree mycorrhizal dominance may be a key control of soil C dynamics in forests.

Keywords

Belowground carbon allocation, mycorrhizal association, rhizodeposition, root exudation.

Ecology Letters (2021) **24**: 626–635

INTRODUCTION

Plants allocate a substantial amount of carbon (C) belowground (Gill and Finzi, 2016), with important consequences for soil C storage. Root-derived inputs influence soil organic matter (SOM) dynamics by promoting soil C formation (Rasse *et al*., 2005; Clemmensen *et al*., 2013; Sokol and Bradford, 2019), stabilisation (Jackson *et al*., 2017) and turnover (Cheng and Kuzyakov, 2005). Thus, roots can both increase and decrease soil C stocks. Despite the critical role of roots in SOM dynamics, we know remarkably little about the magnitude of root-derived inputs, the factors that control these fluxes, and the consequences of root-derived inputs for soil C stabilisation owing to difficulties of tracking belowground inputs (Jones *et al*., 2009; Frey, 2019). Given the importance of soil C storage in regulating global C cycling and mitigating the effects of rising atmospheric CO_2, it is critical to constrain estimates of belowground C supply and understand the fate of root-derived C fluxes in heterogeneous ecosystems (Schmidt *et al*., 2011; Iversen *et al*., 2017).

While estimates of plant-derived C inputs to soil remain sparse, the total amount of C allocated belowground by plants is more commonly studied and can vary across climates, edaphic conditions and species (Gherardi and Sala, 2020). Previous work has revealed broad latitudinal patterns in total belowground C allocation, with 65% of GPP allocated belowground in boreal forests compared to only 30% in tropical forests. These patterns mirror soil N fertility gradients, with greater belowground C allocation occurring in ecosystems will low N availability (Gill and Finzi, 2016). Importantly, most estimates of belowground C allocation are derived primarily from measures of root production and likely underestimate other inputs such as allocation to mycorrhizal partners and root exudates which can be extremely difficult to quantify (Vicca, 2012; Gherardi and Sala, 2020). Within a single site, there is likely considerable variation in belowground C allocation and nutrient uptake (Keller and Phillips 2019a and b) due to interspecific variation in root architectural and morphological traits (Valverde-Barrantes *et al*., 2013), as well as mycorrhizal fungal community composition (Finlay and Clemmensen, 2017). Moreover, there is little evidence of a direct, linear relationship between root productivity and soil C accumulation, reflecting our poor understanding of the fate of belowground C allocation (Lajtha and Bowden, 2014; Jackson *et al*., 2017). Thus, the degree to which belowground C allocation predicts C accumulation in soil has not been tested but is critical to understanding plant community effects on ecosystem C cycling and feedbacks to climate.

Belowground C inputs from plants to soil are comprised of root turnover, root-associated fungal turnover and rhizodeposition (e.g. sloughed root cells, passive exudation and active secretion), making accurate quantitative estimates of this flux challenging (Pausch *et al*., 2012). Traditionally, root turnover has been estimated either using sequential coring or

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minirhizotron approaches, with the remaining rhizosphere C flux approximated using a mass balance approach (Fahey *et al*., 1999, 2005; Hendricks *et al*., 2006). Root exudation can be directly measured from roots in the field using the cuvette method, whereby living roots are excavated from the soil and exudates are captured *in situ* (Phillips *et al*., 2008). However, these methods are time and resource-intensive, necessitating simpler, time-integrated methods for estimating root-derived soil C inputs. The isotopic ingrowth core method takes advantage of the difference in $\delta^{13}C$ signatures between C_3 and C_4 plants (and consequently, the soils they are growing in), providing a quantitative estimate of root-derived soil C accumulation over the course of the study (Hoosbeek *et al*., 2004; Cotrufo *et al*., 2011; Martinez *et al*., 2016). As such, the isotopic ingrowth core method may provide a better estimate of root-derived C inputs compared to traditional methods.

Tree mycorrhizal association has been shown to be an integrative plant functional trait that links plant and soil properties (Phillips *et al*., 2013). In temperate forests, trees associate almost exclusively with one of two groups of mycorrhizal fungi – arbuscular mycorrhizal (AM) or ectomycorrhizal (ECM) fungi – and trait differences between groups could lead to variable root C inputs (Weemstra *et al*., 2016). Isotopic labelling of saplings have revealed greater rhizosphere C fluxes in AM trees (Wurzburger and Brookshire, 2017), in ECM trees (Phillips and Fahey 2005), and equivalent belowground C allocation (Keller and Phillips, 2019b). Similarly, field studies of mature trees have reported greater root C fluxes under ECM trees (Yin *et al*., 2014), under AM trees (Sun *et al*., 2017) , or no differences in fluxes between mycorrhizal types (Brzostek *et al*., 2013; Sun *et al*., 2017). Carbon fluxes from roots are often presumed to increase SOM turnover via priming effects (Cheng *et al*., 2014; Sulman *et al*., 2014), though root-derived inputs may also promote more SOM formation given their effects on microbial efficiency (Sokol and Bradford, 2019). At broad scales, AM-dominated forests tend to have greater soil C (Craig *et al*., 2018; Jo *et al*., 2019) than ECM-dominated soils, yet whether this pattern relates to differences in root C fluxes remains unresolved.

The amount of root-derived C that becomes part of the SOM pool may also differ between AM- and ECM-dominated stands. Labile tissues with fast decay promote greater microbial production, efficiency and turnover. In turn, these products generated during microbial decay are thought to contribute disproportionately to slow-cycling soil organic C pools by forming associations with reactive silts and clays (Grandy and Neff, 2008; Schmidt *et al*., 2011; Kallenbach *et al*., 2016). Accordingly, larger mineral-associated organic matter (MAOM) pools have been measured in AM systems (characterised by fast litter decay) compared to ECM systems (Craig *et al*., 2018; Cotrufo *et al*., 2019). This pattern suggests plant mycorrhizal type may be critical in determining stabilisation of soil C. However, most of the empirical and theoretical work documenting these patterns (Sulman *et al*., 2017; Zhu *et al*., 2018; Jo *et al*., 2019) is premised on the idea that leaf litter quality differences between AM and ECM trees drive this pattern (Keller and Phillips, 2019a). This is in contrast to recent work showing that roots may be the primary source of slow-cycling mineral-associated soil C (Sokol and Bradford, 2019). Thus, there is a critical need to directly test whether tree mycorrhizal dominance affects belowground C inputs, and whether such differences contribute to MAOM formation patterns.

To this end, we measured total root-derived soil C accumulation and root ingrowth across nine-plot gradients of increasing ECM tree dominance within six temperate forests. We asked (1) what is the magnitude of root-derived soil C accumulation? (2) how does root-derived soil C accumulation vary across gradients of ECM tree dominance and (3) what is the contribution of root-derived C to the formation of mineral-associated soil C? We hypothesised that root-derived C accumulation would vary between plot mycorrhizal type and that such mycorrhizal type differences would be magnified in MAOM pools.

METHODS

Site descriptions and experimental design

To examine plant mycorrhizal type and soil type controls on belowground C fluxes in temperate forests, we worked in six eastern U.S. temperate forests within the Smithsonian Forest Global Earth Observatory (ForestGEO) network (Anderson-Teixeira *et al*., 2015): Harvard forest (HF), Lilly-Dickey Woods (LDW), the Smithsonian Conservation Biology Institute (SCBI), the Smithsonian Environmental Research Center (SERC), Tyson Research Center (TRC) and Wabikon Lake Forest (WLF) (Table S1) (Mushinski *et al*., 2020). At each of the six sites, we established nine 20 m × 20 m plots spanning a gradient of ECM tree dominance (by basal area) for a total of 54 plots. At each site, the plots with the three lowest and three highest ECM tree dominance were designated as AM and ECM 'end-member' plots respectively. The remaining three plots per site were designated as AM/ECM 'mixed' plots. Across sites, mean % dominance by basal area of the dominant mycorrhizal type was 88% and 91% AM and ECM canopy trees, respectively. The sites vary in climate, soil type and plant species composition but each host a diversity of AM and ECM-associated canopy tree species (Tables 1 and 2). To measure variation in plant species composition across plots, we calculated Shannon's diversity index (H) by basal area for each plot.

Ingrowth cores

In each plot, we installed five rigid plastic mesh root ingrowth cores (inner diameter 5.77 cm, hole size 0.55 cm, height 15 cm; Industrial Netting product #RN4465), hereafter referred to as 'ingrowth cores', as well as two PVC cores that were impermeable to root and fungal ingrowth, that is 'control cores'. This hole size was selected to allow for acquisitive root foraging into the cores while retaining soil within the core. Cores were randomly placed throughout the plot to 15 cm depth. The top and bottom of each ingrowth core was covered with window-screen mesh, whereas the control cores were covered with 1-micron mesh to prevent root and fungal ingrowth. Cores were left in the field for two full growing seasons (Spring 2017 – Fall 2018).

Table 1 Soil classification and most dominant AM- and ECM-associated tree species at each site

Site	Predominant soil type	Dominant AM trees	Dominant ECM trees
HF	Oxyaquic Dystrudepts	*Acer rubrum*, *A. saccharum, Fraxinus americana*	*Pinus strobus, Tsuga canadensis*
LDW	Typic Dystrudepts and Typic Hapludults	*A. saccaharum*, *Liriodendron tulipifera*	*Quercus montana*, *Q. rubra*
SCBI	Typic Hapludalfs	*L. tulipifera*	*Q. alba*, *Q. rubra*, *Q. veluntina*
SERC	Typic Hapludults and Aquic Hapludults	*Liquidambar styraciflua*, *L. tulipifera*	*Fagus grandifolia*, *Q. alba*
TRC	Typic Hapludalfs and Typic Paleudalfs	*F. americana*, *Ulmus rubra*	*Q. alba*, *Q. rubra*, *Q. velutina*
WLF	Alfic Haplorthods	*A. saccharum*, *F. americana*	*Betula alleghaniensis*, *T. americana*

Table 2 Site properties (± 1SD; $n = 9$) at Harvard Forest (HF), Lilly-Dickey Woods (LDW), Smithsonian Conservation Biology Institute (SCBI), Smithsonian Environmental Research Center (SERC), Tyson Research Center (TRC) and Wabikon Lake Forest (WLF)

Site	MAP* (mm yr^{-1})	Sand-Silt-Clay† (%)	Soil pH‡	Soil C mg g $soil^{-1}$	Soil C:N	N min§ (μg N g^{-1} day^{-1})	Shannon's H	Consistent O-horizon?
HF	1050	63-29-8	3.7 (0.4)	131 (63)	21 (4)	0.66 (0.68)	1.03 (0.5)	Y
LDW	1203	15-76-9	4.4 (1.0)	43 (22)	16 (4)	1.08 (0.4)	0.87 (0.5)	N
SCBI	1001	26-60-14	5.2 (1.0)	34 (7)	14 (3)	0.63 (0.3)	1.12 (0.5)	N
SERC	1068	50-35-15	4.1 (0.8)	26 (4)	13 (1)	0.26 (0.3)	1.06 (0.3)	N
TRC	957	9-82-9	5.6 (0.6)	34 (9)	14 (2)	0.77 (0.4)	1.57 (0.3)	N
WLF	805	37-56-7	4.8 (0.5)	81 (32)	14 (2)	1.19 (1.2)	1.18 (0.3)	Y

*Anderson-Teixeira *et al.*(2015).
†Determined via a standard hydrometer procedure, measured on 5–15 cm soils to avoid organic-rich upper horizon.
‡Measured in 0.01 M $CaCl_2$ solution.
§Measured with 2M KCl extraction, extracts analysed using Lachat QuikChem 8000 Flow Injection Analzyer (Lachat Instruments, Loveland, Colorado, USA).

To quantify plant-derived belowground C inputs to the soil, we used a dual ingrowth-core isotopic technique similar to Panzacchi *et al.* (2016). Each ingrowth core was filled with a C_4 soil/sand mixture (50:50 by volume) to reduce soil compaction, increase detectability of root-derived C inputs and enhance root recovery from ingrowth core soils following harvest. The soil was obtained from an agricultural field at the University of Illinois Energy Farm (40° 03' 046" N, 88° 11' 046" W) where soils are silt-loam Arguidolls. The field had been under a corn-soy rotation for > 100 years, with corn planted most years including the year prior to soil collection. Given that corn is a C_4 plant, the initial soil carried a $\delta^{13}C$ signature of −16.0 ± 0.15 (mean ± SE, $n = 6$), which was significantly enriched in ^{13}C compared to the C_3 root material recovered from the ingrowth cores at the end-member sites (see below) (−28.7 ± 0.15 across all sites, $n = 54$). Surface soils from the farm were collected and transported to the laboratory for ingrowth core preparation. There, soils were sieved to 4mm and organic debris removed. Soils were mixed with carbonate-free sand in a 50:50 ratio by volume and refrigerated until deployment. MAOM % C and $\delta^{13}C$ of the initial sand: soil mix (see below for methodology) were 2.05% and −17.55, respectively. Initial MAOM-C pool size was 0.72 g g^{-1} soil.

At the beginning of the growing season at each site, ingrowth and control cores were installed in each of the 54 plots. At each core location, a soil core of equal diameter to the ingrowth core was taken, soil was removed and replaced by an ingrowth (or control) core filled with the C_4-soil/sand mixture. Care was taken to minimise disturbance of the surrounding soil to prevent significant air gaps between the installed core and forest soil. After two full growing seasons, cores were carefully extracted and transported back to the laboratory for processing.

Roots were removed from each soil core by hand (discarding dead roots), washed, dried at 60 °C for 48 h and weighed to 0.0001 g. The C_4 soil from each core was air-dried, ground and analysed for total C, N and $\delta^{13}C$. While we measured root biomass in all ingrowth cores, only a subset of root samples was analysed for total C, N and $\delta^{13}C$. Specifically, we used roots from all cores in one AM and one ECM end-member plot from each site ($n = 12$). This assumes root $\delta^{13}C$ is conserved across plots for a given mycorrhizal type (i.e. AM or ECM) within a given site. Root tissue and C_4 soil subsamples were ground to a powder using a 2010 GenoGrinder (SPEX® SamplePrep) and analysed for total C and $\delta^{13}C$ using an elemental analyser coupled to a gas-isotope ratio mass spectrometer. Root and C_4 soil samples were analysed at two facilities (the Purdue Stable Isotope Facility with a PDZ Europa Elemental Analyzer coupled to a Sercon 20-22 IRMS, and the BayCEER Laboratory of Isotope Biogeochemistry with a Carlo Erba 1108 Elemental Analyzer coupled to a delta S Finnigan MAT). A subset of samples was analysed at both facilities, confirming the two facilities reported comparable results ($R^2 = 0.96$). Isotope ratio values were expressed with the delta notation (δ):

$$\delta^{13}C‰ = [(R_{sample}/R_{standard} - 1) \times 1000].$$

where R_{sample} and $R_{standard}$ are the ^{13}C: ^{12}C sample and standard ratios, respectively, and $R_{standard}$ is referenced to the Vienna Pee Dee Belemnite (VPDB).

Quantifying belowground C inputs

We quantified root ingrowth as the total root mass recovered within a given core after two years. Fine roots of temperate trees typically turn-over in one year (McCormack *et al*., 2015), and thus roots recovered in the ingrowth cores likely resulted from one and not two years of production, although we acknowledge specific root (and fungal) turnover times likely differ among plots and sites (Withington *et al*., 2006; Mccormack and Guo, 2014; McCormack *et al*., 2014). Consequently, we did not divide our estimates of fine root ingrowth by two. However, we acknowledge our root ingrowth values reflect the balance between root production and root turnover over a 2-year period. We quantified root-derived C accumulation into each core using a two-pool mixing model following Panzacchi *et al*. (2016). Broadly, as C_3 rhizodeposits are incorporated into the C_4 soil core, the $\delta^{13}C$ signature of the C_4 soil becomes more similar to that of the C_3 root-derived inputs. This change in $\delta^{13}C$ of the ingrowth core soil can be used to calculate total root-derived C inputs into the core.

First, the fraction of soil C derived from root inputs (F_{rd}; unitless) was calculated using a two-end member mixing model:

$$F_{rd} = (\delta^{13}C_{ingrowth} - \delta^{13}C_{control})/(\delta^{13}C_{root} - \delta^{13}C_{control}) \quad (1)$$

where $\delta^{13}C_{ingrowth}$ is the $\delta^{13}C$ of C_4 soil collected from individual ingrowth cores after two years in the field and $\delta^{13}C_{control}$ is the average $\delta^{13}C$ of C_4 soil collected from two PVC control cores from the same plot as the ingrowth core after two years in the field. We estimated root $\delta^{13}C$ for AM/ECM 'mixed' plots as a weighted average (based on aboveground basal area) of site-specific AM and ECM $\delta^{13}C$ values. For any given plot, $\delta^{13}C_{root}$ was estimated as the mean $\delta^{13}C$ for a given mycorrhizal plot-type at a given site, acknowledging this assumes mixed plots represent the 'average' of the two mycorrhizal types. The net root-derived C inputs ($C_{rd\text{-}net}$; g C m^{-2}) into surface soils (0-15 cm) was calculated as:

$$C_{rd-net} = \rho * [C] * F_{rd} * 150,000 \quad (2)$$

where ρ is the initial C_4 soil bulk density (g cm^{-3}), [C] is the C concentration (%) of the core after 2 years in the field and following removal of roots, and 150 000 is the conversion factor to transform % C to g C m^{-2} to a depth of 15 cm. Bulk density (1.21 g/cm^{-3}) was measured on the initial C_4 soil: sand mixture and is thus constant across all plots. To estimate an annual net flux (for comparison to annual aboveground net primary production), we divided root-derived C by the number of years cores were in the field (i.e. two years at all sites).

Soil MAOM fraction

We separated the MAOM fraction from the bulk soil to evaluate mechanisms underlying the persistence of root-derived C in ingrowth cores. Due to costs, we selected three of the six sites (HF, LDW, SERC) and processed all samples from the six end-member plots at each site. For each sample, we used a standard size fractionation procedure (Cambardella and Elliott, 1992). Briefly, we dispersed 10 g soil samples in 30 mL of 5% (w/v) sodium hexametaphosphate for 20 h on a reciprocal shaker at 180 rpm and washed slurries through a 53-um sieve using a stream of DI water. The fine fraction that passed through the sieve was considered MAOM. The MAOM fraction was dried (80 °C), weighed and ground to a powder. The MAOM fraction was analysed for C concentrations and $\delta^{13}C$ at the Purdue Stable Isotope Facility as described above. Root-derived MAOM-C (MAOM-C_{rdc}; mg MAOM-C/g bulk soil) was then calculated as:

$$\text{MAOM-}C_{rdc} = \frac{\text{MAOM} - \text{C(mg)}}{\text{bulk soil(g)}} * F_{rd}. \quad (3)$$

Site means for bulk soil, MAOM soil and root %C and $\delta^{13}C$ are presented in Table S2. MAOM-C pool sizes for control and experimental controls are presented in Table S3.

Aboveground litter mass estimates

Plot-specific litter mass was measured in 2017 at all plots. Specifically, two to three litter collectors were placed in each plot, covering a total average area of *c*. 0.5–1.0 m^{-2} per plot. All litter, including leaves, woody debris and reproductive material, was collected two to three times over the course of senescence. Litter was dried at 60 °C for at least 72 h and then weighed to 0.01 g. Plot litter mass C inputs were calculated as the total mass of all litter collected in a given plot in 2017 and converted to units C using a 0.47 conversion factor for biomass to C (Fahey and Knapp, 2007). We acknowledge litterfall mass can vary across years. Still, our field-based observations suggest litterfall at our sites was not subject to extreme events (e.g. drought, pathogen outbreak) in 2017, and thus we are confident these data serve as a useful comparative metric in relation to the magnitude of our belowground C data.

Data analysis

We used multiple linear regression to assess the effects of site, ECM dominance and the interaction between the two on root-derived C or root ingrowth separately. To focus on differences between AM and ECM-dominated plots, we also conducted two-way ANOVA tests using just the six end-member plots (AM or ECM-dominated). Site, plot type and the interaction between the two were included as fixed factors and root ingrowth or root-derived C were dependent variables. In the case of root-derived C and MAOM-C, no significant interaction between site and plot type was observed and the interaction was subsequently excluded from the model. Student's t-tests were used to assess global plot type differences. Tukey's post hoc tests were used to evaluate pair-wise differences in each case. To assess how plant diversity, edaphic and climate factors affect root-derived C accumulation, we also fit a linear mixed model (*lme*() in the *nlme*() package) predicting root-derived C with % ECM, Shannon's diversity index, soil pH, soil % clay, soil N mineralisation rates (0–5 cm) and MAP included as fixed factors and site included as a random intercept. Multiple linear regression and linear mixed model results are presented in Table S2–S4. All analyses were carried out using R version 3.6.1 (R Core Team, 2019).

RESULTS

Across six temperate forests, we quantified total root-derived C accumulation and root ingrowth in 54 plots spanning a gradient of AM-associated vs. ECM-associated tree dominance. Overall, we found that both total root-derived soil C and root-derived MAOM-C were greater in AM-dominated plots, whereas root ingrowth was greatest in ECM-dominated plots. Importantly, annual root-derived soil C accumulation was greater than aboveground litter mass C inputs, highlighting the importance of this often poorly quantified component of ecosystem C budgets.

Root-derived C inputs

Root-derived C accumulation showed a weak, but significant, negative relationship with ECM dominance at the plot-level (Fig. 1a; $R^2 = 0.09$, $P = 0.013$), and ECM dominance and site together predict root-derived C ($R^2 = 0.30$, $P = 0.004$; Table S4). There was no significant relationship between root-derived C accumulation and root ingrowth (Fig. 1b). Moreover, using linear mixed modelling (site included as a random intercept), we found no significant relationship between root-derived C and plant diversity (Shannon's diversity index), edaphic (soil pH, % clay, soil N mineralisation rates), or climate factors (MAP) (Table S6). Comparing the three most AM-dominated and three most ECM-dominated plots only (i.e. 'end-member plots'), root-derived C was greater in AM plots compared to ECM plots across sites ($F_{1,29} = 5.33$, $P = 0.028$) with no statistically significant difference among sites (Fig. 2a). The highest root-derived C inputs were observed in AM plots at HF (715 ± 258 g C m^{-2} $year^{-1}$), whereas the lowest C inputs were observed in ECM plots at TRC (212 ± 52.7 g C m^{-2} $year^{-1}$). Annual root-derived C generally exceeded aboveground litter mass C inputs (Fig. 3; Figure S1). The ratio of annual root-derived C: litter mass C was significantly predicted by site ($F_{5,29} = 3.60$, $P = 0.012$) and plot mycorrhizal type ($F_{1,29} = 7.20$, $P = 0.012$), with no significant interaction between site and mycorrhizal type. The amount of root-derived C recovered in MAOM pools was greater in AM compared to ECM plots ($P = 0.041$; Fig. 4). There was no site or site × plot type effect on root-derived MAOM-C (Table S5).

Root ingrowth

In contrast to the patterns observed with root-derived C inputs, root ingrowth was strongly predicted by site and (to a lesser extent) ECM dominance, with a significant site × ECM dominance interaction ($R^2 = 0.72$, $P < 0.001$; Table S6). Comparing the end-member plots only, root ingrowth varied significantly both by plot mycorrhizal type ($F_{1,24} = 4.66$, $P = 0.041$) and among sites ($F_{5,24} = 15.19$, $P < 0.001$; Fig. 2 b). Overall, root ingrowth was greater in ECM-dominated plots compared to AM-dominated plots. The highest root ingrowth was observed in ECM plots at HF (172 ± 34.2 g C m^{-2} $year^{-1}$), whereas the lowest root ingrowth was observed in ECM plots at SCBI (16.4 ± 1.13 g C m^{-2} $year^{-1}$). While there were no significant pairwise differences between plot mycorrhizal types within a given site, mean root ingrowth values were higher in ECM compared to AM plots at four of the six sites: HF, LDW, SERC and TRC.

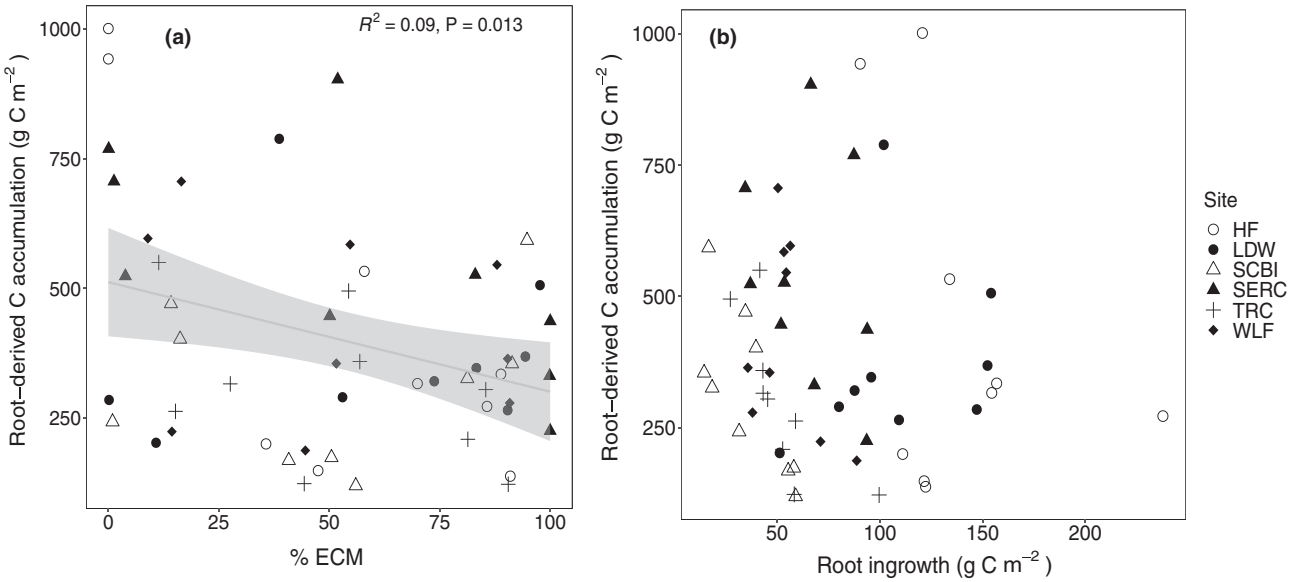

Figure 1 Patterns of root-derived C accumulation related to (a) % ECM tree dominance (by basal area) of the plot and (b) root ingrowth. Each point represents one plot, with distinct sites depicted with different shaped points. Sites include Harvard Forest (HF), Lilly-Dickey Woods (LDW), Smithsonian Conservation Biology Institute (SCBI), Smithsonian Environmental Research Center (SERC), Tyson Research Center (TRC) and Wabikon Lake Forest (WLF). There is a weak negative relationship between root-derived C accumulation and plot % ECM (bivariate relationship: $R^2 = 0.09$, $P = 0.013$) but no relationship between root-derived C accumulation and root ingrowth at a given plot. Significant linear regression shown with shaded 95% confidence interval.

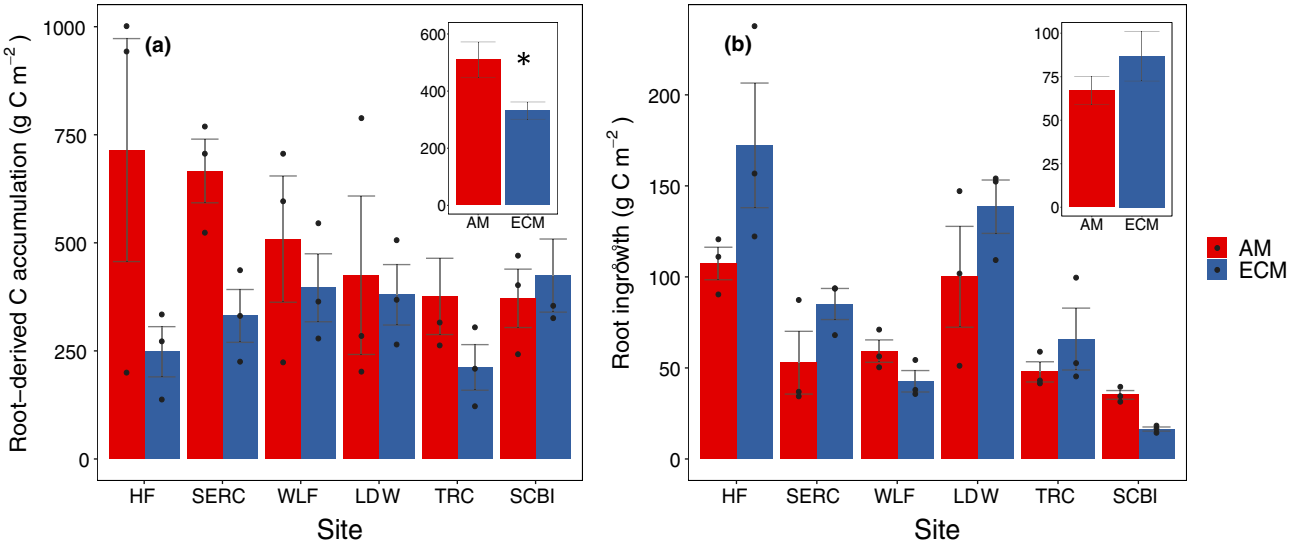

Figure 2 (a) Root-derived C accumulation and (b) root ingrowth related to plot mycorrhizal type. Bars represent means (with standard error bars shown) for the AM-dominated (red) and ECM-dominated (blue) end-member plots at each site. Sites include Harvard Forest (HF), Lilly-Dickey Woods (LDW), Smithsonian Conservation Biology Institute (SCBI), Smithsonian Environmental Research Center (SERC), Tyson Research Center (TRC) and Wabikon Lake Forest (WLF). Insets show AM vs. ECM cross-site means, with * indicating significant difference between mycorrhizal types for root-derived C accumulation ($P = 0.016$). Mycorrhizal type, but not site or the interaction between mycorrhizal type and site, significantly predicted root-derived C accumulation (panel a; $P = 0.014$). Mycorrhizal type and site significantly predicted root ingrowth (panel b; $P = 0.04$ and $P < 0.001$ respectively), whereas the interaction between mycorrhizal type and site was marginally significant ($P = 0.09$). There were no significant pairwise differences between mycorrhizal types for any site in either panel a or b.

DISCUSSION

Nearly half of all primary production enters the soil via roots (Gherardi and Sala, 2020), yet we poorly understand the factors governing how these inputs affect SOM formation and stabilisation. Using an isotopic ingrowth core technique, we quantified root-derived soil C accumulation (in the bulk soil and MAOM fraction) and root ingrowth across gradients of ECM-associated tree dominance in six temperate forests. We found that root-derived C accumulation does not mirror root ingrowth patterns, with greater root-derived C in AM- compared to ECM-dominated plots yet greater root ingrowth in ECM (rather than AM)-dominated plots (Fig. 2). We also recovered more root-derived inputs in the MAOM fraction in AM compared to ECM plots (Fig. 4). Finally, our results highlight the impressive magnitude of root-derived C inputs (199.5 ± 14.7 g C m^{-2} y^{-1}) as compared to leaf litter inputs (168.8 ± 10.77 = g C m^{-2} y^{-1}), emphasising the importance of adequately characterising this plant-to-soil C flux in order to understand how tree community composition influences ecosystem C cycling (Fig. 3).

Given that root ingrowth did not predict root-derived soil C in our study, and that mycorrhizal production is typically greater in ECM plots (Cheeke et al. *in press*), greater root and/or fungal production most likely do not explain the greater root-derived C accumulation in AM plots. Importantly, our measure of root-derived soil C accounts for all root and fungal inputs plus rhizodeposition that persisted in soil after 2 years. Data quantifying rhizodeposition are less abundant, and previous work has found that exudation can be greater in ECM stands (Yin *et al.*, 2014), greater in AM stands (Sun *et al.*, 2017), or similar between mycorrhizal types (Brzostek *et al.*, 2013; Sun *et al.*, 2017). Our results suggest that rhizodeposition may be greater in AM-dominated plots, at least across four of our six sites. While it's possible that ECM roots and fungi, which can accelerate root (Li *et al.*, 2015) and organic matter (Jacobs *et al.*, 2018) decomposition, may have contributed to this pattern, such priming effects are unlikely to account for the root C accumulation patterns in our study. This is because our mixing model accounted for changes in soil C within each core. Thus, greater root inputs in AM soils, as opposed to greater losses in ECM soils, likely drove the greater root-derived C accumulation in the AM-dominated soils.

Additionally, mycorrhizal type differences in root and fungal turnover between AM and ECM trees may contribute to the greater root-derived C in AM plots. AM root litter (See *et al.*, 2019; Jiang et al. 2020) tends to decay more quickly than that of ECM plants, and faster turnover rates of these tissues would result in greater total root-derived C inputs in AM plots when measured over multiple phenological cycles. Mycorrhizal type differences in root turnover may also explain, to some degree, the lack of relationship between root-derived C accumulation and root ingrowth. Turnover of AM fungi can exceed that of ECM fungi by an order of magnitude (Staddon *et al.*, 2003; Tedersoo and Bahram, 2019, but see Schäfer *et al.*, 2019). Differences in fungal turnover rates between mycorrhizal types may be particularly important in driving root-derived soil C accumulation as fungal inputs to soil C have been shown to exceed that of both leaf and root litter (Godbold *et al.*, 2006). The greater recovery of root-derived C in AM soils also reflects mycorrhizal-associated

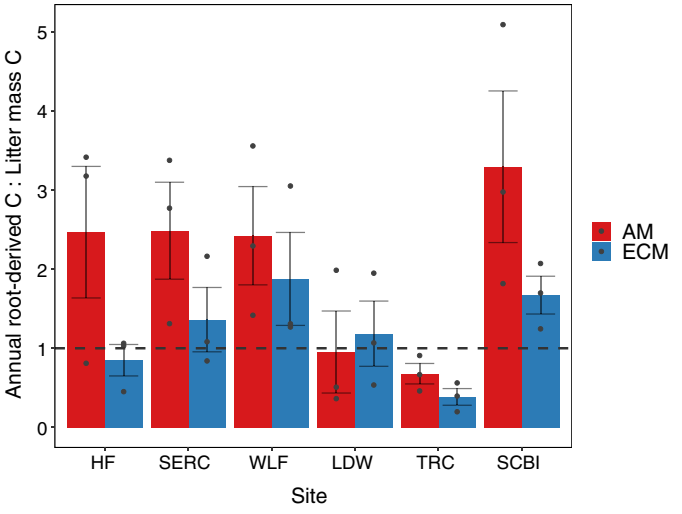

Figure 3 Ratio of annual root-derived C accumulation to annual aboveground litter mass C at the plot level for the AM (red) and ECM (blue) end-member plots at each site. Sites include Harvard Forest (HF), Lilly-Dickey Woods (LDW), Smithsonian Conservation Biology Institute (SCBI), Smithsonian Environmental Research Center (SERC), Tyson Research Center (TRC) and Wabikon Lake Forest (WLF). The 1:1 line is shown as a dashed grey line for reference. Bars represent plot-level means (with standard error bars shown) for each mycorrhizal type at each site. Site and mycorrhizal type (but not the interaction between the two) significantly predicted annual root-derived C accumulation: litter mass C ($P = 0.003$).

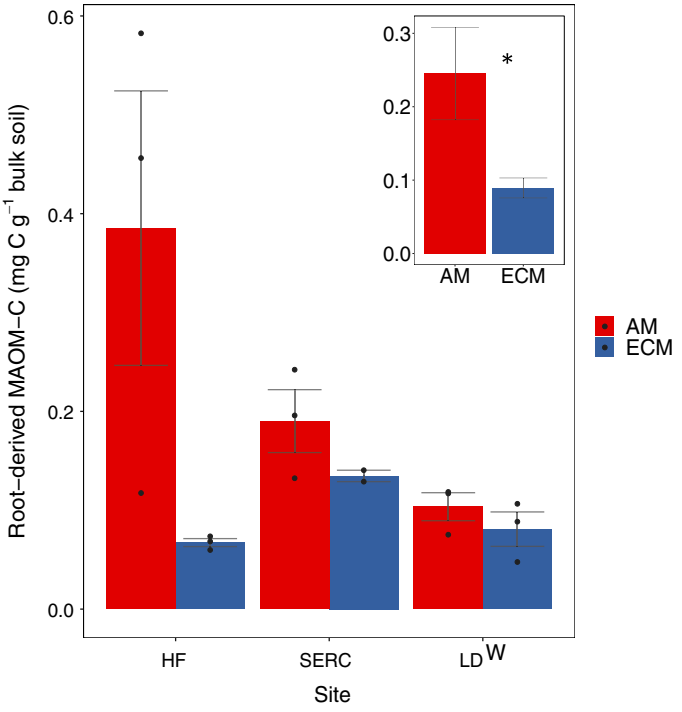

Figure 4 Mean root-derived MAOM-C (mg C/ g bulk soil) for the three AM-dominated (red) and three ECM-dominated (blue) end-member plots at three sites with standard error bars ($n = 3$ for each group). Mycorrhizal type ($P = 0.04$) significantly predicted plot-level root-derived MAOM-C, and the inset shows cross-site differences in AM vs. ECM mean root-derived MAOM-C across all sites. * Indicates significant differences between mycorrhizal types ($P < 0.05$). Sites include Harvard Forest (HF), Lilly-Dickey Woods (LD) and Smithsonian Environmental Research Center (SERC).

differences in soil organic matter formation pathways. Whereas plant inputs to ECM soils tend to accumulate in organic horizons or particulate C pools, there is increasing evidence that AM systems transfer greater amounts of plant-derived C into mineral-associated forms (Cotrufo *et al.*, 2019) and our results support this idea (Fig. 4). Faster decomposition of AM inputs should lead to more microbial products that are precursors to MAOM formation (Cotrufo *et al.*, 2015). To the extent that MAOM cycles slowly and protects C from microbial decomposers (Grandy and Neff, 2008, Bradford *et al.*, 2013, but see Jilling *et al.*, 2018), this could explain the greater root-derived C accumulation in both the bulk soil and MAOM fraction in AM compared to ECM soils. It is also worth noting that AM fungi promote aggregation and stimulate particulate organic matter formation (Rillig, 2004). Thus, future work is warranted to elucidate mycorrhizal group differences on micro- and macro-aggregate stability and slow-cycling particulate organic matter pools (Fernandez and Kennedy, 2015; Rillig *et al.*, 2015).

Our ingrowth core method controlled for edaphic differences (cores were filled with a uniform soil matrix across all plots and sites) and thus differences in soil C cycling dynamics driven by edaphic factors were minimised, although microbial communities within cores may have shifted over the course of the experiment. However, soil C cycling is also driven by distinct plant and microbial traits that can alter both soil C stabilisation and destablisation (Cheng and Kuzyakov, 2005; Schmidt *et al.*, 2011). AM fungi are known to produce an aggregate-promoting glycoprotein (Rillig, 2004), whereas ECM fungi have greater oxidative enzyme capacity to destabilise SOM (Shah *et al.*, 2016). Likewise, differences in mycorrhizal taxa, which can vary across edaphic gradients (Zak *et al.*, 2019), could explain site differences in the magnitude of the mycorrhizal effect among our sites, though this remains an open question. Thus, the observed inverse relationship between root-derived soil C and ECM dominance (Fig. 1a) may not only reflect differences between mycorrhizal types in their input chemistry, but also reflect their capacity to destabilise SOM to acquire nutrients.

Our estimates of root-derived C accumulation across all sites (199 g m^{-2} y^{-1}) are similar in magnitude to studies that used the isotopic ingrowth core technique. In an ECM-dominated 130-year old forest, Martinez *et al.* (2016) estimated root-derived C inputs to be 303 g m^{-2} y^{-1} and Panzacchi *et al.* (2016) reported a similar rate (309 g m^{-2} y^{-1}) in a young hardwood plantation. Moreover, annual root-derived C accumulation was larger on average than leaf litter inputs (Fig. 3; Figure S2), and of a similar magnitude to estimates of aboveground net primary productivity at similar sites (Newman *et al.*, 2006; Keeling and Phillips, 2007; Finzi, 2020). This highlights the importance of belowground C fluxes, and suggests that ecosystem models that presume leaf litter inputs drive soil C dynamics may lead to inaccurate projections of SOM responses to global change.

The isotopic ingrowth core technique has limitations and several assumptions are worth noting. For one, root-derived C accumulation is an operationally defined pool that includes decaying roots, hyphae and rhizodeposits. Thus, our estimates are not easily compared with other estimates of rhizosphere C fluxes. Second, the process of severing roots during core installation may have reduced roots and fungal production (Vogt *et al*., 1998; Hendricks *et al*., 2006; Addo-Danso *et al*., 2016), suggesting our estimates of root-derived C may be conservative. Likewise, ingrowth cores can favour thin-rooted species (Chen *et al*., 2018), which rely less on mycorrhizal fungi for foraging than thick-rooted species (Eissenstat *et al*., 2015; Chen *et al*., 2016), which would reduce rhizodeposition inside the cores compared to field soil. On the other hand, the soil matrix inside the cores differed from forest soils (e.g. less N), which may have increased mycorrhizal proliferation (Eissenstat *et al*., 2015; Liu *et al*., 2015). Third, some dissolved organic C (DOC) may have moved laterally into the experimental but not the solid PVC control cores, elevated estimates of root-derived C. However, this effect was likely minimal, as lateral flows of DOC are typically minor relative to root C fluxes (Michalzik *et al*., 2001).

Overall, our results suggest the magnitude of root-derived soil C inputs is large and can vary significantly across sites and mycorrhizal types. Importantly, we show direct evidence that plant mycorrhizal types differ in their effects on putatively stable mineral-associated SOM pools via differences in root and fungal activities. As eastern forests shift in their relative abundance of AM versus ECM trees (Jo *et al*., 2019), changes in SOM dynamics might also occur. Accurate predictions of ecosystem C cycling in ecosystem and land surface models depend on improved quantification of the belowground C flux from plants to soil C pools, and improved understanding of the factors that control soil C stabilisation. Our results suggest that better estimates of root and fungal contributions to stable SOM pools are needed in order to better understand how vegetation shifts can affect ecosystem C cycling now and in the future.

ACKNOWLEDGEMENTS

We thank the ForestGeo network and the following individuals and their support teams for access to the sites: Dave Orwig (HF), Bill McShea (SCBI), Sean McMahon (SERC), Michael Chitwood (LDW), Jonathan Myers (TRC) and Amy Wolf (WLF). We acknowledge the IU Research and Teaching Preserve (RTP) which includes LDW. We acknowledge and honor the Indigenous communities native to this region, and recognize that IU RTP lands are part of Indigenous homelands and resources. We recognize the Miami, Delware, Potawatomi, and Shawnee people as past, present, and future caretakers of this land. We are grateful to members of the Phillips and Brzostek labs for assistance in the field, and are especially grateful to Elizabeth Huenupi for her efforts in both the field and the lab. Michael Masters enabled collection of corn soil, and Peter Sauer and Janine Sparks assisted with the isotope analyses. We are grateful to members of the Phillips and Brzostek labs for assistance in the field. Funding was provided by the U.S. Department of Energy Office of Biological and Environmental Research, Terrestrial Ecosystem Science Program (Award # DESC0016188), Center for Tropical Forest Science – ForestGEO, and the United States Department of Agriculture, National Institute of Food and Agriculture (no. 2019-67011-29507). JBF contributed to this research from the Jet Propulsion Laboratory, California Institute of Technology, under a contract with the National Aeronautics and Space Administration. MEC contributed to this research from Oak Ridge National Laboratory which is operated by UT-Battelle, LLC, under contract DE-AC05-00O $R^2$2725 with the U.S. Department of Energy.

AUTHORS' CONTRIBUTIONS

All authors contributed to planning the study. ABK, EB and MEC conducted the field work. ABK carried out the laboratory analyses and wrote the first draft of the manuscript. All authors provided feedback on the final manuscript draft.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13651.

DATA AVAILABILITY STATEMENT

Upon acceptance, data from this manuscript will be archived in Figshare (https://doi.org/10.6084/m9.figshare.13212308.v1).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Johannes Knops
Manuscript received 18 May 2020
First decision made 5 November 2020
Manuscript accepted 9 November 2020