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Rapid fine root C and N mineralization in a northern temperate forest soil

F. Santos · K. Nadelhoffer · J. A. Bird

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Abstract While fine roots (≤2-mm diameter) are major suppliers of carbon (C) and nitrogen (N) to northern temperate and boreal forest soils, our understanding of how long-term plant and N inputs affect fine root decomposition rates and the amount of root-derived organic matter (OM) stabilized in forest soils is incomplete. We examined the influence of long-term aboveground and/or belowground litter and inorganic N additions on mineralization and vertical transport of fine root-derived C and N during the first 2 years of decomposition of dead fine root in the field. We used an existing long-term field manipulation experiment located in a northern Michigan forest; with (i) exclusion of above and below-ground inputs, (ii) exclusion of belowground inputs alone, or (iii) inorganic N additions, for 6 years prior to the addition of dual-labeled (^{13}C and ^{15}N) *Acer rubrum* fine roots. After 2 years in soil, labeled fine roots rapidly decomposed in all treatments, with only 20.7 % of root ^{13}C and 35.8 % of root ^{15}N recovered in soil (0–20 cm depth). This was likely because of the combined effects of (1) root litter chemistry, (2) processing of root litter by exotic earthworms, and (3) the low stabilization potential of the coarse-textured soil at the site. Neither the long-term exclusion of litter inputs nor increased inorganic N additions influenced root mineralization rates; and there were no detectable effects of either treatment on CO_2 efflux or on dissolved organic C loss. During the 2-year study, exclusion of litter inputs did not affect root C retention in soil but lowered C:N ratios of roots recovered in that treatment. Inorganic N additions had no significant effect on root-derived C or N retention in the soil. Our results show that fine root litter turns over faster than previously thought in coarse-textured temperate forests soils that lack effective OM stabilization mechanisms.

Keywords ^{13}C · ^{15}N · DIRT · Fine roots decomposition · Litter manipulation treatments · Soil organic matter

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F. Santos
School of Natural Sciences, University of California, Merced, CA 95343, USA

K. Nadelhoffer
Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA

J. A. Bird (✉)
School of Earth and Environmental Sciences, Queens College, City University of New York, Flushing, New York, NY 11367, USA
e-mail: jbird@qc.cuny.edu

J. A. Bird
The Graduate Center of the City University of New York, New York, NY 10016, USA

Abbreviations

DIRTs	Detritus input and removal treatments
DOC	Dissolved organic carbon
NRs	No roots
NIs	No inputs
OM	Organic matter
SOC	Soil organic carbon
SOM	Soil organic matter

Introduction

Fine roots (≤2-mm diameter, hereafter referred to as roots) are a major contributor to forest soil carbon (C) stocks, either through exudate production or decay of dead root tissue (Rasse et al. 2005; Kramer et al. 2010; Rumpel and Kögel-Knabner 2011; Tefs and Gleixner 2012; Clemmensen et al. 2013). The important role of roots as a primary source of slowly degrading plant-derived soil organic C (SOC) has been invoked by several studies (Balesdent and Balabane 1996; Nierop 1998; Rumpel et al. 2002, 2004; Abiven et al. 2005; Bird and Torn 2006; Nierop et al. 2006; Crow et al. 2009; Schmidt et al. 2011; Persson 2012; Xiong et al. 2013; Hatton et al. 2015). While the stability of root-derived litter in soils is co-regulated by initial root chemistry, reactive mineral surfaces, organic matter (OM) inputs, nitrogen (N) deposition, and climate (e.g., Silver and Miya 2001; Zhang et al. 2008; Rumpel et al. 2015), the extent to which and mechanisms of how these variables influence fine root dynamics remain unclear. Consequently, better understanding the dominant controls on root-derived C and N persistence in soils is essential to predict the impacts of environmental disturbances on forest C and N cycling. In this study, we investigated the influence of long-term litter removal and increased N deposition during the first 2 years of root C and N dynamics in a forest soil.

Additions of fresh or labile plant-derived OM to soil often stimulate the mineralization (positive priming) of relatively stable soil OM (SOM; Kuzyakov 2010). For example, additions of root C exudates and cellulose accelerate decomposition of native SOM via co-metabolism, in which energy-limited soil microorganisms utilize easily-available C as a source of energy to decompose older and less easily degradable SOM (e.g., Cheng et al. 2003; Fontaine et al. 2004, 2007, 2011; Bird et al. 2011). However, litter manipulation studies show that the exclusion of litter inputs to soils for decades decreases SOM contents (Paterson et al. 2011; Lajtha et al. 2014a, b). Despite existing knowledge on the priming effects of labile C inputs to soils on SOM decomposition, the long-term impact of reduced fresh litter inputs on SOM (e.g., root litter) turnover remains poorly understood (e.g., Bowden et al. 2014). In this study, we examined the effects of above- and belowground litter exclusion on decomposing root litter C and N dynamics.

Elevated inorganic N deposition to forest soils should inhibit the decomposition rate of fine roots. Litter type may explain much of the contrasting effects of inorganic N additions to soils on litter decay rates; with N additions stimulating the decomposition rates of litter with low lignin concentration, while slowing the decay of lignin-rich litter (Knorr et al. 2005; Janssens et al. 2010). Similarly, experimentally adding inorganic N to forest soils promoted the activity of polysaccharide-degrading enzymes, whereas it suppressed the losses of lignin after 1 year of litter decomposition (Talbot and Treseder 2012). Given the abundance of lignin, cutin and suberin compounds in roots (Kolattukudy 1980; Abiven et al. 2005; Xiong et al. 2013), long-term elevated N deposition could increase the persistence of root litter C in soils. Nevertheless, little data exist on the effects of N additions on fine root degradation in forest soils. In a Norway spruce stand, Majdi (2007) observed an increase in root mass loss from soils that had received N and S additions. Assessing the interactions between N additions and root-derived C and N dynamics is needed to better understand the long-term impact of N deposition on belowground C pools in forest soils.

The objective of our study was to assess the effects of litter inputs and inorganic N additions on the decay dynamics and retention of dual-labeled (^{13}C and ^{15}N) *Acer rubrum* roots in soils during a 2-year decay period within a long-term litter and N manipulation field experiment [detritus inputs and removal treatment (DIRT)] located at the University of Michigan Biological Station (UMBS) in northern lower Michigan (Pellston, MI, USA). Given that heterotrophic respiration (CO_2 production) and leaching [as dissolved organic carbon (DOC)] are pathways for litter C losses (Soong et al. 2015), we assessed root decay dynamics by tracing the ^{13}C-signal of root litter into CO_2 and DOC in the DIRT plots. We hypothesized that the limitation of above- and belowground litter

inputs to soils would decrease root litter C and N retention in surface soils, increase root-derived CO_2 mineralization rates and enhance root-derived DOC exports to lower soil depths. In a second experiment, we examined the effects of inorganic N additions on fine root stability in soils. We hypothesized that the chronic N addition to soils would increase root C and N retention in soils by inhibiting fine root CO_2 mineralization rates and decreasing the loss of root-derived C to lower soil depths as DOC.

Materials and methods

Study site

We took advantage of an existing long-term DIRT litter manipulation experiment located at the UMBS (Pellston, MI; 45°33.6′ N, 84°42.6′ W), in a transition zone between mixed hardwood and boreal forests. The UMBS DIRT plots were established in 2004, and consist of replicated treatments (5 m × 5 m, n = 3) in which the above- and/or belowground litter is either excluded or added (Nadelhoffer et al. 2004), and exposed to natural or increased (30 kg ha^{-1} $year^{-1}$) N fertilization levels. This experimental site is part of a larger network of DIRT experiments (Nadelhoffer et al. 2004; Lajtha et al. 2014a, b), and the Ameriflux network. The forest canopy is dominated by *Populus grandidentata* (Bigtooth aspen), *Quercus rubra* (Northern red oak), *Betula papyrifera* (Paper birch), and *A. rubrum* (red maple). The site is located at 235–238 m elevation, with a mean annual temperature and precipitation of 6.8 °C and 838 mm, respectively (1983–2013). The soils are well-drained sandy spodosols (92.9 % sand, 6.5 % silt, 0.6 % clay), developed on outwash plains, and classified as mixed, frigid Entic Haplorthods (Soil Survey Staff 2014). Reported atmospheric inorganic N deposition for this area was 4.1 kg ha^{-1} in 2012 (National Atmospheric Deposition Program 2014).

^{13}C- and ^{15}N-enriched red maple roots

Red maple saplings were grown and labeled with ^{13}C and ^{15}N between May and September 2009 at Queens College, City University of New York, Flushing, NY. Red maple is an important overstory species present in most mixed forests in the Great Lakes region, and its populations continue to expand in abundance and range in eastern North America (Abrams 1998; Fei and Steiner 2007). The labeling of 2-year old red maples was conducted in a temperature-controlled growth chamber modified from Bird et al. (2003). ^{13}C labeling was accomplished by exposing red maple saplings to enriched $^{13}CO_2$ (25 at.%) once a week for a total of 18 weeks. ^{15}N labeling was accomplished by fertilizing the maple saplings with $^{15}NH_4Cl$ and $K^{15}NO_3$ at (19.3 at.% excess), once a week for a total of 21 weeks. After fall senescence and leaf drop, red maples were removed from the soil media. In this study, we used roots that were <2 mm in diameter and produced during a season of growth. While our diameter-based classification groups roots of different orders and functions, order-based classification may be an important way to consider the effect of litter quality for fine roots (McCormack et al. 2015). Fine root biomass used in our study was formed during the current growing season, with the 'new' root biomass visually distinguished from the 'old' one by color and location in the root system. Fine roots produced during the labeling period were clipped, air-dried, and subsampled for further analyses (Table 1). All roots used in this study had a maximum length of 6 cm. Subsamples of labeled roots were analyzed in duplicates for total organic C (TOC) and N on a CHN gas analyzer (Costech Model 4010, Valencia, CA). ^{13}C and ^{15}N enrichment was measured in duplicates on a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (IRMS, Sercon Ltd., Cheshire, UK). The chemical composition of labeled roots was determined in replicates using proximate C fractions according to Ryan et al. (1990). Calcium (Ca), potassium (K), phosphorous (P), and magnesium (Mg) concentrations of labeled fine roots (n = 3, Table 1) were determined by inductively coupled plasma atomic emission spectrometry following acid digestion (Kalra 1997).

Field study design

In July 2010, 60 mesocosms (10-cm diameter and 22-cm long PVC cylinder) were inserted into the soil (to a depth of 20 cm) of the selected DIRT plots 2 months prior to fine root addition. The sides of the mesocosms had two clusters of 10, 0.4 cm diameter holes that were drilled 0.5–1 cm apart to allow fungal hyphae, fine roots, and earthworms to access the core.

Table 1 Isotopic and elemental composition of *Acer rubrum* fine root (≤2 mm in diameter, dry matter) added to soils

	C	^{13}C	^{15}N	Proximate C fractions[a]							Mass ratios		Nutrients[b]				
				NPE	WS	WS phenol	WS glucose	AHF	AHF glucose	ARF	C:N	ARF:N	N	Ca	K	P	Mg
	(g kg^{-1})	(at.%)		(g kg^{-1})									(g kg^{-1})				
Fine roots	527	5.20	11.5	68	287	25	104	334	200	311	44	26	11.5	3.5	7.4	2.1	1.8

[a] All proximate C values are expressed on an ash-free dry basis. Fractions: *NPE* non-polar extractives (waxes, fats, and chlorophylls), *WS* water-soluble extractives (simple sugars, hydroxyl phenol groups, and amino acids), *WS phenol* water soluble phenol expressed as percent tannic acid equivalents, *WS glucose* water-soluble polysaccharide expressed as percent glucose equivalent, *AHF* acid hydrolysable fraction (plant polysaccharides, proteins, polypeptides, some amino acids, and nuclei acids), *AHF glucose* acid hydrolysable polysaccharides expressed as percent glucose equivalents, *ARF* acid resistant fraction ('lignin')

[b] After nitric- and perchlorid-acid digestion

The clusters of holes were approximately 5 and 18 cm from the top of the mesocosm.

Experimental treatment I: litter inputs

To test the effects of litter additions on the decomposition rate of red maple roots, soil mesocosms were placed within DIRT plots that had no belowground roots (NR), and no below- and aboveground litter additions (NI; Table S1). In the NR treatment, roots are excluded by trenching to 1.1 m depth, placing an impermeable plastic barrier around plot perimeters, and backfilling the trenches with soil removed during trenching. In the NI treatment, the aboveground litter inputs are removed using a mesh screen to collect and remove litterfall, while root ingrowth is excluded as described for NR plots (Nadelhoffer et al. 2004). Treatments with no manipulation of above- and belowground litter inputs served as experimental controls (C).

Experimental treatment II: N additions

To investigate the impacts of N additions on the decomposition of labeled maple roots, mesocosms were placed within plots receiving periodic N additions at a rate of 30 kg N ha^{-1} year^{-1} (as NH_4Cl) in three annual applications (May, August, and November; Table S1). This annual application rate is approximately 7.3 times the background inorganic N deposition reported for this site (National Atmospheric Deposition Program 2014). Treatments with no experimentally added N served as controls.

Addition of ^{13}C and ^{15}N-enriched red maple roots to soils

In September 2010, ^{13}C- and ^{15}N-labeled roots (1.1 g root-C and 0.025 g root-N per soil mesocosm) were placed in the first 4 cm of the mineral soil (A and E horizons), in three field replicates per treatment. Unamended mesocosms were treated as those amended with roots and served as experimental controls.

Sampling and analyses

Root ^{13}C and ^{15}N recovery from soil

Mesocosms were excavated intact from the DIRT plots 1 and 2 years after application of $^{13}C/^{15}N$ labeled roots to soil mesocosms (i.e., September 2011 and August 2012). Following excavation, soil mesocosms were stored at 4 °C until processing and analysis (<7 days). For each mesocosm, soil was separated and subsampled by depth (0–10 and 10–20 cm). For both depth increments, size fractions >2 and <2 mm were separated using a 2 mm sieve. Subsamples were homogenized by ball milling and analyzed for total elemental and stable isotope analyses. Total SOC and N were measured using a CHN gas analyzer (Costech Model 4010, Valencia, CA). Carbon (C) and N isotopic enrichment was measured on an Elementar Vario EL Cube elemental analyzer (Elementar Anal-

ysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20–20 IRMS (Sercon Ltd., Cheshire, UK). Isotopic composition was expressed with respect to the Vienna Pee Dee Belemnite (VPDB) standard for C and relative to atmospheric N_2 for N. The total recovery of applied ^{13}C-derived root in soil was fit to a single exponential model (Olson 1963) as in Eq. (1):

$$^{13}C(S_t) = S_0 e^{(-k * t)}, \quad (1)$$

where S_0 is the proportion (%) of ^{13}C remaining in soil from added root, S_t is the proportion of ^{13}C-derived root remaining in soil at time t, and k is the decay rate constant (day^{-1}). In this study, k was reported in years^{-1} (Table 2). Curve fitting was performed using SigmaPlot for Windows (v. 12; SYSTAT Software, Inc., San Jose, CA, USA).

Soil CO_2 respiration and $^{13}CO_2$ efflux

Total soil CO_2 and $^{13}CO_2$ efflux rates were measured five times during the experiment (22 September 2010, 20 May 2011, 29 June 2011, and 19 August 2011, and 18 August 2012), using a LI-6400 portable infrared gas analyzer and a soil respiration chamber (LI-COR, Lincoln, NE) modified for headspace gas collection (Torn et al. 2003). Soil CO_2 efflux was measured in triplicate per plot for each sampling time. In addition to CO_2 fluxes measurements, CO_2 was sampled at five time points per plot for ^{13}C-CO_2 determination. The δ^{13}C of soil CO_2 efflux was measured on a Delta Plus XP IRMS (ThermoFinnigan, Bremen, Germany) interfaced with a GasBenchII (ThermoFinnigan, Bremen), and calculated using the Keeling plot method (1958). Rates of soil CO_2 efflux were interpolated during the 2-year study to provide an estimate of total losses of SOC and roots as CO_2 (Supplementary material 2, Figs. S1, S2).

Soil C leachate and ^{13}C-dissolved organic C

Zero-tension lysimeters (ZTLs) were installed on one of the three mesocosms for each treatment. The majority of the ZTLs produced consistently insufficient yield for analysis, which did not allow for comparison among all treatments on all sampling dates. However, sufficient sample allowed for DOC measurement from solutions collected between 13 August 2011, and 3 September 2011. ZTL leachate samples were filtered using a pre-ashed (450 °C for 5 h) filters (Whatman GF/F, <0.7 μm), and stored at −20 °C until chemical analysis. DOC concentration was measured on a TOC analyzer (Shimadzu, TOC-V CPH, Kyoto, Japan). Samples were acidified and purged with helium off-line to remove all dissolved inorganic C prior to measurement. The ^{13}C enrichment of DOC was determined using an O.I. analytical TOC analyzer (Model 1030, College Station, TX) interfaced to a PDZ Europa 20–20 IRMS (Sercon Ltd., Cheshire, UK) utilizing a GD-100 gas trap interface (Graden Instruments, Ontario, Canada). The δ^{13}C were expressed with respect to VPDB and analytical precision for this analysis was 0.4 ‰.

^{13}C and ^{15}N calculations

The contribution of ^{13}C and ^{15}N from labeled roots to soil C and N fluxes and pools (f_{root}) was calculated from a mass balance of isotopic signatures (Eq. 2),

$$f_{\text{root}} = \left(\delta_{\text{sample}} - \delta_{\text{control}}\right)/\left(\delta_{\text{labeled root}} - \delta_{\text{control}}\right), \quad (2)$$

where δ denotes the isotopic value (either δ^{13}C or δ^{15}N, ‰) in soil, evolved CO_2 or DOC from treatment with labeled roots (δ_{sample}) and unamended soil (no added labeled fine roots, δ_{control}); and $\delta_{\text{labeled root}}$ is the isotopic value (δ^{13}C or δ^{15}N, ‰) of labeled roots prior to addition to soils. The mass of added labeled root ^{13}C or ^{15}N (hereafter referred to as root C or N) recovered in soil and pools was calculated by multiplying f_{root} by the total amount of C or N in bulk soil, soil fractions, and evolved CO_2 or DOC.

Statistical analyses

The effects of DIRT treatments on root C and N recovered in two soil fractions and depths, as well as on DOC were tested using randomized complete block design for repeated measures and individual one-way analysis of variance (ANOVA) on individual sampling dates. Comparisons between treatments for measured soil CO_2 effluxes were performed using repeated measures one-way ANOVA. We used a $P < 0.05$ as the a priori *error* for statistical significance between means. Given the relatively low statistical power of the experimental design, we also reported $P < 0.10$ in "Results" section (Lovell 2013). All analyses were

Table 2 Recovery of *Acer rubrum* fine root ^{13}C and ^{15}N in soils at different depths (0–10, 10–20 cm) and fractions (> and <2 mm) after 1- and 2-year field study within litter manipulation (Experiment I) and N addition (Experiment II) treatments

Treatments	Years	Mesocosm		0–10 cm					
		Total ^{13}C recovery % of applied ^{13}C or ^{15}N	Total ^{15}N recovery	>2 mm % of applied ^{13}C	<2 mm	Total ^{13}C recovery	>2 mm % of applied ^{15}N	<2 mm	Total ^{15}N recovery
Experiment I									
C	1	35.0 (2.4)	63.2 (4.0)	20.7 (1.6)	12.5 (5.0)	33.3 (3.6)	34.2 (5.4)	24.7 (6.0)	58.9 (1.1)
NR		29.0 (2.6)	44.1 (2.7)	16.4 (1.5)	12.5 (3.4)	28.9 (2.4)	19.3 (1.4)	23.9 (3.7)	43.2 (2.6)
NI		48.1 (10.6)	73.0 (13.7)	31.6 (10.6)	16.9 (3.0)	48.4 (10.6)	38.8 (12.0)	33.6 (5.8)	72.3 (13.5)
C	2	19.5 (3.6)	33.7 (5.4)	5.1 (2.2)	13.7 (3.5)	18.9 (3.7)	6.7 (2.5)	25.4 (5.7)	32.1 (5.3)
NR		28.6 (10.2)	41.3 (14.9)	5.0 (3.1)	23.0 (12.3)	28.1 (10.1)	6.1 (3.6)	33.7 (16.4)	39.9 (14.4)
NI		22.4 (4.7)	45.0 (8.3)	7.9 (1.3)	14.2 (3.5)	22.1 (4.8)	11.1 (1.9)	32.8 (6.6)	43.8 (8.5)
Experiment II									
No N added	1	35.0 (2.4)	63.2 (4.0)	20.7 (1.6)	12.5 (5.0)	33.3 (3.6)	34.2 (5.4)	24.7 (6.0)	58.9 (1.1)
N added		32.8 (5.6)	50.7 (6.1)	21.4 (3.3)	11.7 (2.5)	33.1 (5.6)	28.1 (2.4)	21.7 (4.8)	49.8 (5.9)
No N added	2	19.5 (3.6)	33.7 (5.4)	5.1 (2.2)	13.7 (3.5)	18.9 (3.7)	6.7 (2.5)	25.4 (5.7)	32.1 (5.3)
N added		12.3 (2.4)	23.1 (3.5)	1.7 (0.5)	10.2 (2.7)	11.9 (2.4)	2.6 (0.7)	18.9 (4.1)	21.5 (3.7)

Treatments	Years	Mesocosm		10–20 cm						k[1]
		Total ^{13}C recovery % of applied ^{13}C or ^{15}N	Total ^{15}N recovery	>2 mm % of applied ^{13}C	<2 mm	Total ^{13}C recovery	>2 mm % of applied ^{15}N	<2 mm	Total ^{15}N recovery	^{13}C year^{-1}
Experiment I										
C	1	35.0 (2.4)	63.2 (4.0)	−0.3 (0.2)	2.1 (1.9)	1.8 (2.0)	0.1 (0.0)	4.2 (3.9)	4.3 (3.9)	0.96 (0.08)[2]
NR		29.0 (2.6)	44.1 (2.7)	−0.4 (0.1)	0.5 (0.1)	0.1 (0.2)	0.0 (0.0)	0.9 (0.2)	1.0 (0.2)	0.96 (0.20)[3]
NI		48.1 (10.6)	73.0 (13.7)	−0.4 (0.1)	0.1 (0.0)	−0.4 (0.1)	0.0 (0.0)	0.6 (0.5)	0.7 (0.5)	0.78 (0.06)[4]
C	2	19.5 (3.6)	33.7 (5.4)	0.0 (0.0)	0.6 (0.1)[a]	0.6 (0.0)[a]	0.1 (0.0)	1.5 (0.1)	1.6 (0.1)	
NR		28.6 (10.2)	41.3 (14.9)	0.0 (0.0)	0.5 (0.2)[a]	0.5 (0.2)[a]	0.1 (0.1)	1.3 (0.4)	1.4 (0.5)	
NI		22.4 (4.7)	45.0 (8.3)	0.0 (0.0)	0.3 (0.1)[b]	0.3 (0.1)[b]	0.2 (0.1)	0.9 (0.2)	1.2 (0.3)	
Experiment II										
No N added	1	35.0 (2.4)	63.2 (4.0)	−0.3 (0.2)	2.1 (1.9)	1.8 (2.0)	0.1 (0.0)	4.2 (3.9)	4.3 (3.9)	0.96 (0.08)[2]
N added		32.8 (5.6)	50.7 (6.1)	−0.6 (0.1)	0.4 (0.1)	−0.2 (0.1)	0.1 (0.0)	0.8 (0.1)	0.9 (0.1)	1.12 (0.10)[5]
No N added	2	19.5 (3.6)	33.7 (5.4)	0.0 (0.0)	0.6 (0.1)	0.6 (0.0)	0.1 (0.0)	1.5 (0.1)	1.6 (0.1)	
N added		12.3 (2.4)	23.1 (3.5)	0.0 (0.0)	0.5 (0.1)	0.5 (0.1)	0.1 (0.0)	1.5 (0.2)	1.6 (0.2)	

Also reported: decay constant (k) of root ^{13}C in soils. Values shown are means of three replicate plots ± standard errors (n = 3). Different letters (superscript) denote statistical differences ($P < 0.05$) among treatments. Treatments included: control (C), no manipulation of above and belowground litter inputs, and no experimental N additions; added N, received additions of N as fertilizer; no roots (NR), received no additions of belowground inputs (e.g., no roots); no inputs (NI), received no additions of above or belowground inputs

[1] P values for the model parameter k (decay constant): [2] 0.07; [3] 0.01; [4] 0.22, [5] 0.02

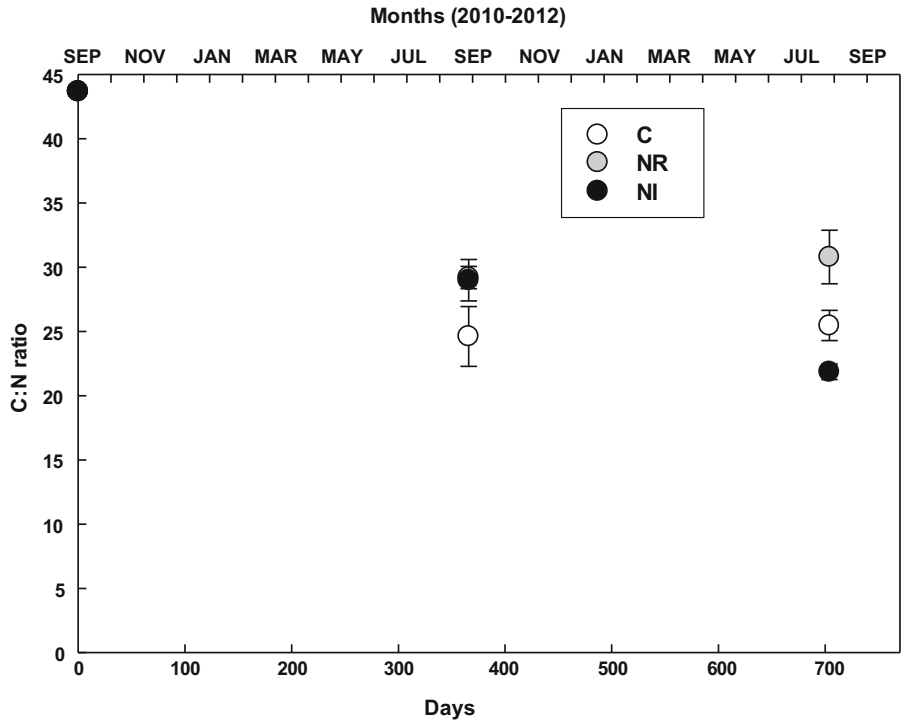

Fig. 1 C:N ratios of dual-labeled (^{13}C and ^{15}N) root litter retained in soil mesocosms (0–20 cm depth) after 1 year (366 days) and 2 years (704 days) in the field within DIRT treatments that received no belowground inputs (*NR* no roots, *gray circle*), no above and belowground litter inputs (*NI* no inputs, *black circle*), and control (C, *white circle*). Data points overlap at time zero. Values shown are means of three replicate plots ± standard errors (n = 3)

conducted using Systat v.10 (SYSTAT Software, Inc., Chicago, IL, USA).

Results

Retention of labeled fine root C and N in DIRT treatments

After 2 years of incubation in the field, 19.5 ± 3.6 % of applied root C and 33.7 ± 5.4 % of applied root N were recovered from soil mesocosms (0–20 cm depth; averages across treatments), with no difference between treatments observed (Table 2). After 2 years in the soil, the majority (73 and 81 %) of remaining root C and N, respectively, were recovered in the <2 mm size fraction of the soil within 0–10 cm depth increment (Table 2).

The C:N ratio of root-derived OM remaining in mesocosms decreased during the 2-year decomposition study (Fig. 1). The initial root C:N ratio (44) declined to an average of 27 ± 0.9 at the end of year 1, and to an average of 25 ± 1.1 at the end of year 2 across all treatments. After 2 years of decomposition, the C:N ratio of root-derived OM recovered from the NI treatments was 12 % lower than in the control ($P = 0.047$); reflecting the 17 % difference found in the <2 mm size fraction isolated from the 0 to 10 cm depth increment ($P = 0.044$). After 2 years in soil, C:N ratios of root-OM in the NR treatment were similar to the control ($P = 0.087$).

After 2 years in soil, only 0.3–0.6 % of applied root C was recovered in the 10–20 cm depth increment across all DIRT treatments (Table 2). Total retention of root C within 10–20 cm depth was 58 % less in NI than in control treatments ($P = 0.03$). Similarly, retention of root C in the bulk soil fraction (<2 mm) within 10–20 cm depth interval was 55 % lower in NI treatments than in control treatments ($P = 0.036$). Despite the negative effects of NI treatments on the retention of root C within 10–20 cm depth interval, less than 0.7 % of root C and N were recovered from that depth interval after 2 years in the field. During the 2-year study, NI treatment increased the total retention

of root N in soil mesocosms ($P = 0.036$), and within 0–10 cm depth interval when compared with control treatments ($P = 0.037$; Table 2). The retention of root N in soil mesocosms was not significantly affected by NR treatments during the 2-year study.

Changes in root N recovery in soil were affected by treatments that received inorganic N additions (Table 2) during the 2-year study. In added inorganic N treatments, 31 % less root N was retained in soils (0–20 cm) than in unamended plots ($P = 0.035$). Despite these differences, the recovery of root N at different depth intervals (0–10 and 10–20 cm) and soil fractions (> and <2 mm) was not affected by N addition.

C mineralization and leaching from labeled fine roots

Rates of root C losses as CO_2 from litter removal (NR or NI) and N addition treatments did not differ from controls during the 2-year field study (Fig. 2). The highest heterotrophic respiration rates of CO_2-C from roots were observed 8 days (September 2010) after application, likely reflecting the minor soil disturbance during application. The fastest and slowest mineralization rates of root C occurred in the summer and fall, respectively, suggesting a seasonal variation of root CO_2 efflux rates. An estimate of total root C-CO_2 effluxes across all DIRT treatments (Fig. S2) suggested that 20 % (NR)–50 % (NI) of added root C was lost as CO_2 during the 2-year study, although caution should be taken when interpreting the modeled data as they were based on four sampling dates. Nonetheless, this estimation suggests that a fraction of root-derived C was lost to lower soil depths likely via leaching (as DOC) and litter redistribution by soil fauna (e.g., earthworms). Similarly to soil CO_2 efflux from roots, losses of root C as DOC in soil leachate collected after two rain events in August and September 2011 were not affected by either NR or NI treatment (Table 3). Losses of root C as DOC for those two sampling dates were up to three orders of magnitude lower than those as CO_2 efflux.

Discussion

In the first 2 years of fine root decomposition, litter C and N losses were large, with ~79 % of the fine root C and 64 % of the fine root N lost from the top 20 cm of soil, averaged across all treatments. These values are considerably higher than those reported from field studies after 1–5 years root decomposition from a sandy eucalypt forest soil (de Miranda Mello et al. 2007) and a sandy conifer forest soil in California (Bird and Torn 2006; Hatton et al. 2015). Our values were also higher than those reported for grassland roots decomposing in temperate soils (Sanaullah et al. 2011), and in both subalpine and altimontane soils (Casals et al. 2010; Garcia-Pausas et al. 2012). Why did maple roots decompose faster in Northern Michigan relative to those reported by previous studies (i.e., pine and wheat roots)? We offer the following explanations of the main factors that influenced our results: the coarse-textured soils, root litter chemistry, and soil mesofauna.

First, the coarse (sandy) texture of the soil in our Northern Michigan site likely contributed to the fast cycling and losses of root C and N we observed. These sandy soils, along with the resulting weakness of SOM stabilization mechanisms, such as adsorption to minerals and physical protection through occlusion or aggregation (Sanaullah et al. 2011; Rumpel et al. 2015), have lower capacity to protect and stabilize soil C than do more developed and finer-textured soils. The effect of soil texture on decomposition rates of litter has been demonstrated by a recent study, which reported that clover leaves decomposed faster in sandy than in clay soil (Frøseth and Bleken 2015). Results from previous studies conducted near our field site support our hypothesis that the coarse texture and resulting weak SOM stabilization capacity contributed to the fast losses of root C and N observed in our study. For example, Garten (2011) reported that the fast-cycling soil C pool at the UMBS was primarily influenced by soil texture. In another study, McFarlane et al. (2012) reported that approximately 53 % of the bulk soil C at the UMBS was found in the free light (unprotected) fraction, whereas only about 10 % was in the "occluded" (protected) fraction. Thus, we posit that the weak protective capacity of the coarse-textured favored the fast cycling of root litter C and N by soil microfauna, mostly bacteria and fungi, the during the 2-year decomposition study.

Second, the low initial C:N and acid-resistant fraction (ARF, referred to as 'lignin' thereafter) to N ratios of maple roots may also have increased their susceptibility to decomposition. The negative

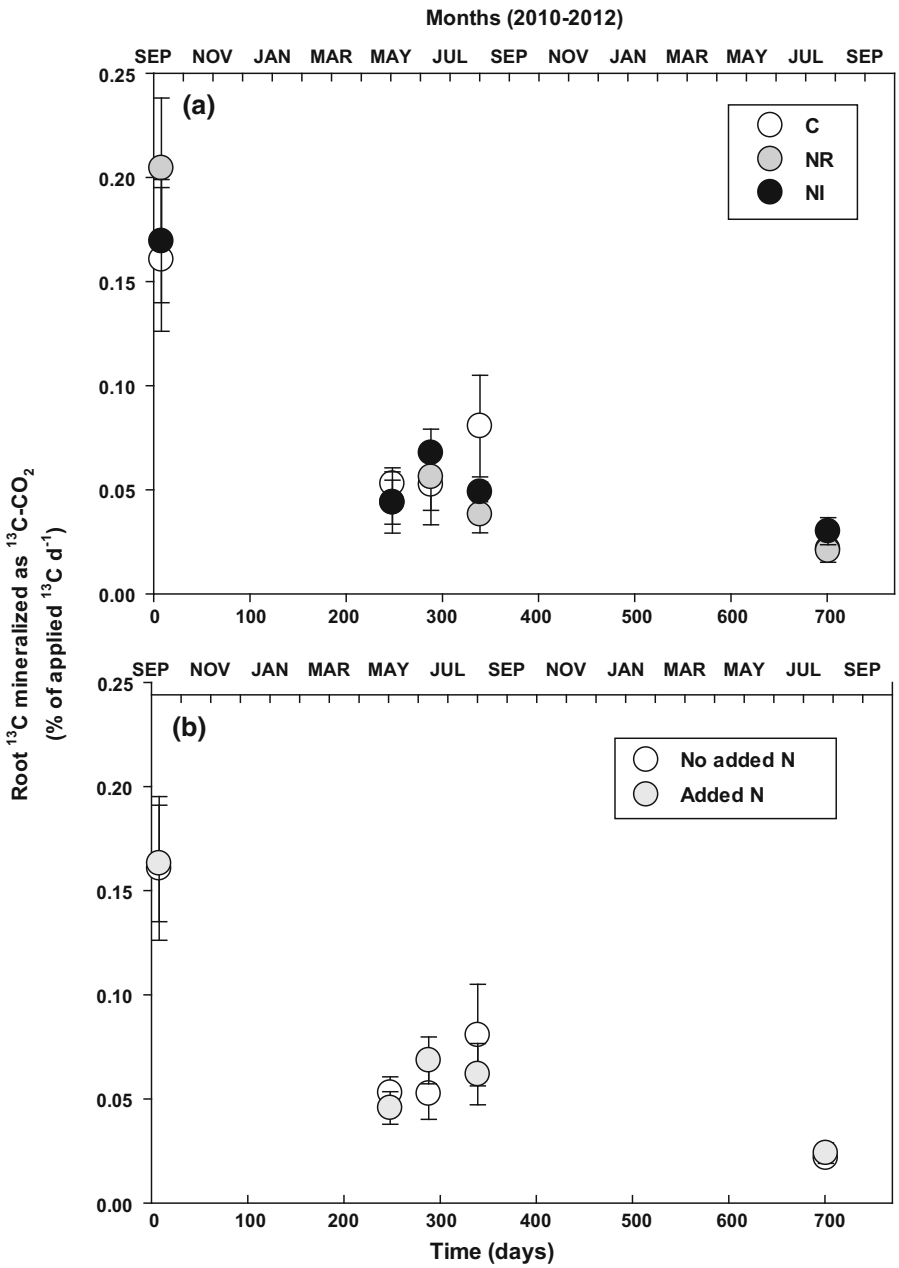

Fig. 2 $^{13}CO_2$ mineralization from applied root C during the 2-year study in DIRT treatments that: (**a**) received no belowground litter inputs (*NR* no roots), no above and belowground litter inputs (*NI* no inputs), and control (C), and (**b**) treatments with or without nitrogen additions as fertilizer. Values shown are means of three replicate plots ± standard errors (n = 3)

correlation between litter decomposition rates and the initial 'lignin':N and C:N ratios has been reported by several studies, some of which conducted in coarse-textured soils (Silver and Miya 2001; Zhang et al. 2008; Tong et al. 2012; Walela et al. 2014; Sariyildiz 2015). For example, in a study conducted by Sariyildiz (2015) in sandy loam soils, fine roots were negatively correlated with initial root litter C:N ratios. We also found that the C:N and 'lignin':N ratios reported for broadleaf and conifer roots were much higher (up to 111 and 69 %, respectively) than those of maple roots reported in this study (Silver and Miya 2001). Similarly, the initial root C:N and 'lignin':N ratios reported in this study were up to 56 and 71 % lower than those reported for 11 temperate tree species in loamy sand soils (Hobbie et al. 2010). Indeed, decomposition rates calculated based on a single exponential model indicated that maple roots in our

Table 3 Losses of root-derived dissolved organic C (DOC) in soil leachate collected from zero-tension lysimeters installed underneath soil mesocosms within litter manipulation (Experiment I) and N addition (Experiment II) treatments

Treatments	DOC	
	13 August 2011 % of applied ^{13}C	3 September 2011
Experiment I		
C	1.02×10^{-3} (6.16×10^{-4})	1.06×10^{-3} (4.08×10^{-4})
NR	2.62×10^{-3} (1.84×10^{-3})	8.04×10^{-4} (2.69×10^{-4})
NI	9.72×10^{-4} (2.79×10^{-5})	3.51×10^{-4} (2.22×10^{-4})
Experiment II		
No N added	1.02×10^{-3} (6.16×10^{-4})	1.06×10^{-3} (4.08×10^{-4})
N added	9.6×10^{-4} (4.8×10^{-4})	8.3×10^{-5} (3.6×10^{-5})

Leachates were collected from a single rain event on 13 August 2011, and on 3 September 2011. Values shown are means of three replicate plots ± standard errors (n = 3). Treatments included: control (C), no manipulation of above and belowground litter inputs, and no experimental N additions; added N, received additions of N as fertilizer; no roots (NR), received no additions of belowground inputs (e.g., no roots); no inputs (NI), received no additions of above or belowground inputs

study decomposed much faster than those reported by Hobbie et al. (2010) and Sariyildiz (2015), supporting the idea that the initial litter chemistry likely favored the relative rapid decay rates of maple roots.

Third, we cannot exclude that earthworms in our site accelerated the initial fragmentation of fine roots. In this study, the fine roots applied to soil were not confined in litterbags, as was the case for other studies cited here (e.g., Sanaullah et al. 2011; Garcia-Pausas et al. 2012), due to artifacts known to result from this mass loss approach (Dornbush et al. 2002). Thus, the root litter in this study was accessible to soil mesofauna, including the exotic earthworms reported in our field site and shown to decompose maple leaf litter (Crumsey et al. 2015). Earthworms have been reported to decrease fine root (1-mm diameter) biomass by approximately 20 % in a temperate forest (Fisk et al. 2004), and in our site they may have contributed to the observed, faster decomposition rates of fine roots.

We recognize that the factors mentioned above, together with other soil conditions such as water availability, fungal and bacterial activity, and pH, may have interacted to influence our results. For example, fungi and bacteria are the major mediators of SOM decomposition, and their relative abundance has been reported near our field sites (DeForest et al. 2004). This would be in agreement with the emerging perspective that the stability of SOM depends on an array of physical, chemical and biological conditions within the soil matrix, and not initial litter chemistry alone (Kleber 2010; Prescott 2010; Schmidt et al. 2011; Dungait et al. 2012). It is beyond the scope of this study to determine the primary factors controlling root decomposition dynamics in our site. Furthermore, we acknowledge that comparisons of our fine root C and N losses data with those from previous studies may be limited for two main reasons: first, the decay rates of litter in direct contact with soil has been reported to be faster than those of litter enclosed in litterbags (Dornbush et al. 2002; Cotrufo et al. 2010; Berhe 2013). Second, we recognize that our definition of root based on diameter (≤2 mm) is broad and does not capture the morphological, chemical and functional heterogeneity of fine roots (e.g., see McCormack et al. 2015). For example, the decay rates of lower-order roots have been reported to be slower than those for higher-order roots (Xiong et al. 2013). This finding has been attributed to the influence of root order on the chemical composition of roots: lower-order roots contain higher concentration of acid-insoluble fraction than do higher-order roots (Xiong et al. 2013).

In this study, the removal of above- and belowground litter for 8 years in the DIRT experiments decreased the C:N ratios of maple root litter remaining in soils, indicating a high degree of microbial processing. In addition, litter exclusion treatment significantly reduced root C retention in bulk soil within 10–20 cm depth after 2 years of decomposition. We hypothesize that subsurface soils in litter exclusion treatments were more energy-limited than those in control treatments. Thus, the release of soluble C and N fractions derived from maple root

litter to presumably C- and nutrient-limited lower soil depths could have increased the fungal and bacterial substrate use efficiency in those subsurface soils. While an increase in substrate-use efficiency could result in higher retention of microbially-derived OM in mineral soils (Cotrufo et al. 2013), the low stabilization capacity of the coarse-textured soil studied here does not favor the selective preservation of necromass and other microbial by-products. Our results support the idea that microbial activity in mineral subsoil horizons is generally limited in energy (i.e., fresh C supply) that is needed to decompose OM (Fontaine et al. 2007). This energy limitation has also been reported for permafrost mineral horizons that received additions of organic compounds (Wild et al. 2014). It is possible that pulses of labile C (i.e., soluble) fraction released from the decaying maple root created a microbial hotspot at lower soil depths (Kuzyakov and Blagodatskaya 2015), stimulating microbial activity in this presumably energy-limited subsoil horizon.

Nitrogen addition effects

Our data showed that inorganic N additions had no effect on the retention of red maple root C. The absence of treatment effects on root C mineralization rates further support our conclusion that the mineralization rates of root C were unaffected by the additions of inorganic N in the DIRT plots. These results are consistent with those from several studies that showed no responses of litter decomposition to N additions (Hobbie and Vitousek 2000; Johnson et al. 2000). In contrast to our results, N fertilization in the form of ammonium sulphate has been shown to increase the decomposition rates of a Norway spruce root and root lignin (Madji 2007). In an incubation study, the addition of inorganic N to agroforestry soils also increased the decomposition rates of pine roots, but did not stimulate (and sometimes inhibited) the decomposition of poplar roots (Mao et al. 2011). We hypothesize that soil texture influenced our results, given that coarse-textured soils are often reported to retain less N than fine-textured soils (Lajtha et al. 1995; Castellano et al. 2012, 2013). In addition, our results may have been affected by fast leaching rates of added N due to the coarse texture of the soil, or possibly, uneven application of the N fertilizer to soils.

The addition of inorganic N for eight years in the DIRT plots decreased the amount of maple root N retained in soils after 2 years. Our results contrast with those reported by Talbot and Treseder (2012), who found no effect of N fertilization on the proportion of litter N lost after 1 year of decay. In our study, the addition of inorganic N to soils may have stimulated the mineralization of root N by soil microorganisms. However, the extent to which experimentally added N to soils affected the metabolic activity of microorganisms deserves further investigation.

Conclusions

Our results showed that fine root litter in coarse-textured northern temperate forest soils may be a much faster-cycling SOM pool than previously thought. In addition to the coarse soil texture, we attributed this fast turnover rate to the high litter quality (low initial C:N and 'lignin':N ratios) and the presence of earthworms in our field site. The rapid decomposition of roots observed in this study suggests (a) a slow SOM accumulation rate in this northern temperate forest, and (b) that in the short-term, root litter may not be a dominant source of stabilized OM in this ecosystem. We demonstrated that 8 years of inorganic N additions to soils and the removal of above and belowground litter for 8 years had no influence on fine root C dynamics. Taken together, our results highlight the need for long-term studies on C and N dynamics of root litter and the environmental factors that affect root decomposition in different forest ecosystems. Progress in root litter research would improve our mechanistic understanding of belowground C and N stabilization processes, and would facilitate predictions of forest SOM turnover under different environmental conditions. Finally, further studies that focus on the biotic and abiotic mechanisms that regulate the root-C responses to changes in aboveground and belowground litter inputs and N additions are needed to more fully understand the impact of environmental disturbances on SOM dynamics.

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