Forest Ecology and Management 258 (2009) 2224–2232

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Increased coniferous needle inputs accelerate decomposition of soil carbon in an old-growth forest

Susan E. Crow [a,b,*], Kate Lajtha [a], Richard D. Bowden [c], Yuriko Yano [d], Justin B. Brant [e], Bruce A. Caldwell [a], Elizabeth W. Sulzman [e]

[a] Botany and Plant Pathology Department, Oregon State University, Corvallis, OR 97330, USA
[b] ^{14}CHRONO Centre, Queen's University Belfast, BT9 6AX, UK
[c] Department of Environmental Science, Allegheny College, Meadville, PA, USA
[d] Municipality of Anchorage, Health and Human Services, Anchorage, AK 99501, USA
[e] Crop and Soil Science Department, Oregon State University, Corvallis, OR 97330, USA

ARTICLE INFO

Article history:
Received 17 July 2008
Received in revised form 15 December 2008
Accepted 8 January 2009

Keywords:
Andisol
Carbon balance
Coniferous forest
Priming effect
Soil priming

ABSTRACT

Changes in temperature, precipitation, and atmospheric carbon dioxide (CO_2) concentration that are expected in the coming decades will have profound impacts on terrestrial ecosystem net primary production (NPP). Nearly all models linking forest NPP with soil carbon (C) predict that increased NPP will result in either unchanged or increased soil C storage, and that decreased NPP will result in decreased soil C storage. However, linkages between forest productivity and soil C storage may not be so simple and direct. In an old-growth coniferous forest located in the H.J. Andrews Experimental Forest, OR, USA, we experimentally doubled needle litter inputs, and found that actual soil respiration rates exceeded those expected due to the C added by the extra needles. Here, we estimated that this 'priming effect' accounted for 11.5–21.6% of annual CO_2 efflux from litter-amended plots, or an additional 137–256 g C m^{-2} yr^{-1} loss of stored C to the atmosphere. Soil priming was seasonal, with greatest amounts occurring in June–August coincident with peaks in temperature and dry summer conditions. As a result of priming, mineral soil was more resistant to further mineralization during laboratory incubations. Soil lignin-derived phenols in the Double Litter plots were more oxidized than in the control, suggesting that the soil residue was more degraded. Our hypothesis that excess dissolved organic C produced from the added litter provided the link between the forest floor and mineral soil and a substrate for soil priming was not supported. Instead, the rhizosphere, and associated mycorrhizal fungi, likely responded directly to the added aboveground litter inputs. Our results revealed that enhanced NPP may lead to accelerated processing of some stored soil C, but that the effects of increased NPP on ecosystem C storage will be based on a net balance among all ecosystem C pools and are likely to be ecosystem-dependant. Forest C models need to include these complex linkages between forest productivity and soil C storage.

1. Introduction

Changes in ecosystem net primary productivity (NPP) and thus litterfall are predicted under climate change scenarios (Melillo et al., 1993; King et al., 1997; Raich et al., 2006). As a result, alterations of microbial (i.e. bacterial or fungal) biomass and activity also can be expected (Frey et al., 2004; Waldrop et al., 2004). Enhanced microbial respiration in response to additional plant litter inputs can release a portion of the newly added C as well as increase the rate of release of stored soil organic matter. This pattern, termed the "priming effect" was described as early as 1926 (Löhnis, 1926) and is the 'non-additive interactions between decomposition of the added substrate and of soil organic matter (SOM)' such that positive priming results in the acceleration of SOM decomposition and negative priming results in the retardation of SOM decomposition (Kuzyakov et al., 2000). Soil priming recently has received increased attention (see reviews by Kuzyakov et al. (2000) and Fontaine et al. (2003)) as the impacts of global change on terrestrial C dynamics are explored more thoroughly.

Microorganisms play a central role in determining if soil C pools increase or decrease and changes in microbial biomass or activity that resulted from alterations in inputs were frequently associated with soil priming (Kuzyakov et al., 2000). One hypothesis for the mechanism underlying the positive priming effect is that fast-growing microbes specializing in utilization of fresh inputs respond rapidly and produce extracellular enzymes that metabo-

* Corresponding author at: 42 Fitzwilliam Street, ^{14}CHRONO Centre, Queen's University Belfast, Belfast BT9 6AX, UK. Tel.: +44 28 9097 3085.
E-mail address: s.crow@qub.ac.uk (S.E. Crow).

0378-1127/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2009.01.014

lize not only fresh material, but also existing SOM (Fontaine et al., 2004a). Priming effects often have been attributed to enhanced microbial biomass and exoenzyme production in response to water-soluble sugar components of added litter (Schimel and Weintraub, 2003; Rasmussen et al., 2007, 2008). Alternatively, Fontaine et al. (2003) proposed a conceptual model for soil priming whereby the addition of fresh inputs establishes a competition between fast-growing species specialized in metabolizing fresh material and slow-growing species specialized in metabolizing SOM (but that also can utilize fresh material). When SOM-specialized microbes out-compete fresh litter-specialized microbes, e.g. under nutrient limiting conditions (Fontaine et al., 2004b), soil priming occurs.

In an old-growth coniferous forest at the H.J. Andrews Experimental Forest in the Pacific Northwest region of the U.S., Sulzman et al. (2005) reported that the annual CO_2 flux associated with the experimental doubling of aboveground litter increased by an additional 186 g C m^{-2} yr^{-1}, or a 34% increase, beyond what was expected based on rates of decay for the added litter. This elevated CO_2 flux suggested that positive soil priming occurred as a result of the added aboveground litter. In this region of the U.S., dry summer months are followed by a long wet season. Re-wetting of the forest floor and soil profile typically occurs in late October–November and results in a flush of dissolved organic carbon (DOC) in soil solution (Lajtha et al., 2005). Approximately one-third of water soluble leachates from fresh coniferous litter from this site were easily degradable carbohydrates (e.g., polysaccharides, and simple sugars) (Yano et al., 2004). In a seasonal experiment, Brant et al. (2006a) observed a shift in soil microbial community associated with the litter addition only in November.

Based on these collective observations at H.J. Andrews, we hypothesized that if fast-growing microbes specializing in the utilization of fresh inputs responded rapidly to added litter and resulted in overall positive soil priming, then the observed priming effect would be greatest in the fall when a flush of DOC from the forest floor provided an easily-accessible substrate for soil microbes and was associated with the shift in microbial community observed when extra litter was added to the forest floor. By this conceptual model, we expected DOC transport to provide the link between forest floor litter and mineral soil priming. To refine the relationships among increased CO_2 efflux, altered microbial communities, and DOC transport, we synthesized previously collected data in a novel analysis to investigate the potential impact of increased aboveground NPP on old-growth coniferous forest soil dynamics.

2. Methods

2.1. Field site

Plant litter inputs were manipulated as part of the on-going Detritus Input Removal and Transfer (DIRT) Experiment in the H.J. Andrews Experimental Forest in OR, USA (44°13′N, 122°13′W, 531 m elevation) since 1997. The H.J. Andrews DIRT site was established in an undisturbed old-growth (>500 yr) western hemlock [*Tsuga heterophylla* (Rafinesque) Sargent] and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] stand. Other significant tree species at the site include vine maple (*Acer circinatum* Pursh.) and western red cedar (*Thuja plicata* D. Don). Mean annual temperature is 8.7 °C and annual precipitation is 2370 mm yr^{-1}(average from 1973 to 2002), which occurs mostly as rain. Over 70% of the precipitation occurs during a wet season between November and March (Sollins et al., 1980). Nitrogen deposition to this area is ~0.2 g N m^{-2} yr^{-1} (Vanderbilt et al., 2003). Soils are derived from volcanic parent materials and classified as coarse loamy mixed mesic Typic Hapludands. The soil C/N ratio is 35, 19, and 16 for the 0–5, 5–10, and 10–20 cm increments of the mineral soil (Keirstead, 2004). In the A horizon, the bulk density is 0.82 Mg/ha), the texture is loamy with 13% clay, and the pH is 5.4 (Dixon, 2003). Mean annual soil temperature for 2001–2003 was 9.5 °C at 5 cm and mean annual soil moisture for 2001–2003 was 29% (Sulzman et al., 2005).

The DIRT Experiment treatments include the addition or removal of above- and belowground litter inputs with the goal of understanding long-term controls on soil organic matter formation and stability (Nadelhoffer et al., 2004). Six litter input/exclusion treatments, replicated three times, were randomly assigned to the plots. Plots are approximately 10 m × 15 m and include trees; there is a small range in plot sizes due to available space and obstacles. Litter manipulation treatments include combinations of aboveground litter addition, screens placed atop the soil surface to collect aboveground litter, and use of trenches and root barriers to remove roots (Table 1).

In this study, we utilized data from the Control, Double Litter, No Litter, and No Roots treatments, but focus on the Control and Double Litter treatments. To obtain a doubled needle and fine litter inputs for the Double Litter treatment, we used litter obtained from the No Litter plots; litter was excluded with 1-mm-mesh screens, and was transferred to Double Litter plots 2–5 times per year. Large branches and stems or lichen/moss masses that fell on screens were discarded. Over the first six years, 490 g C m^{-2} of additional litter has been added to the double needle plots; in 2005, the O-horizon depth was 1.9 cm on the Double Litter plots compared to 1.5 cm on the Control plots (Lajtha et al., 2005). In 2003, litter transfers were made on April 25 and July 17, but flux measurements for those months were taken before the litter addition occurred.

Daily precipitation totals and mean air temperature for 2003 were taken from the H.J. Andrews primary meteorological station (PRIMET) which is located at the nearby Experimental Forest headquarters (44°21′N, 122°26′W, 430 m elevation). Soil moisture was measured at the DIRT site at 10 cm in the A horizon at 30-min intervals (Onset Tidbit Temperature Data Logger, Onset Computer Corporation, Bourne, MA).

2.2. Field CO_2 flux and priming estimation

Soil CO_2 efflux was measured at least monthly in 2003 with a portable infrared gas analyzer (Li-6250, LI-COR Inc., Lincoln, NE) incorporated into a photosynthesis system (Li-6200), and attached to a closed, dynamic soil respiration chamber (LI-6200-09) designed for use with the Li-6200. For each measurement, the soil respiration chamber was placed on a 10 cm diameter by 5 cm height polyvinyl chloride (PVC) collar that was installed permanently 2 cm into the mineral soil. The forest floor and O-horizon was left intact within each PVC collar. There are five permanently

Table 1
Treatments and methods of the Detritus Input Removal and Transfer (DIRT) Experiment.

Treatment	Method
Control	Normal litter inputs are allowed.
No Litter	Aboveground inputs are excluded from plots with netting.
Double Litter	Aboveground leaf/needle inputs are doubled by adding litter removed from No Litter plots.
Double Wood	Aboveground wood inputs are doubled by adding large shredded wood pieces, both fresh and highly decayed, based on measured input rates of woody debris fall.
No Roots	Roots are excluded with impermeable plastic barriers extending from the soil surface to the top of the C horizon.
No Inputs	Aboveground inputs are prevented as in No Litter plots; belowground inputs are prevented as in No Roots plots.

installed PVC collars in each treatment plot. These data were included in a three-year dataset published previously in Sulzman et al. (2005). Here, we utilize the seasonal soil CO_2 efflux data from 2003. For each plot, data collected from the five PVC collars was averaged, and then the three replicate plots from the DIRT site were averaged for each month in 2003. Due to the unexpected passing of our colleague and subsequent inaccessibility of raw data, only these monthly average values and no variability estimates were available for analysis within this paper. Monthly data are presented so that trends established over time are apparent and the influence of outliers is lessened by the increased transparency of data.

Two methods were used to estimate the priming effect on the Double Litter plots. The first approach (Method A) used a first-order decay model for litter decomposition to estimate the amount of CO_2 efflux expected from the added litter and compared that to the actual measured amount of extra CO_2 efflux from the Double Litter plots. The second approach (Method B) used the DIRT treatments to partition aboveground, belowground, and root/rhizosphere sources of total CO_2 efflux and compared the expected amount of CO_2 efflux from the Double Litter plots to the measured amount.

In Method A, we calculated the expected amount of litter remaining in 2003 from that added during the first six years of the experiment (1997–2002) (a total of 55 g C m^{-2} remained) using a first-order decay constant for Douglas-fir and western hemlock litter from Harmon et al. (2004). We then calculated the expected respiration from the Double Litter plots in 2003 attributable to the remaining litter from previous years' additions and added it to the flux from the Control plots. Then we subtracted the expected flux from the measured flux from the Double Litter plots:

$$DL_{CO_2} - EXPECTED_{CO_2} = PRIMING_{CO_2}$$

where DL_{CO_2} is the measured CO_2 flux (g C m^{-2} $month^{-1}$), $EXPECTED_{CO_2}$ is the expected flux from decay of added litter plus the measured flux from the Control plots, and $PRIMING_{CO_2}$ is the difference. The priming effect was then calculated:

$$PE = \left(\frac{PRIMING_{CO_2}}{DL_{CO_2}}\right)100,$$

where PE is the priming effect (%) shown as the percent of total CO_2 flux from the Double Litter plots attributable to priming.

In Method B, the CO_2 flux attributed to roots/rhizosphere, aboveground litter, and belowground SOM was calculated in a series of differences in CO_2 flux between the DIRT plots (Bowden et al., 1993; Sulzman et al., 2005):

$$CTL_{CO_2} - NR_{CO_2} = ROOTS_{CO_2},$$

$$CTL_{CO_2} - NL_{CO_2} = AG_{CO_2},$$

$$CTL_{CO_2} - AG_{CO_2} - ROOTS_{CO_2} = BG_{CO_2},$$

where CTL_{CO_2} is the measured CO_2 flux (g C m^{-2} $month^{-1}$) from the Control plots, NR_{CO_2} is the measured flux from the No Root plots, NL_{CO_2} is the measured flux from the No Litter plots, $ROOTS_{CO_2}$ is the flux attributable to root/rhizosphere respiration, AG_{CO_2} is the flux attributable to decomposition of aboveground litter, and BG_{CO_2} is the flux attributable to decomposition of belowground C. We assumed that these fluxes remained constant and the flux due to aboveground litter decay doubled in the Double Litter plots to estimate the expected amount of CO_2 flux from the Double Litter plots ($EXPECTED_{CO_2}$). As in Method A, we subtracted the expected flux from the measured flux from the Double Litter plots to estimate flux due to priming ($PRIMING_{CO_2}$) and expressed it as the percent of total CO_2 flux from the Double Litter plots attributable to the priming effect (PE).

These calculations are a slight modification of the methods used in Sulzman et al. (2005), i.e. instead of calculating priming as a fraction of CO_2 flux from the Control plots, we calculate it as a fraction of CO_2 flux from the Double Litter plots. This accounts for a small discrepancy between our results and the previously reported annual means.

2.3. DOC collection and fractionation

O-horizon material was collected in August of 1999 from three mature Douglas-fir stands in the H.J. Andrews Experimental Forest that had thick (~4 cm) organic horizons that could be separated into Oi, Oe, and Oa horizons with a knife. Litter was extracted in a 1:40 litter-to-water ratio placed on a shaker at 100 rpm at 22 °C for 48–68 h followed by centrifugation at 7000 rpm for 15 min. The supernatant of each extract was filtered (Whatman GF/F) and stored frozen until chemical fractionation.

In summer 2000, one zero-tension lysimeter (20 cm × 20 cm plastic containers) was installed at the bottom of the O-horizon in each DIRT Control plot to collect O-horizon leachate. An area of about 30 cm × 30 cm of the O-horizon was removed, lysimeters were installed, and then the piece of O-horizon was put back gently upon the lysimeter. O-horizon leachates were collected from the zero-tension lysimeters installed on the DIRT control plots for chemical fractionation on an approximately monthly basis during November 2001 through May 2002 on a total of 5 dates.

Five Prenart Superquartz tension lysimeters, three at 30 cm and two at 100 cm, were installed in each plot in 1997 at a 30° angle. Samples were not collected from the 30 cm tension lysimeters during the first year, allowing the lysimeters time to equilibrate. Soil water was collected approximately monthly during the first few wet seasons, and several times per season in subsequent years, except when access was blocked by snow. Dissolved organic carbon concentration data collected from the 30 cm tension lysimeters from 1999 to 2004 were reported previously in Lajtha et al. (2005) within a larger dataset and are presented again here to compare DOC concentration of soil solutions between the Control and Double Litter plots.

To minimize biological and chemical alteration of the DOC collections, all samples were retrieved within 72 h after the application of tension (for tension lysimeters) or after the beginning of water collection (for zero-tension lysimeters). All samples were transferred on ice to Oregon State University and stored frozen until analysis for DOC and chemical fractionation. Initial experiments with filtering soil solutions demonstrated that tension lysimeters samples did not need to be filtered, but O-horizon leachates were filtered through Whatman GF/F filters (0.7 μm nominal pore size) before being stored.

Dissolved organic matter in soil solutions (O-horizon leachates and 30 cm tension lysimeters) and Oi, Oe, Oa extracts was characterized by fractionation into 6 operationally defined fractions by a method modified from Qualls and Haines (1991) and Leenheer (1981). The method fractionates DOM by its affinity to three different types of resins (Amberlite XAD-8, non-inonic; Amberlite AG MP-50, cation exchange; and Duolite A-7, anion exchange) and is described in detail in Yano et al. (2004). The recovered fractions include (1) phenolics (weak hydrophobic acids), small phenolic compounds (i.e. tannins and flavonoids), (2) strong hydrophobic acids (HoA), mainly microbially altered plant-derived material rich in aromatic C of larger molecular size, and may contain bound amino acids and carbohydrates, (3) hydrophilic acids (HiA), microbially synthesized and partly plant-derived material of smaller molecular size with high carboxyl-to-C ratios, (4) hydrophobic neutrals (HoN), less microbially altered plant-derived material and contains waxes, fatty acids, and microbial lipids, (5) hydrophilic neutrals (HiN), highly biodegradable carbohydrates and polysaccharides, mainly of microbial origin,

and may contain simple sugars and (6) bases, free amino acids, peptides, and proteins.

The data collected for litter leachates and O-horizon lysimeters were published within larger datasets in Yano et al. (2004). Tension lysimeter (30 cm) data are presented here for the first time and the data previously have not been reported together.

2.4. Soil collection and incubation

A composite of six 5-cm^2 cores taken to a depth of 5 cm per treatment plot was made for a total of ~750 g of mineral soil collected from each plot in June 2002. Each composite moist sample was sieved to remove material >2 mm and stored at 4 °C in tightly sealed bags until density fractionation. Soil was physically divided into two density fractions based on flotation in a 1.6 g cm^{-3} solution of sodium polytungstate (SPT, SOMETU, Van Nuys, CA) (Monnier et al., 1962; Greenland and Ford, 1964). Light fraction material includes partially degraded organic debris, including wood, roots, leaf/needles, and bark (Crow et al., 2007). An estimate of the 'recalcitrant' C pool was made by acid hydrolysis with refluxing of bulk soil in 6 M HCl at 116 °C for 18 h (Paul et al., 2006). Organic C concentrations of bulk soil, light fraction, and acid hydrolysis residue were determined by dry micro-Dumas combustion (NA1500 C/H/N Analyzer, Carlo Erba Strumentazione, Milan) at the Stable Isotope/Soil Biology Laboratory of the University of Georgia, Institute of Ecology.

Approximately 20 g of bulk mineral soil was incubated for one year (dark conditions, 23 °C) in bench top filtration units (Falcon Filter, Becton Dickinson Labware) modified after Nadelhoffer (1990). At the start of the incubation, soil was re-wetted by adding 10 mL of an inoculum solution prepared from fresh soil of the respective site shaken in distilled water for 1 h (1:10, soil:water) and filtered with a Whatman GF/F (0.7 μm pore size). Moisture content was maintained by adding distilled, deionized water to each chamber weekly to maintain a constant weight over the incubation period.

CO_2 efflux for each chamber was measured on days 3, 5, 8, 12, 17, 26, 53, 151, 267, and 361. At each measurement, chamber headspace was purged with CO_2-free air and sealed for approximately 240 min while respired CO_2 accumulated. A 500 μL-calibrated syringe was used to mix the headspace gas several times before extracting a sample, which was immediately injected into a Hewlett Packard 5700A gas chromatograph fitted with a 2 m Poropak R 80/100 column and thermal conductivity detector. Respiration rate was plotted against time and cumulative respiration was calculated for each substrate in SAS (SAS Institute, v. 9.1, Cary, NC) by using PROC EXPAND to approximate the area under the curve using the trapezoidal method. Mineralization data collected from the incubation experiment were previously reported in Lajtha et al. (2005) within a larger dataset and are presented again here to directly compare C mineralization between the Control and Double Litter plots.

2.5. Lignin-derived phenols

Alkaline cupric-oxide (CuO) oxidation (Hedges and Mann, 1979) was used to quantify lignin-derived phenols in bulk soil samples. The biopolymer extractions utilized Monel reaction vessels (Prime Focus, Inc., Seattle, WA, USA). Following the initial alkaline reaction and prior to the solvent extraction phase, ethyl vanillin was added as internal recovery standards for the lignin phenols. A Hewlett-Packard (5971) quadrupole mass spectrometer interfaced to a 5890 series II gas chromatograph was used to quantify individual compounds by extracted ion calibration curves. Lignin phenols were quantified by analysis of the trimethylsilane (TMS) derivatives (Hedges and Ertel, 1982) of vanillyl (V)-based (i.e. vanillin, acetovanillone, and vanillic acid); syringyl (S)-based (i.e. syringaldehyde, acetosyringone, and syringic acid); cinnamyl (Ci)-based (i.e. *p*-hydroxycinnamic acid and ferulic acid) monomers using extracted-ion internal calibration curves. The ratios of acid and aldehyde monomers within the S and V classes ($Ac/Al_{S,V}$) can be used as an index for the degree of lignin oxidation (degradation) (Kögel, 1986). In this study, SVCi-lignin (the sum of S, V, and Ci-based phenols, in mg 100 mg^{-1} C_{org}) is used to express the concentration of lignin-derived phenols.

2.6. Statistical analyses

Student's *T*-tests were used to compare mean values between the Control and Double Litter treatments when appropriate (PROC TTEST in SAS v.9.1; SAS Institute, Inc., Cary, NC). Samples were observed for normality, skewness, and kurtosis, but the low sample number limited the usefulness of these parameters. The two-tailed *T*-test is a robust analysis that can withstand some non-conformity to the assumption of normality (Zar, 1999) and we observed no obvious outliers in our samples. Statistical significance was set at 0.05. Because natural heterogeneity in forest soils is high and sample is size low due to constraints associated with the maintenance of long-term experimental plots, all *P*-values <0.10 are reported and discussed as trends.

3. Results

3.1. Seasonal patterns in CO_2 efflux and priming

Total soil CO_2 efflux at the field site was greatest during the spring months of April–June (with a peak in May) for the Control plots and the late spring/summer months of May–July (with a peak in July) for the Double Litter plots (Fig. 1). Soil CO_2 efflux for all of

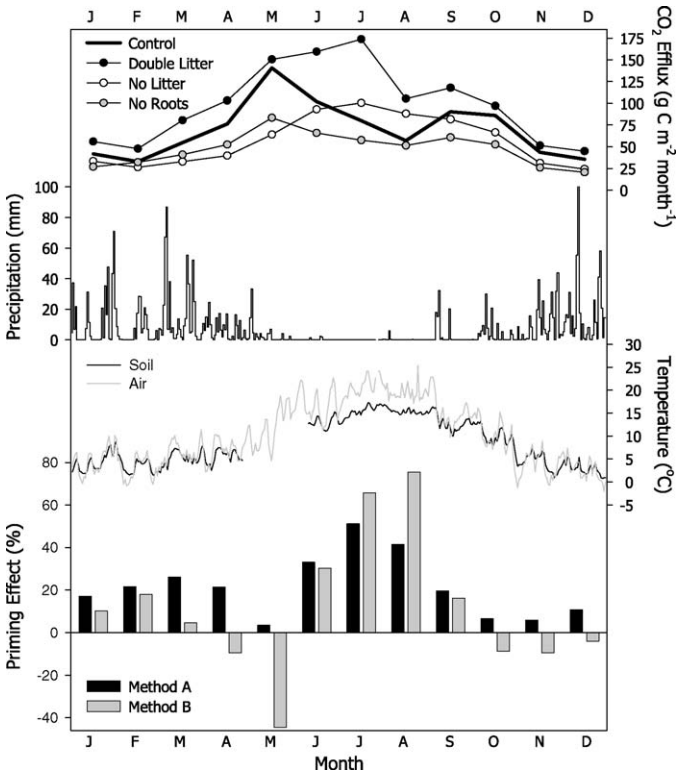

Fig. 1. Field-measured CO_2 efflux from the H.J. Andrews DIRT plots, precipitation, soil and air temperature, and percent of total CO_2 efflux from the Double Litter plots that is attributable to the priming effect, calculated by two methods. Values for soil CO_2 efflux and the priming effect are means of the three replicate plots.

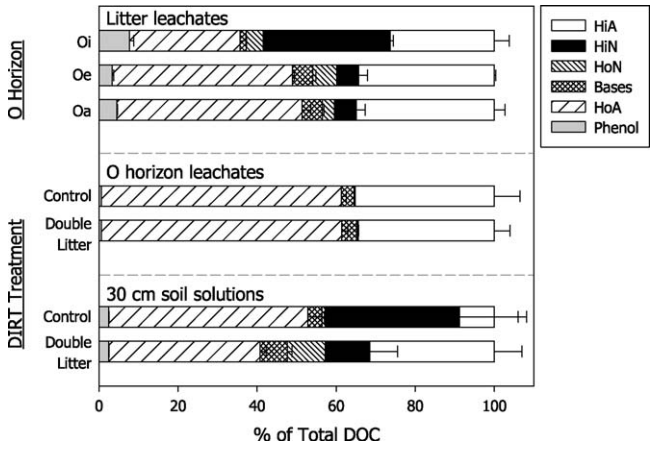

Fig. 2. Chemical composition of litter layer leachates, O-horizon leachates, and soil solutions collected from the Control and Double Litter DIRT plots. Values are means ± one standard error for the three replicate plots.

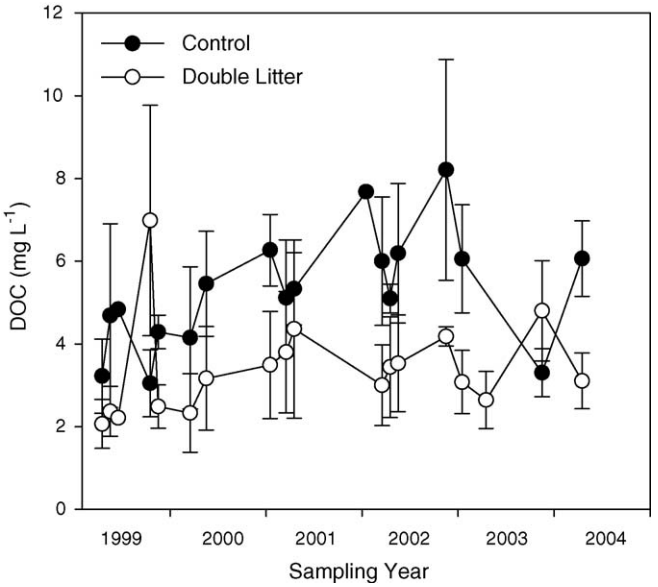

Fig. 3. Six years of DOC concentrations in soil solutions collected at 30 cm in the A horizon from the H.J. Andrews Control and Double Litter DIRT plots. Values are means ± one standard error for the three replicate plots.

the treatments generally increased throughout the spring months while precipitation was still present and air and soil temperatures increased following winter. However, during the warmest and driest months of late summer (July–August) soil CO_2 efflux declined. In September, precipitation increased and soil CO_2 efflux increased again before declining during the fall and winter months. This yearly pattern persisted at this site over the course of three years (2001–2003) (Sulzman et al., 2005). Effluxes from the Double Litter plots were greater than Control plots every month and, with two exceptions, the litter removal plots were less than the Control plots.

The priming effect estimated by Method A generally agreed with Method B each month, with reported low values for May, October, November, and December, intermediate values for January–April, and high values for June–August (Fig. 1). The decline in soil CO_2 efflux during the warm, dry, late-summer months coincided with the greatest percent of total CO_2 efflux attributed to priming as estimated by both methods.

3.2. DOC: chemical fractions and concentration

The relative abundance of hydrophilic neutral compounds decreased whereas hydrophobic and hydrophilic acid compounds increased in water extracted from increasingly degraded layers of the O-horizon (Oi, Oe, Oa) (Fig. 2). O-horizon leachates were dominated by the hydrophobic and hydrophilic acid groups (together constituting >92% of total DOC) and no differences in composition were apparent among the Control and Double Litter plots.

On every sampling date but two from 1999 to 2004, the DOC concentration in soil solutions collected from tension lysimeters at the 30 cm depth was greater in the Control plots than in the Double Litter plots (Fig. 3). In soil solutions collected from the 30 cm depth of the mineral horizon, the proportion of hydrophilic neutral compounds was elevated compared to the O-horizon leachates (Fig. 2). The relative abundances of hydrophilic neutral and hydrophobic acid compounds were lower and hydrophilic acid and hydrophobic neutral compounds were greater in the Double Litter plots compared to Control plots.

3.3. Soil properties and incubation

Variability in bulk soil C concentration was large and the means for Control and Double Litter plots were not significantly different (Table 2). The percent of bulk soil C recovered within the light fraction was greater in the Double Litter soil than the Control ($P = 0.070$). Although the concentration of lignin-derived phenols in bulk soil was the same in the Control and Double Litter plots, the decay state (ratio of acid to aldehyde lignin-derived phenols) of the vanillyl (V) phenol classes, which is the most abundant class in gymnosperm plant tissue (Hedges and Mann, 1979), was significantly greater in bulk soil from the Double Litter plots compared to the Control (Table 2).

During the one-year incubation of mineral soil, respiration rates were consistently lower from the Double Litter plots than from the Control plots (Fig. 4). As a result, there was a trend towards more cumulative C mineralized from the Control plots than the Double Litter plots ($P = 0.092$). Respiration rates generally leveled off after day 150. Therefore, we defined the 'labile' C pool as the cumulative C respired up to that point. The 'labile' C pool was smaller for the Double Litter plots than the Control plots, but not significantly so

Table 2
Soil carbon and lignin-derived phenol properties of mineral soil at the H.J. Andrews DIRT site.

	Control	Double Litter	*P*-value
C_{SOC} (g C kg^{-1} soil)	67.9 ± 10.7	95.9 ± 19.5	n.s.
C in light fraction (% of bulk soil C)	15 ± 1*	22 ± 3*	*0.070*
SVCi-lignin concentration (% of bulk soil C)	3.78 ± 0.70	4.03 ± 0.96	n.s.
Lignin-decay state (Ac/Ad_V)	0.45 ± 0.03**	0.54 ± 0.02**	*0.042*
'Labile' C, respired after 150 days (% of bulk soil C)	3.5 ± 0.2	2.8 ± 0.5	n.s.
'Recalcitrant' C, 6 N HCl residue (% of bulk soil C)	73.2 ± 4.0	80.0 ± 3.3	n.s.

Values are mean ± one standard error.
* Means that are trends at the $P < 0.10$ level.
** Means that are significantly different at the $P < 0.05$ level.

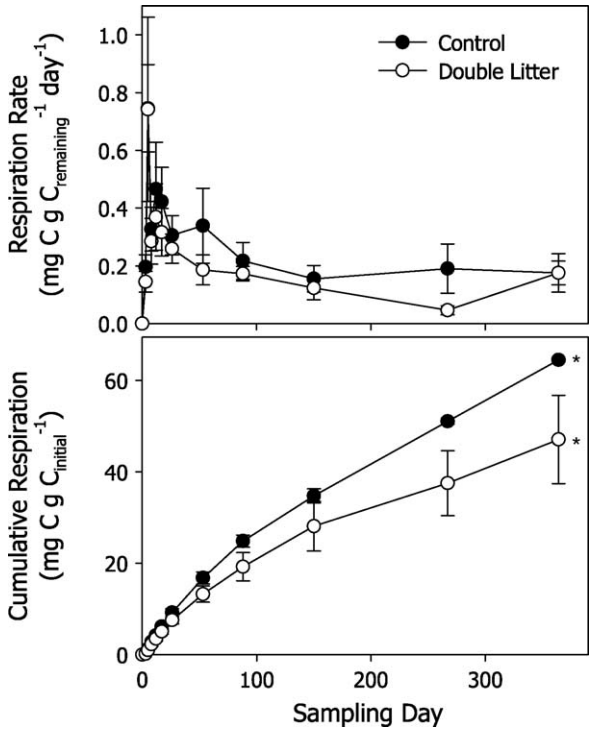

Fig. 4. Respiration rates (upper panel) and cumulative C mineralized (lower panel) during one-year incubation of bulk mineral soil collected from the H.J. Andrews Control and Double Litter DIRT plots. Values are means ± one standard error for the three replicate plots, an asterisk indicates a trend for the cumulative amount of C mineralized after one year ($P = 0.092$).

(Table 2). The 'recalcitrant' C pool, measured within the 6 N HCl acid digestion residues, was greater for the Double Litter plots than the Control plots, but also not significantly so.

4. Discussion

4.1. Microbial communities and seasonality in priming effects

Based in part on the observed shift in microbial community on the litter addition plots compared to the Control plots at H.J. Andrews in November 2003 (Brant et al., 2006a), we hypothesized that the greatest amount of priming would occur during autumn, when a fresh flush of needlefall and DOC (Lajtha et al., 2005), increased soil moisture (Sulzman et al., 2005), and an altered microbial community (Brant et al., 2006a) would suggest strong linkages between microbial processing and available organic matter. However, this hypothesis was not supported. We found that the least priming occurred in the months of October, November, and December and that the greatest priming occurred during the late spring and summer months (June, July, and August) (Fig. 1), during which time no difference in microbial community between the Control and Double Litter treatments was previously observed (Brant et al., 2006a).

For 2003, we estimated that on average 21.6% (Method A) or 11.5% (Method B) of the annual CO_2 efflux from the Double Litter plots was due to soil priming, which was equivalent to an additional 256 g C m^{-2} yr^{-1} (Method A) or 137 g C m^{-2} yr^{-1} (Method B) loss of soil C to the atmosphere. The dry summer typical of the Pacific Northwest reduced the CO_2 efflux but promoted priming in the Double Litter plots. The peak in priming coincided with the time of highest air and soil temperature and lowest precipitation (Fig. 1). In 2003, transfer of litter onto the Double Litter plots occurred in both April and July. Because priming was not similarly elevated in April–May, the point-source addition of litter is not likely a direct explanation for the high rates of priming that we observed during July–August. Instead, elevated priming in July–August likely was due to the cumulative added litter over six years and higher temperature, increased enzyme activity, and greater root activity, results that agree with other studies that found the greatest priming effect corresponded to peaks in litter decomposition and temperature (Subke et al., 2004).

4.2. Priming by ecosystem type

Our results are comparable to work in a Norway spruce stand, where existing populations of rhizosphere microbes were linked to soil priming following litter addition (Subke et al., 2004). Similar to our estimates, up to 19% of CO_2 efflux was attributable to soil priming following litter addition in this study. However, our results are in contrast to Cleveland et al. (2004), working in a tropical forest, who found that opportunistic members of the soil community, specifically members of the Gammaproteobacteria and Firmicutes groups, responded strongly to added substrates. The low nutrient status of the soils at our old-growth forest is associated with a high occurrence of ectomycorrhizal fungi and large overall contribution of belowground components to total soil CO_2 efflux (over 80%) compared to more nutrient rich sites (Sulzman et al., 2005). These observations suggest that processes controlling soil priming are different among ecosystems of differing climate, nutrient status, and vegetation type.

In our forest, a negative correlation exists between soil moisture and CO_2 efflux due primarily to the fact that in winter soil conditions are near saturation and, even during the dry summer, soil volumetric water content rarely falls below 20% (Sulzman et al., 2005). Measured over three years, soil temperature was not different between the Double Litter and Control plots. However, soil moisture was consistently lower in the Double Litter plots compared to the Control during the summer. Further, the Double Litter plots in late summer were the only plots to drop below 20% volumetric water content (Sulzman et al., 2005), the threshold below which other studies have shown a positive correlation between soil moisture and CO_2 efflux (Davidson et al., 1998; Rey et al., 2002).

Coniferous forests often are more fungal dominated than deciduous forests (e.g. Frey et al., 2004), which may help explain the difference in functionality of the microbial community among ecosystem types. In soil collected in July 2003 from the same H.J. Andrews site, Brant et al. (2006a) observed that the Control and Double Litter plot soils were positively associated with fungal PLFA biomarkers, but no significant differences in either fungal or bacterial biomass existed between the treatments. In an old-growth Douglas-fir–western hemlock forest in western Washington, Moore-Kucera and Dick (2008a) found a significant decline in PLFA biomarkers for both fungi and bacteria and an increase in stress biomarkers in late August compared to mid-June, suggesting that the microbial community was declining under water-limiting conditions. These results are in contrast with many other studies that have linked increases in microbial biomass and activity to priming (see review by Kuzyakov et al., 2000).

4.3. Coniferous litter as a substrate for priming

Much research has shown soil priming to occur in response to added sources of labile C (Kuzyakov et al., 2000; Brant et al., 2006b; Cleveland et al., 2007), although Rasmussen et al. (2008) also showed that additions of recalcitrant C can result in priming, especially when SOM is recalcitrant already. Litter decomposition rates are generally lower in coniferous litter than in deciduous litter (see Berg and McClaugherty, 2007). However, the hydrophilic neutral fraction was abundant in fresh litter from the Oi horizon relative to other compounds (Fig. 2) and is highly biodegradable

(Qualls and Haines, 1992; Jandl and Sollins, 1997). Don and Kalbitz (2005) found that C mineralization from DOC extracted from fresh pine and spruce litter was actually greater than mineralization from maple and beech-derived DOC; this indicates the potential of leachates from coniferous needles as a source of easily accessible organic matter inputs.

At H.J. Andrews, water-extractable DOC decreased significantly from Oi (385 mg/L), Oe (147 mg/L), and Oa (38 mg/L) horizons (Yano et al., 2004). Hydrophilic neutral compounds disappeared from soil solution with depth in the O-horizon and were replaced by hydrophobic and hydrophilic acid compounds (Fig. 2), which are comprised of more microbially altered compounds (Qualls and Haines, 1992). The concentration of DOC in O-horizon leachates was not significantly different for the Double Litter plots (51.1 mg/L) than the Control plots (39.8 mg/L) (Yano et al., 2004) and the chemical composition of O-horizon leachates was not distinguishable between the treatments (Fig. 2). This suggests that at this site, microbial activity extensively processes DOC before it enters the mineral horizon.

Kalbitz et al. (2007) proposed that added litter promoted priming in the Oe/Oa horizons, resulting in enhanced microbial DOC production from C already stored in the O-horizon. We did not find increases in DOC concentrations from plots with added litter, but in the added litter plots, we did find an increase in the relative abundance of DOC fractions of microbial origin and indicative of decomposition processes. The coniferous material appears to contain large initial amounts of labile material that may stimulate microbial respiration in the O-horizon, however this labile material disappears as the soil solution passes into mineral soil. Hence, labile C from aboveground litter is not likely to be a direct cause of priming in the mineral soil.

4.4. Evidence for mineral soil priming

By the time that we had conducted the laboratory incubation, the field experiment had been in operation for five years. If priming had been occurring *in situ* in the Double Litter plots over that time, then the soil used for the laboratory incubations should have contained C that already was more degraded and resistant to decomposition than the Control soil. Correspondingly, we found that respiration rates were consistently lower for the soil collected from the Double Litter plots than the control plots, leading to less cumulative C mineralization over the course of the year incubation (Fig. 4). The lignin-derived phenols in soil from the Double Litter plots were significantly more degraded than lignin-derived phenols from the Control plots, providing direct evidence that some SOM was degraded and further supporting the idea that priming had occurred in mineral soil, and not just O-horizon material (Table 2).

We expected DOC in soil solution to provide a substrate for the microorganisms responsible for soil priming. Although DOC from added litter did not directly provide the additional easily-accessible input to mineral soil that we expected, DOC concentrations in soil solutions collected from the 30 cm depth tension lysimeters consistently were elevated in the Control plots compared to the Double Litter plots throughout our five-year measurement period (Fig. 3). As a result, annual DOC flux from the 30 cm depth of mineral soil was lower in the Double Litter plots than the Control plots (Lajtha et al., 2005). However, the difference between treatments was not significant at 100 cm, suggesting that the net export of DOC to stream flow, which is a proxy for C losses from soil to streams, is not affected by litter additions. Thus, there was evidence that DOC in mineral soil horizons was utilized in excess on the Double Litter plots compared to Control plots, but this did not affect the overall soil C balance because it did not translate into decreased C loss through DOC.

In the mineral soil, root-derived C (i.e. root exudates and rhizosphere organic matter) provided fresh sources of different chemical classes of DOC. In the Control soils, we found that amount of hydrophilic neutral compounds (highly biodegradable material) collected in soil solution was substantially greater at the 30 cm depth in the mineral soil than it was immediately below the O-horizon (Fig. 2). However, in the Double Litter plots this easily degradable DOC fraction was present in lower relative amounts in soil solution than in the Control plots. In place of hydrophilic neutral compounds, hydrophobic neutral (plant-derived material including waxes, fatty acids, and microbial lipids) and hydrophilic acid (both microbially synthesized and plant-derived material of smaller molecular size with high carboxyl-to-C ratios) fractions were elevated (Qualls and Haines, 1991). Our results are similar to those found in a grassland site, where soil priming reduced the amount of fresh plant-derived DOC in the mineral soil between 10 and 20 cm and decreased DOC export when litter was added experimentally (Steinbeiss et al., 2008). This shift from easily degradable compounds to more recalcitrant plant-derived and microbially synthesized together with the decrease in DOC concentration in soil solution is consistent with mineral soil priming in the soil with additional litter inputs.

4.5. Link between O-horizon and mineral soil

Our evidence revealed that increased aboveground litter results overall in positive mineral soil priming, but the link between forest floor processes and mineral soil priming remains unclear. Subke et al. (2004) also found that adding litter alone was not sufficient to induce soil priming, but that the priming effects in a Norway spruce forest were related to the presence of roots and an active rhizosphere. Our results similarly suggest that the rhizosphere and litter additions are connected mechanistically and result in the observed elevation in soil CO_2 efflux as a result of rhizosphere priming, but that DOC does not provide a direct supply of easily degradable substrate between the forest floor and mineral soil that could have induced priming when litter was added.

Instead, biotic connections between the forest floor and mineral soil may have influenced processes that control priming. For example, the O-horizon typically is invaded by fine roots (Ehrenfeld et al., 1997). Across a variety of coniferous forests, Ehrenfeld et al. (1992) found that 30–60% of fine roots were found within the O-horizon. By some estimates, up to 80% of fine root biomass is located within the top 30 cm of soil at H.J. Andrews (Harmon, unpublished data). Fungal transport of litter residue and nutrients to mineral soil also has been shown (Frey et al., 2003; Williams et al., 2006) and Moore-Kucera and Dick (2008b) observed fungal hyphae emerging from the mineral soil into litter bags placed on the forest floor. Further, Brant et al. (2006b) found that fungi were primarily responsible for priming during a soil incubation experiment; adding a phenol substrate induced the strongest priming effect in soils from H.J. Andrews. Together with the increased decay state of the soil lignin-derived phenols, our results suggest that rhizosphere priming may be driven in part by lignin-degrading fungi in this old-growth coniferous site. Thus, roots and their associated mycorrhizal fungi potentially provide the link between the forest floor and mineral soil priming in our old-growth coniferous forest.

4.6. Net effect of soil priming

The net effect of increased litter additions to soil C depends on the sum of numerous soil processes. Our work indicated that soil priming accelerated processing of some soil C in the mineral horizon of this old-growth forest, but we also found early evidence of increased total soil C and recalcitrant C with added litter

(Table 2). Additionally, soil C was more resistant to decay and the 'labile' C pool showed signs of being smaller in the Double Litter plots compared to the Control plots. Douglas-fir and western hemlock needles are highly concentrated in cutin acids (Goni and Hedges, 1990; Crow et al., 2009), which are chemically recalcitrant and accumulate in soil (e.g. Nierop, 1998; Lorenz et al., 2007). Thus, additional needle inputs provide an added source of potentially stabilized soil C (Crow et al., 2009). Although some of these differences were not yet significant, they may become more prominent over time with continuous litter amendment.

Dividing soil into light and heavy fractions did not successfully separate C pools with different rates of turnover, i.e. the radiocarbon-based mean residence time of light fraction was 117 yr and the heavy fraction was 93 yr for the Control soil (Crow et al., 2007). Therefore, the observation that light fraction C increased with litter addition suggests an increase in what typically would be considered an intermediate (century-scale) soil C pool. Using sequential fractionation of the same soil at increasing densities, Sollins et al. (2006) found all C recovered in fractions <2.28 g/mL density had mean residence times of <200 yr. SOM associated with minerals >2.28 g/mL in density did have a mean residence time >680 yr, but this material comprised less than 5% of total soil C. Unless soil priming substantially decreased the amount of C in the most recalcitrant C pools, the effective impact of priming on overall C storage in this ecosystem is likely to be small. Thus, the net effect of soil priming on total C storage and dynamics induced by increased aboveground NPP remains unclear.

Relationships among net primary production, increased litter production, and net soil C storage are complex. Although priming may mineralize some recalcitrant soil C, increased inputs of C to soil may also move into stabilized pools of soil C (Hyvönen et al., 2007). To quantify net C exchange in soil, it will be critical to understand and to quantify all soil C flux processes. Importantly, soil mineralogy also factors into C stabilization. Rasmussen et al. (2007) found that in 90-day incubations, mineralogy was the dominant control on soil C priming in three coniferous forests. In addition, high soil C/N, low N availability, and high amounts of SOM stabilized by Fe oxyhydroxides, all characteristic of the old-growth forest soils at H.J. Andrews, affected the amount of C that was susceptible for priming (Rasmussen et al., 2007). The net balance of soil C storage in response to increased forest productivity will be depend upon rates of microbial processing of added of labile and recalcitrant C compounds, fluxes of DOC into soil C pools, and stabilization of soil organic C.

Acknowledgements

We thank Weixin Cheng and two anonymous reviewers for helpful comments on the manuscript. This project was supported by the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service, grant number 2002-35107-12249 and by National Science Foundation (NSF), Division of Environmental Biology (DEB) grant number 0087081. Air temperature and precipitation datasets were provided by the Forest Science Data Bank, a partnership between the Department of Forest Science, Oregon State University, and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, Oregon. Funding for these data and this project was provided by the National Science Foundation Long-Term Ecological Research program award to the H.J. Andrews Experimental Forest (DEB-02-18088).

References

Berg, B., McClaugherty, C., 2007. Plant litter: decomposition, humus formation, carbon sequestration, 2nd ed. Springer, NY.

Bowden, R.D., Nadelhoffer, K.J., Boone, R.D., Melillo, J.M., Garrison, J.B., 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Canadian Journal of Forest Research 23, 1402–1407.

Brant, J.B., Myrold, D.D., Sulzman, E.W., 2006a. Root controls on soil microbial community structure in forest soils. Oecologia 148, 650–659.

Brant, J.B., Sulzman, E.W., Myrold, D.D., 2006b. Microbial community utilization of added carbon substrates in response to long-term carbon input manipulation. Soil Biology & Biochemistry 38, 2219–2232.

Cleveland, C.C., Neff, J.C., Townsend, A.R., Hood, E., 2004. Composition, dynamics, and fate of leached dissolved organic matter in terrestrial ecosystems: results from a decomposition experiment. Ecosystems 7, 275–285.

Cleveland, C.C., Nemergut, D.R., Schmidt, S.K., Townsend, A.R., 2007. Increases in soil respiration following labile carbon additions linked to rapid shifts in soil microbial community composition. Biogeochemistry 82, 229–240.

Crow, S.E., Lajtha, K., Filley, T.R., Swanston, C.W., Bowden, R.D., Caldwell, B.A. 2009. Sources of plant-derived carbon and stability of of soil organic matter: implications for global change. Global Change Biology, doi:10.1111/j.1365-2486.2009.01850, in press.

Crow, S.E., Swanston, C.W., Lajtha, K., Brooks, J.R., Keirstead, H., 2007. Density fractionation of forest soils: methodological questions and interpretation of incubation results and turnover time in an ecosystem context. Biogeochemistry 85, 69–90.

Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biology 4, 217–227.

Dixon, J.J., 2003. Applying GIS to soil-geomorphic landscape mapping in the Lookout Creek valley, Western Cascades, Oregon. MS Thesis. Department of Crop and Soil Science, Oregon State University, Corvallis.

Don, A., Kalbitz, K., 2005. Amounts and degradability of dissolved organic carbon from foliar litter at different decomposition stages. Soil Biology & Biochemistry 37, 2171–2179.

Ehrenfeld, J.G., Kaldor, E., Parmelee, R.W., 1992. Vertical-distribution of roots along a soil toposequence in the New-Jersey Pinelands. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 22, 1929–1936.

Ehrenfeld, J.G., Parsons, W.F.J., Han, X.G., Parmelee, R.W., Zhu, W.X., 1997. Live and dead roots in forest soil horizons: contrasting effects on nitrogen dynamics. Ecology 78, 348–362.

Fontaine, S., Mariotti, A., Abbadie, L., 2003. The priming effect of organic matter: a question of microbial competition? Soil Biology & Biochemistry 35, 837–843.

Fontaine, S., Bardoux, G., Benest, D., Verdier, B., Mariotti, A., Abbadie, L., 2004a. Mechanisms of the priming effect in a savannah soil amended with cellulose. Soil Science Society of America Journal 68, 125–131.

Fontaine, S., Bardoux, G., Abbadie, L., Mariotti, A., 2004b. Carbon input to soil may decrease soil carbon content. Ecology Letters 7, 314–320.

Frey, S.D., Six, J., Elliott, E.T., 2003. Reciprocal transfer of carbon and nitrogen by decomposer fungi at the soil–litter interface. Soil Biology and Biochemistry 35, 1001–1004.

Frey, S.D., Knorr, M., Parrent, J.L., Simpson, R.T., 2004. Chronic nitrogen enrichment affects the structure and function of the soil microbial community in temperate hardwood and pine forests. Forest Ecology and Management 196, 159–171.

Goni, M.A., Hedges, J.I., 1990. Potential applications of cutin-derived CuO reaction-products for discriminating vascular plant sources in natural environments. Geochimica Et Cosmochimica Acta 54, 3073–3081.

Greenland, D.J., Ford, G.W., 1964. Separation of partially humified organic materials from soils by ultrasonic dispersion.In: 8th International Congress of Soil Science, Bucharest, 2, pp. 137–147.

Harmon, M.E., Bible, K., Ryan, M.G., Shaw, D.C., Chen, H., Klopatek, J., Li, X., 2004. Production, respiration, and overall carbon balance in an old-growth Pseudotsuga-Tsuga forest ecosystem. Ecosystems 7, 498–512.

Hedges, J.I., Ertel, J.R., 1982. Characterization of lignin by gas capillary chromatography of cupric oxide oxidation-products. Analytical Chemistry 54, 174–178.

Hedges, J.I., Mann, D.C., 1979. Characterization of plant-tissues by their lignin oxidation-products. Geochimica Et Cosmochimica Acta 43, 1803–1807.

Hyvönen, R., Agren, G.I., Linder, S., Persson, T., Cotrufo, M.F., Ekblad, A., Freeman, M., Grelle, A., Janssens, I.A., Jarvis, P.G., Kellomaki, S., Lindroth, A., Loustau, D., Lundmark, T., Norby, R.J., Oren, R., Pilegaard, K., Ryan, M.G., Sigurdsson, B.D., Stromgren, M., van Oijen, M., Wallin, G., 2007. The likely impact of elevated CO_2, nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. New Phytologist 173, 463–480.

Jandl, R., Sollins, P., 1997. Water extractable soil carbon in relation to the belowground carbon cycle. Biology and Fertility of Soils 25, 196–201.

Kalbitz, K., Meyer, A., Yang, R., Gerstberger, P., 2007. Response of dissolved organic matter in the forest floor to long-term manipulation of litter and throughfall inputs. Biogeochemistry 86, 301–318.

Keirstead, H., 2004. Quantifying C and N contents and isotope signatures of SOM pools in the HJ Andrews DIRT plots. M.S. Thesis. Department of Crop and Soil Science, Oregon State University, Corvallis.

King, A.W., Post, W.M., Wullschleger, S.D., 1997. The potential response of terrestrial carbon storage to changes in climate and atmospheric CO_2. Climatic Change 35, 199–227.

Kögel, I., 1986. Estimation and decomposition pattern of the lignin component in forest humus layers. Soil Biology & Biochemistry 18, 589–594.

Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. Soil Biology & Biochemistry 32, 1485–1498.

Lajtha, K., Crow, S.E., Yano, Y., Kaushal, S.S., Sulzman, E., Sollins, P., Spears, J.D.H., 2005. Detrital controls on soil solution N and dissolved organic matter in soils: a field experiment. Biogeochemistry 76, 261–281.
Leenheer, J.A., 1981. Comprehensive approach to preparative isolation and fractionation of dissolved organic-carbon from natural-waters and wastewaters. Environmental Science & Technology 15, 578–587.
Löhnis, F., 1926. Nitrogen availability of green manures. Soil Science 22, 253–290.
Lorenz, K., Lal, R., Preston, C.M., Nierop, K.G.J., 2007. Strengthening the soil organic carbon pool by increasing contributions from recalcitrant aliphatic bio(macro)-molecules. Geoderma 142, 1–10.
Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B.I., Vorosmarty, C.J., Schloss, A.L., 1993. Global climate change and terrestrial net primary production. Nature 363, 234–240.
Monnier, G., Turc, L., Jeanson-Luusinang, C., 1962. Une methode de fractionnement densimetrique par centrifugation des matieres organiques du sol. Annals of Agronomy 13, 55–63.
Moore-Kucera, J., Dick, R.P., 2008a. PLFA profiling of microbial community structure and seasonal shifts in soils of a Douglas-fir chronosequence. Microbial Ecology 55, 500–511.
Moore-Kucera, J., Dick, R.P., 2008b. Application of C-13-labeled litter and root materials for in situ decomposition studies using phospholipid fatty acids. Soil Biology & Biochemistry 40, 2485–2493.
Nadelhoffer, K.J., 1990. Microlysimeter for measuring nitrogen mineralization and microbial respiration in aerobic soil incubations. Soil Science Society of America Journal 54, 411–415.
Nadelhoffer, K.J., Boone, R.D., Bowden, R.D., Canary, J.D., Kaye, J., Micks, P., Ricca, A., Aitkenhead, J.A., Lajtha, K., McDowell, W.H., 2004. In: Foster, D., Aber, J. (Eds.), Forests in Time: The Environmental Consequences of 1000 Years of Change in New England. Yale University Press, pp. 300–315.
Nierop, K.G.J., 1998. Origin of aliphatic compounds in a forest soil. Organic Geochemistry 29, 1009–1016.
Paul, E.A., Morris, S.J., Conant, R.T., Plante, A.F., 2006. Does the acid hydrolysis-incubation method measure meaningful soil organic carbon pools? Soil Science Society of America Journal 70, 1023–1035.
Qualls, R.G., Haines, B.L., 1991. Geochemistry of dissolved organic nutrients in water percolating through a forest ecosystem. Soil Science Society of America Journal 55, 1112–1123.
Qualls, R.G., Haines, B.L., 1992. Biodegradability of dissolved organic-matter in forest throughfall, soil solution, and stream water. Soil Science Society of America Journal 56, 578–586.
Raich, J.W., Russell, A.E., Kitayama, K., Parton, W.J., Vitousek, P.M., 2006. Temperature influences carbon accumulation in moist tropical forests. Ecology 87, 76–87.
Rasmussen, C., Southard, R.J., Horwath, W.R., 2007. Soil mineralogy affects conifer forest soil carbon source utilization and microbial priming. Soil Science Society of America Journal 71, 1141–1150.
Rasmussen, C., Southard, R.J., Horwath, W.R., 2008. Litter type and soil minerals control temperate forest soil carbon response to climate change. Global Change Biology 14, 2064–2080.
Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P.G., Valentini, R., 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. Global Change Biology 8, 851–866.
Schimel, J.P., Weintraub, M.N., 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biology and Biochemistry 35, 549–563.
Sollins, P., Grier, F.M., McCorison, K., Cromack, K., Fogel, R.K., Fredricksen, R.L., 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecological Monographs 50, 261–285.
Sollins, P., Swanston, C., Kleber, M., Filley, T., Kramer, M., Crow, S., Caldwell, B.A., Lajtha, K., Bowden, R., 2006. Organic C and N stabilization in a forest soil: evidence from sequential density fractionation. Soil Biology & Biochemistry 38, 3313–3324.
Steinbeiss, S., Temperton, V.M., Gleixner, G., 2008. Mechanisms of short-term soil carbon storage in experimental grasslands. Soil Biology & Biochemistry 40, 2634–2642.
Subke, J.A., Hahn, V., Battipaglia, G., Linder, S., Buchmann, N., Cotrufo, M.F., 2004. Feedback interactions between needle litter decomposition and rhizosphere activity. Oecologia 139, 551–559.
Sulzman, E.W., Brant, J.B., Bowden, R.D., Lajtha, K., 2005. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO_2 efflux in an old growth coniferous forest. Biogeochemistry 73, 231–256.
Vanderbilt, K.L., Lajtha, K., Swanson, F., 2003. Biogeochemistry of unpolluted forested watersheds in the Oregon cascades: temporal patterns of precipitation and stream nitrogen fluxes. Biogeochemistry 62, 87–117.
Waldrop, M.P., Zak, D.R., Sinsabaugh, R.L., Gallo, M., Lauber, C., 2004. Nitrogen deposition modifies soil carbon storage through changes in microbial enzymatic activity. Ecological Applications 14, 1172–1177.
Williams, M.A., Myrold, D.D., Bottomley, P.J., 2006. Carbon flow from C-13-labeled straw and root residues into the phospholipid fatty acids of a soil microbial community under field conditions. Soil Biology & Biochemistry 38, 759–768.
Yano, Y., Lajtha, K., Sollins, P., Caldwell, B.A., 2004. Chemistry and dynamics of dissolved organic matter in a temperate coniferous forest on Andic soils: effects of litter quality. Ecosystems 8, 286–300.
Zar, J.H., 1999. Biostatistical Analysis, 4th edition. Prentice Hall, New Jersey.