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Litter and Root Manipulations Provide Insights into Soil Organic Matter Dynamics and Stability

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Understanding controls on C stored in soil organic matter (SOM) is of critical importance to models of biospheric C sequestration. Although ecosystem C models assume a strong relationship between plant litter inputs and soil C accumulation, there is little experimental evidence to support this assumption. The Detritus Input and Removal Treatments (DIRT) experiment at Harvard Forest was designed to assess how rates and sources of plant litter inputs control the accumulation and dynamics of organic matter in soils across decadal time scales. Carbon and SOM quantity and quality were measured in O horizon and mineral soil in five treatments: control, double litter, no litter, no roots, and no inputs. After 20 yr of manipulation, doubling litter inputs did not increase bulk soil C or N content, light or heavy fraction pools of C, or measures of labile C. However, the activities of two key enzymes (β-glucosidase and phosphomonoesterase) increased 30% with litter additions. Exclusion of either aboveground litter or root inputs resulted in sharp declines in O-horizon C and N but smaller decreases in total mineral soil C and N. However, decreases in light fraction C and soil respiration were significant in removal treatments. Litter exclusion resulted in an 18% decline in total profile mineral soil C, whereas root exclusion resulted in a 9% decline, indicating the importance of aboveground inputs to long-term C pools. Soil C pools in this forest do not respond linearly or immediately to aboveground or belowground litter inputs, and thus efforts to sequester C by managing productivity and associated litter inputs will probably not result in increased C storage in short time frames.

Abbreviations: DL, double litter; NI, no inputs; NL, no litter; NR, no roots; OA-less; plots with the O and A horizons removed and replaced with mineral soil; SOM, soil organic matter.

Globally, soils contain more than three times as much as C as the atmosphere and four and a half times more C than the world's biota (Lal, 2004). Despite their importance, however, soil C stocks have been degraded through land use change and unsustainable forest management practices (Lal, 2004; Vågen et al., 2005). Although C sequestration in soil is often suggested as a management technique to reduce the rate of atmospheric CO_2 increases, mechanisms of soil C sequestration, the amounts of C that may potentially be sequestered in soils, and the long-term dynamics of C sequestered in soils are poorly understood (Baldock and Skjemstad, 2000; Six et al., 2002; von Lützow et al., 2006, 2008).

Increasing the aboveground biomass necessarily sequesters C from the atmosphere, but changes in C masses stored in biomass do not necessarily lead to immediate or long-term changes in soil C storage (Sulzman et al., 2005; Crow et al.,

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2009a). For example, many forests show little or no change in total soil C content following harvest (Yanai et al., 2003; Nave et al., 2010), even though forest harvest clearly causes an immediate decrease in the C content of the stand. The response of soil organic matter (SOM) to changes in forest biomass and litter inputs might have a significant temporal lag; Holub et al. (2005) found no effect of above- and belowground organic inputs on SOM in two different forest soils after 4 or 11 yr. Although most ecosystem C models assume a strong linkage between net primary productivity, litter inputs, and soil C accumulation (Gottschalk et al., 2012), soils have finite capacities to sequester C and might "saturate" or achieve maximum equilibrium levels under different combinations of soil texture, mineralogy, and climatic regimes (Chung et al., 2010; Stewart et al., 2009; Six et al., 2002; Mayzelle et al., 2014). The C saturation deficit is the difference between current C content and the point of C saturation (Hassink, 1997), and thus C accumulation potential depends on litter input rates, decomposition rates, soil mineralogy, soil C content, and soil C saturation capacity.

Altering above and belowground inputs may also have complex effects on SOM pools due to changes in microbial respiration rates (Fontaine et al., 2003, 2004; Sulzman et al., 2005; Brant et al., 2006; Crow et al., 2009a). Increases in labile C inputs to soil can cause disproportionate increases in microbial respiration rates, known as *positive priming*. Sulzman et al. (2005) saw a positive priming effect of 187% in response to litter additions in an old-growth forest after 13 yr of litter manipulations, which agrees with other studies in forest ecosystems (Nottingham et al., 2012; Phillips et al., 2012; Sayer et al., 2007; Langley et al., 2009). The quality of litter inputs and the source of the material can have nonlinear effects on soil C fluxes and microbial composition (Cheng et al., 2012). The priming effect could be short-lived (Hoosbeek and Scarascia-Mugnozza, 2009) and thus may not be evident in longer duration litter manipulation studies. However, a recent meta-analysis of soil responses to increases in litter inputs due to experimental CO_2 enrichments of croplands, grasslands, and forests showed sustained and large priming effects increasing SOM turnover rates across ecosystem types (van Groenigen et al., 2014). There is a clear need for more long-term, comprehensive studies to elucidate plant litter controls on soil C dynamics at both short- and long-term time scales.

The Detritus Input and Removal Treatments (DIRT) experiment was designed to assess how rates and sources of plant litter inputs control the accumulation and dynamics of organic matter and nutrients in forest soils at decadal time scales (Nadelhoffer et al., 2004; Lajtha et al., 2005). The experiment is based on a study designed by Francis Hole at the University of Wisconsin Arboretum in 1956 using plots with additions and removals of above- and belowground litter. The DIRT network consists of eight active sites, with five in the United States and three located internationally.

The objective of this study was to determine the effects of changing litter and root inputs on the quality and quantity of SOM and on microbial activity in DIRT experimental plots at the Harvard Forest after 20 yr of experimental manipulation. We hypothesized that: (i) as high-quality aboveground inputs (litter) increased, C and N in the most labile SOM fractions would increase; (ii) litter and root exclusions would lead to decreased total C and increased proportions of biochemically resistant C; (iii) stable SOM pools would not increase because they are controlled by processes functioning at time scales longer than 20 yr; and (iv) excluding belowground root inputs would have a larger effect on both labile and longer cycling SOM pools than excluding aboveground litter inputs. This final hypothesis was derived from recent studies suggesting a greater impact of root inputs vs. aboveground litter on SOM stabilization (Rasse et al., 2005; Wilson et al., 2009; Clemmensen et al., 2013).

MATERIALS AND METHODS

Site Description

The Harvard Forest DIRT site is located in the Tom Swamp tract in Petersham, MA (42.29° N, 72.11° W), which is a transitional mixed hardwood–white pine–hemlock forest. The dominant tree species at the DIRT site are northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and paper birch (*Betula papyrifera* Marsh.), which represent 43, 19, and 15% of the total basal area of the stand, respectively. From 1733 to 1850, the site was permanent pasture. In 1908, it was classified as old-field white pine (*Pinus strobus* L.), and then as a white pine transition–hardwood in 1923 (Bowden et al., 1993). The soils are well to moderately well-drained Inceptisols of the Peru–Marlow association, are extremely stony, and are developed from friable, coarse-loamy, eolian deposits over dense, coarse-loamy, lodgment till derived from granite and mica schist (NRCS, 2014). The bedrock is primarily granite, gneiss, and schist. The soil texture is sandy loam from the surface of the A horizon to the 1.65-m depth. Slope ranges from 3 to 15%. The average soil depth is 3 m, with a forest floor depth of 3 to 8 cm and a thin Oa horizon (1–3 cm). Mean temperature ranges from −7°C in January to 20°C in July, and the mean annual precipitation is 110 cm (Nadelhoffer et al., 1999). Soil pH (1:1 fresh soil/distilled water) ranged from 3.8 to 4.4 in the O horizon and 4.1 to 4.9 in the 0- to 10-cm-depth mineral soil.

Litter and root manipulations began in September 1990 and include five input–exclusion treatments and a control, each replicated three times. Plots are 3 by 3 m, and none include trees or saplings. Core treatments are the control, double litter (DL), no litter (NL), no roots (NR), no inputs (NI), and OA-less (Table 1).

Control plots receive normal aboveground and belowground inputs. Aboveground inputs include leaves, twigs, seeds, flowering parts, and woody inputs <1 cm in diameter. Belowground inputs include roots and root exudates. In NL and NI plots, aboveground litter is excluded using a plastic mesh fabric placed on the plots from late September until late October (when 95% of all litterfall occurs). After senescence is complete, the leaves are removed from the plots. Any aboveground litter that falls on the plots outside of the autumn or winter period is

Table 1. Description of litter treatments at the Harvard Forest DIRT experiment plots.

Treatment	Description
Control	natural above- and belowground litter inputs are allowed
Double litter	aboveground inputs are doubled by adding litter removed annually and allocated proportionately from the no-litter plots
No litter	aboveground inputs are removed from plots during autumn senescence and periodically throughout the year
No roots	roots are excluded with trenching that extends from the soil surface to the 140-cm depth
No inputs	aboveground inputs are excluded as in no-litter plots, belowground inputs are prevented as in no-roots plots
OA-less	top 30 cm of soil was replaced with mineral soil in 1990

removed occasionally by hand. Living roots were excluded from the NR and NI treatments. Trenches were excavated around each plot to a depth of 1.4 m, approximately 0.4 m below the depth of the deepest tree roots observed at the site; roots entering the plots were thus severed from nearby trees, but roots within the plots themselves were not removed. Trenches were lined with fiberglass or with impervious plastic root barriers and then refilled. The DL plots receive twice the annual input of aboveground litter; litter collected monthly or during autumn senescence from a nearby NL or NI plot is placed on the DL plots. No trees exist within any of the plots. The surfaces of all plots are kept free of ground vegetation via hand weeding. In the NI and NL plots, shade cloths or light burning with a propane torch was used to control mosses that grew directly on the mineral soil. On these plots, 20 yr of aboveground litter exclusion has resulted in the complete loss of the O horizon. We also used OA-less plots, established to follow the trajectory of SOM formation from soils containing lower organic matter contents. The OA-less plots were created by removing the O and A horizons and then replacing this soil with 0- to 10-cm B horizon soil obtained immediately nearby.

Collection Methods

Soils were collected in October 2010. Two 20- by 20-cm O horizon samples per plot were collected by hand from all plots (except for the NL and NI plots, which do not have O horizons). Fine roots were hand picked from O horizon soils and separated into <1- and 1- to 2-mm pools. Two mineral soil cores were collected from each plot with a 9.52-cm-diameter diamond bit corer mounted on a power auger and separated into 0- to 10-, 10- to 20-, 20- to 30-, and 30- to 50-cm pools. In some cases, the deepest sample depth extended to only 40 cm, where glacial till prevented deeper coring. Rocks (>2 mm) were removed using 2-mm sieves; rock volume was determined via water displacement, and the remaining soil was weighed for estimates of soil mass per area. Due to the rockiness of the area (often >40% rock), a single rock content and a single bulk density of the fine soil mass was calculated for each horizon, and the mean soil mass of each horizon across the site was used to convert C concentration data to an areal basis. The exception to this protocol was that a separate bulk density was used for surface horizons in the OA-less plots because these soils had a significantly greater bulk density than the other plots as they are derived from B horizon soils. Samples were kept in airtight plastic bags at 4°C for transport to Oregon State University. Subsamples used for the year-long incubation remained field moist at 4°C until measurements began. The remaining soil was air dried and stored in airtight plastic bags until analysis. All samples for C and N analysis were dried and ground in a Spex Certimill 8000 and analyzed for total C and N using a Costech CHN elemental analyzer.

Respiration Analysis

Soil respiration was measured in a laboratory incubation of the mineral soils from the 0- to 10- and 10- to 20-cm depths. Moist soil (70 g dry-weight equivalent) from each soil core of the mineral horizons was placed in 150-mL volume microlysimeters, based on the design described by Nadelhoffer (1990). Soils were saturated with 0.01 mol L^{-1} $CaCl_2$ and allowed to drain for 4 h, after which drainage had stopped. This moisture level was defined as field capacity, and 60% of this field capacity was maintained throughout the experiment by periodic additions of deionized H_2O. We measured respiration on Days 1, 3, 7, 15, 25, 33, 55, 63, 96, and 242 with a Li-Cor LI-6400 portable photosynthesis system and a custom soil respiration attachment to fit our microcosms. Between measurements, the microcosms were stored in the dark at room temperature (approximately 20°C). The time needed to respire 1% of the C initially measured in the soil was used as an index of labile C (Conant et al., 2008).

Density Fractionation and Acid Hydrolysis

Mineral soils from the 0- to 10- and 10- to 20-cm depths were density fractionated using sodium polytungstate at three densities (1.85, 2.4, and 2.8) following Sollins et al. (2009). Soils were also analyzed for labile C following the acid hydrolysis method of Paul et al. (2006), with minor adjustments; specifically, particulate organic matter was removed with sodium polytungstate at a density of <1.85 g cm^{-3} before hydrolysis.

Enzyme Analyses

The activities of two key soil enzymes involved in litter breakdown and P acquisition were measured using the method of Caldwell et al. (1999). Levels of β-glucosidase (EC 3.2.1.21) and phosphomonoesterase (EC 3.1.3.2) were measured by modifying conventional *p*-nitrophenyl-ester-based assays in the surface mineral soil only. Assays were run without conventional buffers to measure enzyme activity under actual soil matrix conditions.

Statistical Analyses

One-way ANOVA was performed using the Statplus statistical package for Apple, with detrital treatment as the explana-

tory variable. Post-hoc Tukey honestly significant difference tests were used to determine the significance of differences among pairwise combinations of treatments using a significance level of $p < 0.05$. Analyses were conducted for each depth (0–10, 10–20 cm, etc.) and for the whole profile.

RESULTS

Total C and N concentrations (g kg^{-1} soil) and contents (g m^{-2}) of organic horizons differed among treatments (Table 2). The O horizon C and N concentrations and contents were significantly greater in DL than in control, OA-less, and NR treatments. There were also significant differences in fine root mass among treatments; DL and control plots had significantly more fine root mass than all other treatments. Although few, there were still measurable fine roots in the NR plots, indicating that roots had passed the barriers, most likely from underneath.

Although litter exclusion for 20 yr resulted in an 18% decline in total profile (to 50 cm) mineral soil C and root exclusion resulted in a 9% decline in C, these differences were not statistically significant (Table 2). However, C and N concentrations and contents in OA-less plots were significantly lower than all other treatments, both in surface horizons and in total soil mineral horizons. Trends for N contents were similar to trends in C contents, although differences in N contents were more variable.

Cumulative C respiration (g C g^{-1} soil) in surface soil (0–10 cm) incubations was lower in all three input exclusion

Table 2. Carbon and N concentrations and contents, bulk density of fine materials, rock content, and fine root mass of soils from the Harvard Forest DIRT experiment plots. Although bulk densities for each treatment are reported, there were no significant differences among litter manipulation treatments (other than OA-less plots, where the top 30 cm of soil was replaced with mineral soil) and thus a mean cross-site bulk density (0.64 g cm^{-2} for 0–10 cm, 0.87 g cm^{-2} for deeper horizons) was used to calculate C and N on an areal basis. A single cross-site rock content was used for each individual horizon for all treatments. At depths of 20 cm and greater, N content was too near detection limits to report values with certainty.

Depth	Control	Double litter	No inputs	No litter	No roots	OA-less
cm						
			Organic C concentration, g C kg^{-1} soil			
O horizon	324.6 ± 11.0 a†	427.3 ± 9.5 b			308.0 ± 43.9 a	244.8 ± 28.5 c
0–10	72.4 ± 6.7 a	68.5 ± 1.9 a	61.6 ± 5.0 a	58.0 ± 7.5 a	67.5 ± 7.6 a	26.9 ± 4.0 b
10–20	35.1 ± 3.0 a	35.7 ± 3.0 a	33.0 ± 2.0 a	33.2 ± 4.7 a	33.4 ± 4.5 a	15.4 ± 0.4 b
20–30	26.2 ± 1.2	23.55 ± 3.0	21.6 ± 2.8	20.4 ± 1.2	24.2 ± 5.7	16.7 ± 2.0
30–50	19.8 ± 0.1	17.7 ± 0.1	14.7 ± 0.3	13.7 ± 0.03	14.9 ± 0.2	14.6 ± 0.03
			Total N concentration, g N kg^{-1} soil			
O horizon	14.4 ± 0.4 a	17.1 ± 0.4 b			14.6 ± 1.9 a	10.8 ± 1.2 a
0–10	2.1 ± 0.4 a	2.2 ± 0.2 a	1.8 ± 0.3 a	1.6 ± 0.1 a	1.9 ± 0.4 a	0.5 ± 0.4 b
10–20	0.6 ± 0.3	0.6 ± 0.2	0.2 ± 0.1	0.4 ± 0.3	0.6 ± 0.5	‡
			Bulk density, g cm^{-3}			
0–10	0.59 a	0.59 a	0.66 a	0.71 a	0.66 a	0.87 b
			Rock content (all treatments), % (v/v)			
0–10			5.7			
10–20			18.4			
20–30			19.6			
30–50			30			
			C content, g C m^{-2}			
O horizon	1687 ± 237 a	2736 ± 608 b			318 ± 18 c	411 ± 22 c
0–10	4367 ± 380 a	4132 ± 140 a	3717 ± 272 a	3500 ± 346 a	4072 ± 334 a	2212 ± 223 b
10–20	2489 ± 190 a	2533 ± 158 a	2340 ± 213 a	2533 ± 238 a	2547 ± 281 a	1095 ± 28 b
20–30	1834 ± 96	1647 ± 180	1509 ± 139	1423 ± 63	1688 ± 320	1161 ± 127
30–50	2401 ± 102	2156 ± 172	1786 ± 384	1667 ± 34	1820 ± 283	1774 ± 33
Total mineral soil	11091 ± 491 a	10469 ± 356 a	9352 ± 514 a	8943 ± 583 a	10126 ± 742 a	6242 ± 274 b
			N content, g N m^{-2}			
O horizon	75 ± 4a	110 ± 9 b			15 ± 0.3 c	22 ± 5 d
0–10	129 ± 27 a	133 ± 8 a	108 ± 18 a	99 ± 25 a	140.6 ± 18 a	24 ± 13 b
10–20	42 ± 16	40 ± 10	21 ± 10	29 ± 11	43 ± 16	‡
			Root mass in O horizon, g m^{-2}			
Roots <1 mm	128.6 ± 23.4 a	236.4 ± 33.1 b	50.4 ± 5.1 c	34.9 ± 6.6 c	13.1 ± 6.7 d	33.4 ± 22.0 c
Roots 1–2 mm	33.0 ± 30.7 a	20.5 ± 8.3 a	4.4 ± 2.1 b	7.3 ± 4.5 b	0.4 ± 0.4 c	1.5 ± 1.5 b

† Means ± SE. Means followed by different letters are significantly different according to Tukey's honestly significant difference ($\alpha = 0.05$).

‡ Could not be expressed because N was not within detection limits.

treatments and OA-less treatments than in the DL treatment and controls, which did not differ from each other (Fig. 1a). Patterns in the 10- to 20-cm soil incubations (Fig. 2b) were less clear. The control and DL soils were not significantly different from one another, but the OA-less treatment had significantly higher respiration rates per gram of soil than all other treatments ($p < 0.001$). Respiration rates expressed per gram of soil C, a measure of the decomposability of C in the soil, followed patterns of respiration expressed per gram of soil. The amount of time to respire 1% of the soil C followed patterns of total C respired after 242 d (Table 3).

The light soil fraction (densities <1.85 g cm^{-3}) was the pool most responsive to litter input manipulation (Fig. 2). Control and DL treatments had significantly more light-fraction material than the exclusion treatments ($p < 0.001$); there were no significant differences among the exclusion treatments. Other density fractions did not differ among treatments. In deeper (10–20-cm) soils, variability in density pool recovery was very high and only the NI treatments were significantly less than the control ($p = 0.01$).

There were no significant treatment effects on non-hydrolyzable C or N concentrations in soils from either depth, and the data were extremely variable (Table 3). Values in the top 10 cm of soil ranged from 0.2 to 3.3% non-hydrolyzable C and 0 to 0.4% non-hydrolyzable N.

Enzyme activity varied significantly among treatments (Table 4); β-glucosidase and phosphomonoesterase were 30% higher in DL plots than in control plots ($p = 0.01$), and activities were significantly ($p = 0.03$ for β-glucosidase; $p = 0.04$ for phosphomonoesterase) reduced in litter removal plots. Enzyme activities in OA-less soils were significantly lower than the controls. Declines in β-glucosidase with root removals (NR and NI treatments) were greater than declines in phosphomonoesterase.

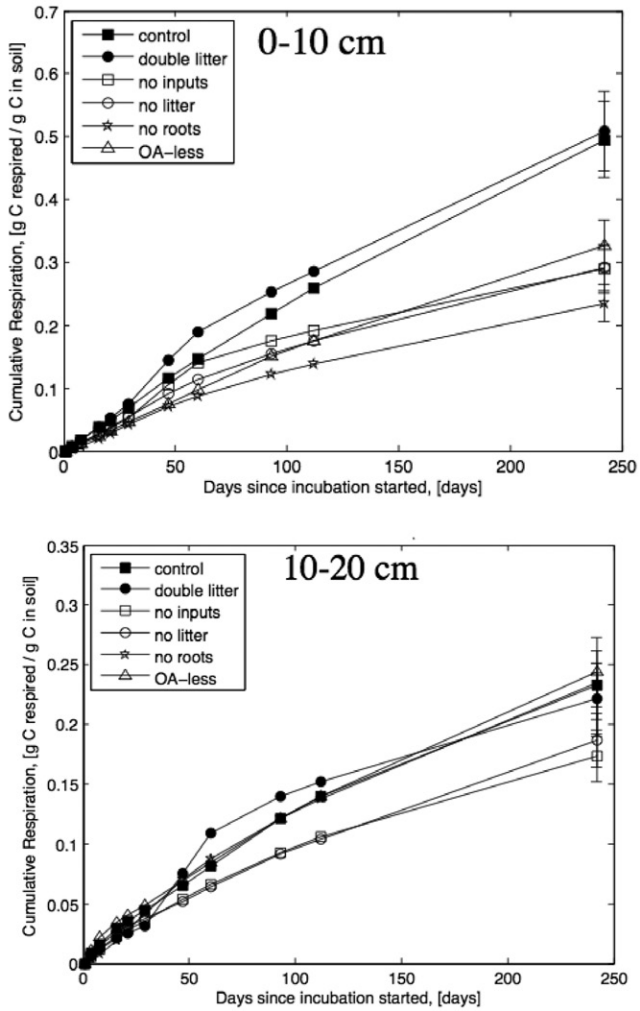

Fig. 1. Cumulative respiration for the 0- to 10- and 10- to 20-cm Harvard Forest soils from the DIRT experiment in laboratory incubations. The top 30 cm of soil was replaced with mineral soil in the OA-less treatment.

DISCUSSION

Soil Carbon Content

We were surprised that two decades of double litter inputs, which increased O horizon C, had no significant effect on mineral soil C content. However, these results are consistent with recent results from DIRT experiments in an old-growth Douglas-fir forest in Oregon and a mixed deciduous forest in Pennsylvania, both of which showed no significant differences in C content with doubled litter inputs within the first 20 yr of litter amendments (Sulzman et al., 2005; Bowden et al., 2014). However, Fekete et al. (2014) found an increase in C content with litter additions in an oak forest in Hungary after 10 yr, and Lajtha et al. (2014) saw a significant increase in total soil C in the deciduous forest DIRT site in Wisconsin, sampled after both 28 and 50 yr of DL treatments. Elevated enzyme activity at the Harvard Forest site, and higher rates of field soil respiration measured in the DL plots early in the experiment (Bowden et al., 1993), indicate that microbes responded to the elevated resource levels by increasing rates of litter decomposition, thus emitting C that could have been transferred to and stored in mineral soil pools.

None of the younger U.S. DIRT sites (Harvard Forest in Massachusetts, Bousson Experimental Research Reserve in Pennsylvania, and H.J. Andrews Experimental Forest in Oregon) showed increases in mineral soil C with litter additions. In fact, C contents in DL treatment plots were lower, although not sig-

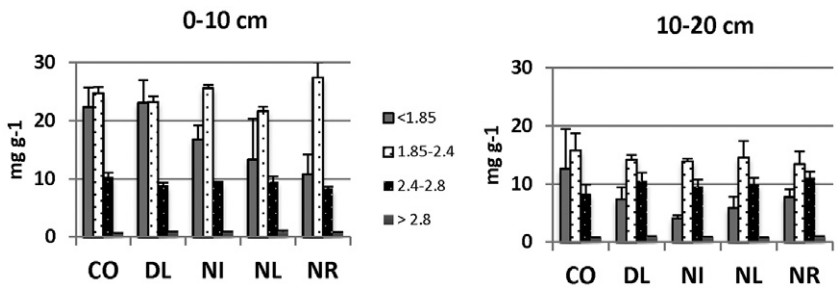

Fig. 2. Soil C concentrations in density fractions in the 0- to 10- and 10- to 20-cm soils of the control (CO), double-litter (DL), no-inputs (NI), no-litter (NL), and no-roots (NR) treatments at the Harvard Forest DIRT experiment plots.

Table 3. Number of days before 1% of soil C was respired, and non-hydrolyzable C and N concentrations for soils in Harvard Forest DIRT experiment plots; OA-less plots had the top 30 cm of soil removed and replaced with mineral soil.

Depth	Control	Double litter	No inputs	No litter	No roots	OA-less
cm						
			Time to 1% respired, d			
0–10	18.5	15.6	26.3	27.5	34.7	16.6
10–20	16.5	29.7	16.7	20.4	9.6	8.5
			Non-hydrolyzable C, %			
O horizon	24.0 ± 12.0†	23.9 ± 14.7	–	–	17.1 ± 7.5	15.7 ± 11.5
0–10 cm	7.9 ± 3.7	6.7 ± 4.8	5.1 ± 2.8	5.6 ± 2.1	10.9 ± 6.6	6.2 ± 7.7
10–20 cm	6.0 ± 5.8	3.6 ± 1.6	3.0 ± 0.8	7.5 ± 6.3	5.0 ± 4.1	1.1 ± 0.3
			Non-hydrolyzable N, %			
O horizon	1.2 ± 0.5	1.1 ± 0.6	–	–	0.9 ± 0.4	0.8 ± 0.5
0–10	0.5 ± 0.3	0.4 ± 0.2	0.3 ± 0.1	0.3 ± 0.1	0.6 ± 0.4	0.3 ± 0.4
10–20	0.3 ± 0.3	0.2 ± 0.1	0.2 ± 0.1	0.4 ± 0.2	0.3 ± 0.2	0.1 ± 0.02

† Means ± SE.

nificantly, than in controls at all three sites. Priming was detected directly in the 6th yr at the Oregon DIRT site (Sulzman et al., 2005), and the lower mean C content values in the DL plots across all the sites suggests that priming probably occurred in the early years at all the sites. In response to elevated litter inputs, priming may initially lower mineral soil C, and it may take several decades before elevated litter inputs are able to replenish the C released by priming and increase mineral soil C. Priming, considered to be a short-term effect (Guenet et al., 2012), is eventually balanced by incorporation and stabilization of new C inputs, and this crossover balance point probably occurs at different times in different forests. After 28 yr in the original Wisconsin forested DIRT sites, both forests (Noe and Wingra Woods) showed significant increases in soil C content in DL plots (Lajtha et al., 2014). This suggests that priming either occurred for a shorter period of time than for the other DIRT sites or else was never apparent. Significant increases in soil C content were found in a litter addition experiment in a moist tropical forest (Leff et al., 2012), suggesting that soil C dynamics in tropical soils, even with very high rates of decomposition, may not exhibit a priming effect from new C inputs.

Following total litterfall estimates of Bowden et al. (1993) and Davidson et al. (2002), about an additional 3000 g C m^{-2} was added to the DL plots during 20 yr. Although none of this was detectable in the mineral soils, DL O horizons accumulated approximately an additional 1000 g C m^{-2}, or about one-third of what was added. Given that much of the added C was respired, this suggests that more time might be needed to detect significant incorporation of litter C into mineral soils. In comparison, N additions via leaf litter were about 2 to 2.5 g N m^{-2} yr^{-1} following these same litterfall estimates. This amounts to an additional N input to DL plots of 40 to 50 g N m^{-2} during 20 yr, an addition of almost 20% of the total soil N. Although we could not detect any change in N content in the mineral soil, the O horizon of DL soils contained an extra 35 g N m^{-2} compared with the controls, suggesting that most added N during the 20-yr period remained in the O horizon.

Virtually all litter manipulation experiments have shown a relatively rapid decrease in mineral soil C with either root or aboveground litter removal (Sayer, 2006; Leff et al., 2012; Bowden et al., 2014; Fekete et al., 2014). Several studies have suggested that roots may contribute to the more stable C pools more than aboveground residues (i.e., Oades, 1988; Clemmensen et al., 2013; Rasse et al., 2005) and that rhizosphere microbes contribute substantially to soil C stabilization (Wilson et al., 2009). However, root exudates and mycorrhizae can also have the opposite effect by stimulating SOM decomposition (Cheng et al., 2012). After 20 yr in the Harvard Forest DIRT plots, there was approximately an 18% decrease in mineral soil C content (0–50 cm) with leaf litter removal and approximately a 9% decrease in C content with root exclusion. If the O horizon is included in these profile estimates, the loss of C with litter exclusion is 28% and the loss with root exclusion is 18%. The less significant C loss with root exclusion might indicate that aboveground litter has a more significant role in soil C stabilization than roots, contrary to other recent reports, or it might reflect the decomposition of roots left in the soil of NR plots followed by incorporation into SOM. Trends in loss during the next few decades will help to differentiate between these alternate hypotheses. After 50 yr of leaf litter exclusion in the Wisconsin site, Lajtha et al. (2014) measured a >50% reduction in C content in surface soils, although most of the loss in C was in the first 28 yr. Although this suggests that soils at the Harvard Forest are more resistant to C loss than those at the Wisconsin Arboretum, due to either climatic, mineralogic, or inherent biochemical reasons, clearly 30 more yr of observation are needed for a direct comparison.

The OA-less treatment, which had the O and A horizons removed, received organic matter inputs from both aboveg-

Table 4. Enzyme activities and percent change in enzyme activities compared to control in surface soils (0–10 cm); OA-less plots had the top 30 cm of soil removed and replaced with mineral soil.

Enzyme	Control	Double litter	No litter	No roots	No inputs	OA-less
			Enzyme activity, mmol *para*-nitrophenol kg^{-1} h^{-1}			
Phosphomonoesterase	18.7 ± 1.2 a†	24.5 ± 1.9 b	10.8 ± 1.5 c	15.8 ± 2.2	13.8 ± 1.0 d	15.0 ± 2.3 d
β-glucosidase	3.5 ± 0.4 a	4.5 ± 0.3 b	1.1 ± 0.2 c	2.8 ± 0.3 d	1.5 ± 0.1 e	2.0 ± 0.5 f
			Change compared with control, %			
Phosphomonoesterase	–	30.9	−15.5	−26.0	−42.5	−19.6
β-glucosidase	–	30.8	−19.0	−56.2	−68.1	−43.9

† Means ± SE. Means followed by different letters are significantly different according to Tukey's honestly significant difference ($\alpha = 0.05$).

round and belowground sources naturally for 20 yr and accumulated about 56% of the C content of the control plots. This reflects the slow nature of C accumulation in soils in general (Schlesinger, 1990) and also the more-than-a-century age of most SOM (e.g., Baisden et al., 2002; Crow et al., 2007). The O horizon of the OA-less soils contained only about one-quarter of the C content of control O horizon soils, which was surprising, given that coniferous O horizon soils generally have mean residence times of 20 to >40 yr (Fröberg et al., 2011) and deciduous forests soils probably have significantly lower mean residence times. However, the 0- to 10-cm OA-less mineral soil gained about 1000 g of C during the 20-yr period, substantially more than the 411 g C m^{-2} that accumulated in the O horizon. This reinforces a strong role for stabilization of organic matter by organic matter–mineral associations (Sollins et al., 2009). It also suggests that forest floors (well-developed O horizons), where present, play a critical role in retaining SOM and that forest floor removal leads to increased processing of litter inputs within the upper layers of mineral soils.

Soil Carbon Quality

The light fraction (<1.85 g cm^{-3}) of soil has generally been found to be the most reactive fraction to management or disturbance (Bremer et al., 1994; Liao et al., 2006; Spielvogel et al., 2006; Throop et al., 2013), although other studies have suggested that C accumulation occurs primarily in heavy-fraction, slow-turnover pools (Grandy and Robertson, 2007). As expected, decreased litter inputs caused decreases in light-fraction pools, showing that this pool is more rapidly depleted than higher density fraction pools, which are composed of soil C stabilized in aggregates (intermediate density fractions) or by strong organo-mineral associations (heaviest fractions) (Hatton et al., 2012; Mayzelle et al., 2014). Litter additions, however, did not result in parallel increases in either total soil C or any of the density pools; rapid respiration of O or mineral soil horizon organic matter, due to enhanced microbial activity or to increased rhizospheric activity, may have prevented soil C increases (Spears and Lajtha, 2004).

We calculated respiration in laboratory incubations both on a per gram basis, representing simple C production rates, as well as on a C respired per gram soil C as a measure of C quality, which is a measure of C decomposability. As expected, C decomposability was greater in control and DL plots than the litter removal plots, although differences were slight. Had any significant amount of added litter accumulated in the mineral soil of the DL plots, we would have expected greater respiration per gram of C in these soils because more of the total C would have been derived from fresh litter. However, given the lack of response of total C, or even light-fraction C in the mineral soil, to detrital additions, the lack of response in respiration rates was expected. At both the Andrews and Bousson DIRT sites (at 6 yr in the Andrews site and 12 yr at Bousson), lower rates of respiration in the DL soils than the controls suggested that priming had already occurred early in the experiment, thus depleting labile C in the mineral soil (Crow et al., 2006, 2009b).

We also expected high relative rates of respiration (g C respired g^{-1} initial soil C) in the OA-less treatment because most C in these plots is derived from litter that is 20 yr old or younger. We were surprised, therefore, that respiration of OA-less soil was significantly lower than control and DL plot soil and similar to rates in soils from the litter removal treatments. These results suggest that soil microbial function in these plots has not fully recovered. Additionally, we observed low root mass in the OA-less plots, thus the rhizospheric community may not yet be fully reestablished in this treatment. This was unexpected, given that tree roots, even if they had been disturbed during plot installation, have had 20 yr to reoccupy these soils.

After 20 yr of eliminating new organic inputs, we expected the proportions of non-hydrolyzable C and N to be higher in soils under litter exclusion, where there was presumably less labile material. During acid hydrolysis, compounds such as proteins, nucleic acids, and polysaccharides are digested, leaving compounds that are resistant to digestion, including aromatic components and wax-derived long-chain aliphatics (Paul et al., 2006). Although our respiration measurements suggest that litter removal soils had less labile C, we did not see significant differences among treatments. This might be a methodological issue; differences in respiration measurements could have been due to differences in light-fraction material among plots, and we removed light-fraction material before acid hydrolysis and thus measured a hydrolyzable fraction only in mineral-associated SOM, which did not differ among treatments. Plante et al. (2006) also found that C hydrolyzability in grassland and agricultural soil was invariant with treatments that should have increased SOM recalcitrance with decreasing SOM content, suggesting that "recalcitrance" may not be tightly coupled to the biochemistry of preserved organic fractions.

Soil Enzyme Activity

Because extracellular soil enzymes are directly responsible for the initial processing of detrital C and organic-bound nutrients (Sollins et al., 1996), treatment impacts on soil enzyme activities should indicate initial functional response(s) of the microbial community to a fresh litter supply. Many studies have suggested that soil enzyme activities are generally the most sensitive indicators of changes in the belowground microbial community from agricultural residue management (Dick, 1992, 1994; Gregorich et al., 1994; Jordan et al., 1995). In a field experiment in Costa Rica, both β-glucosidase and phosphomonoesterase responded more strongly to litter removal than did total soil organic C (Caldwell et al., 1999). The soil enzymes examined in this study are closely associated with the microbial processing of detrital C and P; β-glucosidase is a key enzyme in cellulolytic activity during the breakdown of plant litter, while phosphomonoesterase mineralizes ortho-P from organic phosphate esters and is commonly used as a general indicator of microbial activity. It was not surprising, therefore, that the response of these enzymes was greater than the response of total C, density fractions, or even respiration to litter manipulation.

SUMMARY

Taken together, our results suggest that soil C pools in this forest were remarkably and surprisingly resistant to C increases but were susceptible to decreases in C inputs. Clearly, soil C pools do not respond uniformly to increases or decreases in litter inputs and thus will not be tightly coupled to short-term changes in inputs. In mature forests, it may thus prove difficult to use productivity enhancements to increase soil C, but environmental changes or management activities that reduce litter inputs might result in the loss of soil C.

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