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Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO_2 efflux in an old growth coniferous forest

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Abstract. In an old growth coniferous forest located in the central Cascade Mountains, Oregon, we added or removed aboveground litter and terminated live root activity by trenching to determine sources of soil respiration. Annual soil efflux from control plots ranged from 727 g C m^{-2} $year^{-1}$ in 2002 to 841 g C m^{-2} $year^{-1}$ in 2003. We used aboveground litter inputs (149.6 g C m^{-2} $year^{-1}$) and differences in soil CO_2 effluxes among treatment plots to calculate contributions to total soil efflux by roots and associated rhizosphere organisms and by heterotrophic decomposition of organic matter derived from aboveground and belowground litter. On average, root and rhizospheric respiration (R_r) contributed 23%, aboveground litter decomposition contributed 19%, and belowground litter decomposition contributed 58% to total soil CO_2 efflux, respectively. These values fall within the range of values reported elsewhere, although our estimate of belowground litter contribution is higher than many published estimates, which we argue is a reflection of the high degree of mycorrhizal association and low nutrient status of this ecosystem. Additionally, we found that measured fluxes from plots with doubled needle litter led to an additional 186 g C m^{-2} $year^{-1}$ beyond that expected based on the amount of additional carbon added; this represents a priming effect of 187%, or a 34% increase in the total carbon flux from the plots. This finding has strong implications for soil C storage, showing that it is inaccurate to assume that increases in net primary productivity will translate simply and directly into additional belowground storage.

Introduction

Soils are a major pool of global carbon storage (Schimel 1995), and annually store and release enough carbon to influence global climate. Current fluxes of carbon from soil to the atmosphere via decomposition of organic matter plus root respiration are approximately 10-fold greater than fossil fuel and deforestation sources combined (Schimel et al. 2000); hence, even small changes in total fluxes will influence atmospheric chemistry and heat balance. Considerable

effort has been devoted to quantifying fluxes of CO_2 from soils (e.g., Houghton 1999; Schimel et al. 2000; Goodale et al. 2002), however, quantifying factors that influence C fluxes is challenging because soil CO_2 efflux has three origins: root respiration plus microbial respiration derived from rhizodeposition, microbial respiration of litter from aboveground sources, and microbial respiration of belowground litter.

Quantifying contributions from microbial decomposition of complex soil organic matter and co-located rhizosphere respiration is important because microbial decomposition of residual organic matter influences the amount of carbon ultimately stored in soil. However, the desired partitioning is challenging and at this time no perfect method is available for accomplishing it (Hanson et al. 2000; Högberg et al. 2004, 2005). In addition, it is probably empirically impossible to truly separate autotrophic respiration from respiration associated with rhizosphere organisms, and thus Högberg et al. (2004) distinguished those organisms that receive photosynthates more or less directly from the plant canopy ('functional autotrophs') vs. those that receive their carbon mainly through decomposition of dead or dying organic matter ('functional heterotrophs'). Throughout this paper R_r will be used to indicate activity of functional autotrophs (dependent upon recent C in the rhizosphere), whereas R_h will be reserved for functional heterotrophs.

Autotrophic and heterotrophic respirations respond differently to environmental factors. For example, Boone et al. (1998) suggested that root respiration and microbial respiration might have different Q_{10} values, Högberg et al. (2005) reported rapid response of heterotrophic, but not autotrophic, respiration to short-term temperature decreases, and Goulden et al. (1996) showed that heterotrophic respiration decreased more than autotrophic respiration during extended drought in a temperate deciduous forest. However, weak relationships between temperature and decomposition rates of soil organic matter have also been reported (e.g., Giardina and Ryan 2000; Janssens et al. 2001; Curiel Yuste et al. 2004). Despite attention given recently to separating components of soil CO_2 efflux, there still exists great uncertainty and variability among estimates within forest ecosystems (e.g., Hanson et al. 2000; Högberg et al. 2001; Kutsch et al. 2001; Widén and Madji 2001; Rey et al. 2002; Lavigne et al. 2003; Lee et al. 2003). Partitioning the components of soil respiration within different ecosystems and defining the variables controlling each component is necessary to quantify carbon fluxes between soils and the atmosphere.

The objective of this study was to determine the contributions of heterotrophic (R_h) and 'autotrophic' respiration (loosely defined as roots + associated mycorrhizae as described above: R_r) to total soil CO_2 efflux in an old growth coniferous forest of central Oregon, USA. In addition, we examined the influence of doubling litter inputs, due to increased aboveground productivity, on respiratory losses from soil.

Methods

Framework for the study

The current study is part of a long-term inter-site project (Detritus Input and Removal Treatments, DIRT) that is assessing how rates and sources of plant inputs control accumulation and dynamics of soil organic matter (SOM) and nutrients in forest soils. The original DIRT treatments, designed by the late Dr. Francis Hole at the University of Wisconsin Arboretum in 1956, consist of chronically altering plant inputs to forest soils by regularly removing surface litter from permanent plots and adding it to others. Our network of DIRT sites now includes five temperate forest sites including an oak forest at the Harvard Forest, MA (established 1990), a black cherry/sugar maple-dominated forest in the Bousson Experimental Forest, PA (1991), an old growth coniferous forest at the H.J. Andrews Experimental Forest, OR (1997), an oak forest at the Michigan Biological Laboratory, Pellston, MI (2004), and an oak forest in Síkfőkút Forest, Eger, Hungary (2000).

Study site

Plant litter inputs have been manipulated at the DIRT plots in the H.J. Andrews Experimental Forest (HJA), Oregon (44°15′ N, 122°10′ W, 531 m elevation) since 1997. Mean annual temperature at the headquarters site of HJA is 8.7 °C (1973–2002) and mean annual precipitation over the same period is 2370 mm $year^{-1}$, mostly as rain. In general over 70% of the precipitation occurs during a 'wet season', between November and March. Two of the study years, 2001 and 2002, received only 78 and 75% of the long-term mean annual precipitation, respectively. Rainfall in 2003 was 98% of the long-term mean. Study years 2001 and 2003 were warm compared to the long-term mean (9.4 and 10.1 °C, respectively). Nitrogen deposition to this area is ~ 0.2 g N m^{-2} $year^{-1}$ (Sollins et al. 1980). The DIRT site was established in an undisturbed old-growth Douglas-fir (*Pseudotsuga menziesii*) – western hemlock (*Tsuga heterophylla*) stand. Other important tree species at the site include western red cedar (*Thuja plicata*) and vine maple (*Acer circinatum*). Soils are derived from volcanic parent materials and have strong andic properties: high amorphous Al hydroxide and aluminosilicate contents (oxalate-extractable Al = 1.1%) and a pH in 1 N NaF near 11 (Yano et al. in press). They are classified as coarse loamy mixed mesic Typic Hapludands (Dixon 2003). Basic soil characteristics of the site are presented in Table 1.

Experimental manipulations

In 1997 six litter input/exclusion treatments (three replicates per treatment, Table 2) were located randomly at the site. Plots are typically 10 m × 15 m,

Table 1. Soil and environmental characteristics of H.J. Andrews DIRT site.

Taxonomic subgroup	Typic Hapludands[a]
Depth (cm)	90+ cm
pH of mineral surface horizon	5.4
C:N (0–5 cm)	28.6
Bulk density mineral surface horizon (Mg/m^3)	0.82
Texture of A horizon	Loam
% clay in A horizon	9–20% (mean = 13%)
Mean annual soil temperature at 5 cm (°C)[b]	
2001	9.5
2002	9.8
2003	9.1
Mean annual soil moisture at 10 cm (%)	
2001	31.0
2002	25.9
2003	30.1
Mean annual air temperature (°C)	
2001	9.4
2002	7.7
2003	10.1
Mean annual precipitation (mm)	
2001	1852.1
2002	1773.1
2003	2332.8

Soil data are averages of 14 pits described to at least 60 cm. Data from Dixon (2003) and Keirstead (2004).

[a]Small areas of Andic Dystrudepts and Vitrandic Dystrudepts also underlie the treatment plots.

[b]Note that air temperature does not follow the same interannual pattern as soil temperature.

Table 2. Treatment methods of the Detritus Input and Removal (DIRT) plots.

Treatment	Method
Control	Normal litter inputs are allowed.
No Litter	Aboveground inputs are excluded from plots.
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 based on measured input rates of woody debris fall.
No Roots	Roots are excluded with impenetrable 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.

although there is a small deviation in size in some plots due to available space or obstacles. On No Litter and No Input plots, litter was excluded with 1 mm-mesh screens. To double the input of needles and fine litter, litter from No Litter plots was transferred to Double Litter plots 4–5 times per year: at the end of the dry season, twice or more during the wet season (November–March), and at the beginning of the dry season (typically June). Large branches

and stems or lichen/moss masses that fell on screens were discarded. To double the mass of woody debris in the forest floor of Double Wood plots, several buckets of roughly 2.5 cm^2 chips of Douglas-fir logs are evenly spread every other year. No Root and No Input plots were established by trenching the perimeter to 1 m, inserting a 10 mil (0.35 mm) thick polyethylene sheet along the bottom and sides of the trench, then back-filling the trenches. The same mesh screen as for the No Litter plots was also used for the No Input plots. New vegetation was continually removed from the No Roots and No Inputs plots. Mosses re-grew rapidly, and were removed semi-annually.

Soil CO_2 flux

Soil CO_2 efflux was measured roughly every other week (June–September) to once per month (remainder of the year) from July 2001 to December 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 (Norman et al. 1992). 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. There are five permanently-installed PVC collars in each treatment plot. The volume of the chamber + collar head space at every location was measured frequently and up-to-date values were used to calculate fluxes with minimal measurement error. A foam gasket made an air-tight seal between chamber and collar. Air entering the chamber was partially scrubbed to below ambient levels before starting the readings, and allowed to build to just above ambient during a measurement sequence. Carbon dioxide concentration was recorded every 5 ppm increase, for a total of three readings at each location. During each respiration measurement soil temperature was measured at 10 cm (Li Cor thermocouple) and soil moisture was measured at 12 cm using a hand-held time-domain reflectometer at four locations outside each soil collar (Hydrosense probe, Decagon Devices). Litterfall at our site was obtained using long-term litterfall data from stands of similar age, species composition, and elevation at HJA LTER (HJA LTER 2004a). Those data were collected from 6×1 m^2 traps monthly in each stand from 1977 to 1985. As a verification of litterfall at our site, during the second half of 2002 and the first half of 2003, we collected litterfall at 16 locations within the DIRT study area each time soil CO_2 fluxes were measured. Traps were 0.16 m^2 nursery trays lined with mesh screen. The mean annual air temperature at the H.J. Andrews during the two litterfall collection periods was statistically indistinguishable.

Statistical analysis and annual summation

Measurements of flux, temperature, and moisture at the time of each respiration measurement were used along with continuous soil temperature data at 5 cm

depth from the DIRT site (Hobo probe, Onset Computer Corporation, Bourne, MA) and continuous soil moisture at 10 cm depth from a nearby meteorological station (Primet: HJA 2004b) to model daily soil respiration. There was a strong correlation between temperature measured at individual treatment plots and the continuous temperature probe located on-site (slope of regression line with all data 1.05, R^2 = 0.95), so the continuous data were used without adjustment as a parameter in the flux model. Soil moisture at the meteorological site was lower than soil moisture at the DIRT site, probably because the measurement tower is in a clearing. However, the meteorological soil moisture followed the same pattern that we measured at our site. To estimate daily soil moisture at our measurement site for days between measurements, we assumed that the daily soil moisture pattern at the station matched the daily soil moisture signal at the measurement site. We then inserted the same soil moisture pattern at the station to the soil moisture at our site to create plot-specific daily moisture patterns (Figure 1). Individual curves were created for each plot (n = 17) in each year (n = 3), for a total of 51 independent soil moisture curves. Lastly, we used continuous temperature and moisture data in plot-specific annual multiple linear regression models; flux data were log transformed because of non-normality (Splus version 6.1, Insightful Corp.). The simplest model that explained most of the variance was:

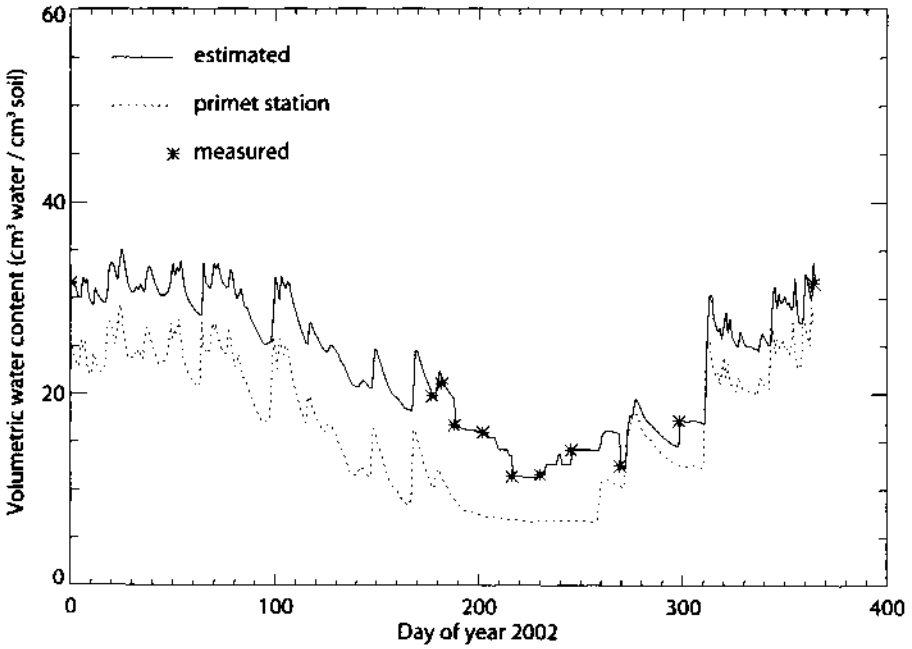


Figure 1. Modeled and measured soil moisture for one of three replicate DIRT plots at H.J. Andrews of the Double Litter treatment in 2002. Continuous moisture data were created for all 17 plots of the six treatments for each year (2001–2003).

$$\ln(\text{resp}) = \text{moisture} + \text{temperature} + \text{temperature} * \text{moisture} \quad (1)$$

Models were developed (Table 3) for each sampling plot ($n = 3$ per treatment except for No Litter) for each year (2001–2003). One of the plots with No Litter treatment was excluded from the analyses because it is surrounded by vine maple (*Acer circinatum* Pursh), which has been shown to dramatically alter soil pH, C, and N content (Tashe and Schmidt 2003). We also found that respiration values from this plot were fundamentally different from other plots of this treatment. This is the only location in this part of the forest that has a high concentration of vine maple, and so is not representative of the forest as a whole. As the No Litter plots are not used in the budget partitioning, excluding this plot did not impact any of our conclusions. Model estimated daily flux rates were averaged by treatment and summed to create an annual treatment-specific value. This study was analyzed as a Completely Randomized Design with each treatment as the replicate experimental unit, and each plot as a repeatedly measured unit within each treatment. The statistical significance of treatment, year, and the interaction between treatment and year were analyzed with analysis of variance (ANOVA) using PROC MIXED (SAS version 8.1, SAS Institute, Inc). In instances where the interaction between treatment and year was not significant ($p > 0.05$), the interaction was removed and the analysis was repeated using all three years of data. When ANOVA resulted in a p-value

Table 3. Multiple linear regression model parameters using soil moisture (β_1) and temperature (β_2) to predict soil CO_2 efflux at the H.J. Andrews LTER DIRT plots.

Year	Treatment	Constant	β_1 (se) moisture	β_2 (se) temperature	β_3 (se) moist:temp	F	R^2
2001	NI	−3.48	−0.006 (0.004)	0.321 (0.145)	0.073 (0.060)	70.01	0.98
	NR	3.31	0.006 (0.001)	−0.127 (0.060)	−0.088 (0.025)	50.67	0.97
	NL	−4.97	−0.009 (0.004)	0.346 (0.124)	0.154 (0.066)	9.70	0.91
	CO	−0.72	−0.002 (0.002)	0.117 (0.072)	0.026 (0.031)	8.78	0.84
	DN	−0.01	−0.001 (0.002)	0.122 (0.058)	0.009 (0.028)	22.84	0.93
	DW	−1.93	−0.005 (0.002)	0.256 (0.055)	0.061 (0.021)	15.86	0.92
2002	NI	0.55	0.004 (0.001)	−0.053 (0.050)	−0.028 (0.019)	4.17	0.58
	NR	0.94	0.008 (0.001)	−0.103 (0.019)	−0.036 (0.007)	30.49	0.91
	NL	11.72	0.027 (0.004)	−0.761 (0.114)	−0.378 (0.051)	6.62	0.64
	CO	1.06	0.005 (0.001)	−0.070 (0.036)	−0.038 (0.018)	12.39	0.82
	DN	−0.81	0.002 (0.001)	0.086 (0.036)	0.034 (0.016)	12.20	0.82
	DW	1.60	0.007 (0.001)	−0.091 (0.035)	−0.048 (0.014)	7.10	0.68
2003	NI	−2.67	0.012 (0.001)	−0.052 (0.046)	0.017 (0.025)	14.90	0.86
	NR	4.34	0.008 (0.001)	−0.241 (0.028)	−0.119 (0.012)	2.95	0.56
	NL	3.39	0.010 (0.001)	−0.168 (0.026)	−0.130 (0.011)	10.38	0.82
	CO	3.03	0.012 (0.001)	−0.223 (0.034)	−0.105 (0.015)	9.98	0.79
	DN	0.27	0.005 (0.001)	0.018 (0.041)	−0.016 (0.021)	17.08	0.88
	DW	0.12	0.0080 (0.001)	−0.061 (0.019)	−0.024 (0.007)	3.17	0.54

One replicate plot from each treatment is presented as an example. Models are of the form: ln(respiration) = moisture + temperature + moisture*temperature.

<0.05, pre-planned comparisons between the six treatments were made using orthogonal contrasts. Treatment differences in moisture content were analyzed using the same method.

Partitioning soil CO_2 flux

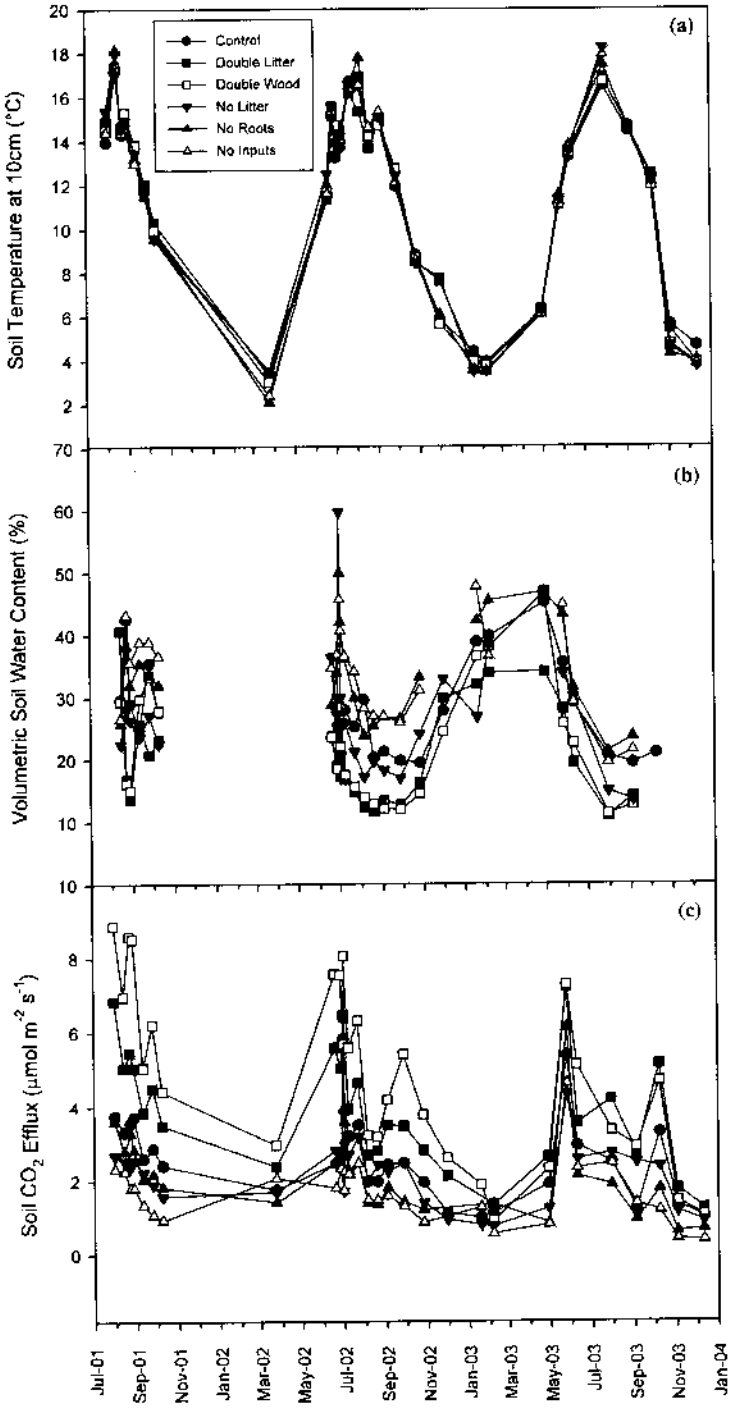
Annual sums of modeled daily effluxes were used to determine the proportion of efflux coming from functionally autotrophic (root plus associated rhizosphere organisms, R_r) and heterotrophic (aboveground plus non-root derived belowground litter, R_h) sources. To accomplish this there are a number of assumptions that must be made. First, we assumed that soil C stores are at steady state over the short term, and that annual aboveground litter inputs (average of 1976–1985 data for six locations within each of two old growth stands of the same species composition at same elevation as the DIRT plots: 149.6 g C m^{-2} $year^{-1}$; HJA LTER 2004a) at steady state are equal to total respiration losses due to decomposition of current and previously deposited leaf litter. Our on-site litterfall data (153.1 g C m^{-2} $year^{-1}$) are within the standard deviation of the long-term mean of the two off-site plots, validating our use of the long-term data as the best estimate for steady state litter input rates for our site.

A number of additional assumptions are important to our partitioning of soil respiration sources. First, we assume that severed roots in trenched plots are contributing little, if any, to total respiration, given that this respiration study began four years post-trenching. Similarly, we assume that the disturbance effect caused by treatment installation is no longer significant. We also assume that root re-growth is minimal, although we have not conducted a post-experiment sampling for residual root density. Observations from DIRT plots in Pennsylvania, which were re-trenched 10 years after plot installation, suggest that this assumption is reasonable. We also assume that rhizosphere respiration is a constant proportion of the total respiration on days when no measurements were made. Finally, we assume that soil microbes do not switch carbon sources when we alter carbon inputs due to our experimental treatments.

We calculate the carbon dioxide from each source as follows:

Aboveground litter: Equivalent to long-term annual aboveground litterfall
Rhizospheric respiration: Control Plots – No Roots Plots
Belowground Litter: Total Respiration – Aboveground litter – Rhizospheric respiration

Figure 2. Soil CO_2 efflux, moisture, and temperature for the six treatments. Closed circle is Control, solid square is Double Litter, open square is Double Wood, closed inverted triangle is No Litter, closed triangle is No Roots, open triangle is No Inputs. (a) Soil temperature (not statistically different among treatments, $p = 0.997$); (b) Volumetric water content (0–12 cm); (c) Soil CO_2 efflux.


(a)
Control
Double Litter
Double Wood
No Litter
No Roots
No Inputs
Soil Temperature at 10cm (°C)
(b)
Volumetric Soil Water Content (%)
(c)
Soil CO_2 Efflux (μmol m^{-2} s^{-1})
Jul-01
Sep-01
Nov-01
Jan-02
Mar-02
May-02
Jul-02
Sep-02
Nov-02
Jan-03
Mar-03
May-03
Jul-03
Sep-03
Nov-03
Jan-04

Results

Soil temperature and moisture

Soil temperature and soil moisture varied greatly with season, with the lowest temperatures and highest soil moisture during winter (Figure 2). Mean daily soil temperature at 5 cm depth did not differ across treatments ($p > 0.05$). Although there were no significant differences in soil moisture among treatments on an annual basis ($p > 0.05$), in the wet season (November–March) No Roots and No Inputs plots were wetter than plots containing roots ($p < 0.0001$). During the dry season (June–September) Double Litter and Double Wood treatments were typically the driest plots, but there was an interaction with year and a significant difference among years as well (Figure 3).

Soil CO_2 efflux

Variability in annual soil CO_2 efflux was small in the wet season, but large in the dry season (Figure 4). In 2001, peak efflux occurred in August, whereas in 2002, the driest year of the study, the peak was lower and occurred in July. In 2003, the warmest year of the study, soil respiration was highest in May (Figure 4).

Efflux was highest in the plots with doubled inputs (Double Litter and Double Wood), and most similar (although still statistically different) across treatments in winter, when low temperatures and very high moisture content (ca. 50+ %) apparently limited respiration (Figure 2). Soil CO_2 efflux was not adequately predicted by temperature alone; a simple exponential relationship between soil temperature and efflux accounted for 17–50% of the observed variation for the No Root and No Litter treatments. In contrast, when the model for each year (Figure 5) included moisture and the interaction between temperature and moisture, the variability in the data explained by the model increased (R^2 = 0.56–0.98; Table 3).

Modeled fluxes and respiration budgeting

Daily estimates of CO_2 efflux created with the site-specific model were averaged by treatment and summed annually (Figure 6). Soil CO_2 effluxes from No Inputs treatment plots were significantly lower than from Control plots; double inputs plots (Double Litter, Double Wood) exhibited significantly higher CO_2 fluxes than the Control plots on an annual basis ($p = 0.0002$); fluxes were not statistically different across years. We expected that treatment differences would be minimal in winter, however we found as many significant treatment

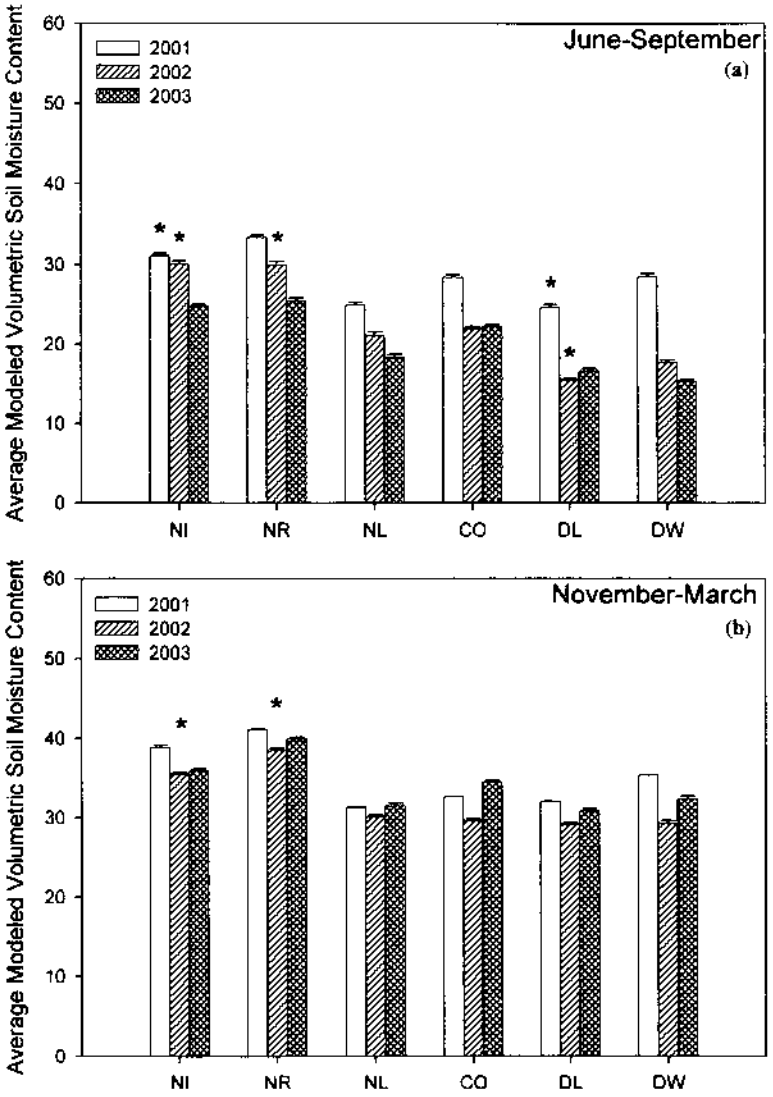


Figure 3. Dry (a) and wet (b) season mean soil volumetric water content as a function of DIRT litter manipulation treatment for all three years. In (a) there is an interaction between year and treatment. Stars show treatments that are different from the Control in that year. In (b) there is no interaction, thus if one star is over the treatment, that treatment is different from the Control using all three years of data.

differences in the cool/wet season (November–March) as in the warm/dry season (June–September).

Budgets constructed from the annual sums show that the contribution of roots to total soil CO_2 efflux was 23 ± 8% over our three-year study period

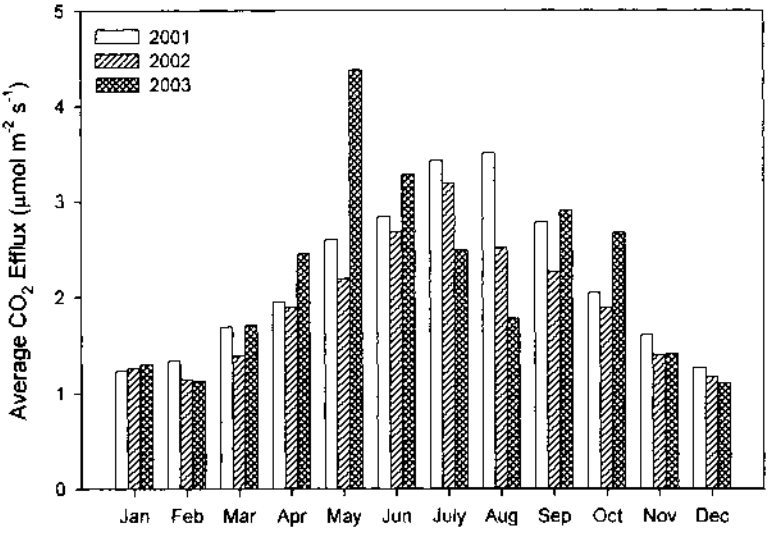


Figure 4. Seasonal and interannual variability in soil CO_2 efflux from the Control plots.

(Figure 7). The largest source of CO_2 to the atmosphere from this system is derived from belowground litter (58 ± 10%; Figure 7). Interannual variability in efflux from control plots varied by more than 100 g C m^{-2} $year^{-1}$ during the study period, with annual totals ranging from 727 g C m^{-2} $year^{-1}$ in 2002, to 841 g C m^{-2} $year^{-1}$ in 2003 (three-year mean 800 ± 126 g C m^{-2} $year^{-1}$; Table 4).

Discussion

Effect of soil temperature and soil moisture on soil CO_2 efflux

The seasonal pattern of soil CO_2 efflux generally matched that of soil temperature, and despite significant interannual differences in mean annual air temperature at the site (Table 1), there were no significant differences in either mean annual soil temperature (5 cm depth) or the corresponding soil CO_2 fluxes. Calculated Q_{10} values for our treatment plots are much lower and have a much poorer fit to the data than have been reported elsewhere (e.g., Q_{10} = 1.9, R^2 = 0.44 for Double Litter). However, these other studies were either laboratory incubations (Kirchbaum 1995; Fang and Moncrieff 2001), field studies in deciduous ecosystems (Boone et al. 1998; Davidson et al. 1998; Rey et al. 2002; Janssens and Pilegaard 2003), or coniferous evergreen systems with a distinct period of freezing temperatures (Widén and Madji 2001; Pumpanen et al. 2003). The oft-cited compilation by Raich and Schlesinger (1992) included Q_{10} values for heathland, winter wheat, dry savanna, and tallgrass prairie, as well as several reports of red pine and evergreen-broadleaf

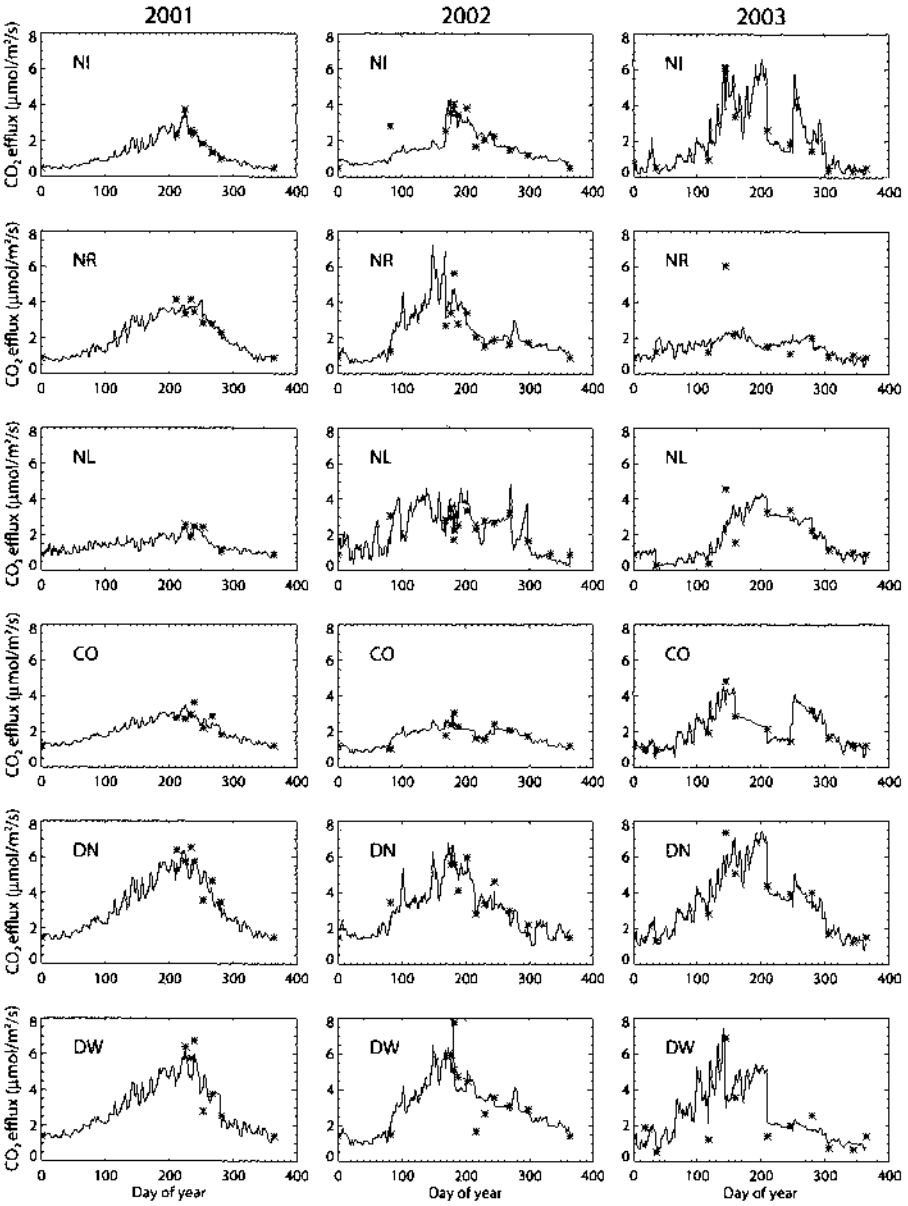


Figure 5. Modeled (curve) and observed (asterix) values of soil CO_2 efflux for each DIRT treatment in each of three years. Data are from a single plot of the three replicates for each treatment. All three replicate plots of each treatment were processed in a similar fashion. End points (January 1 and December 31) were estimated based on the average winter (November–February) values for that treatment.

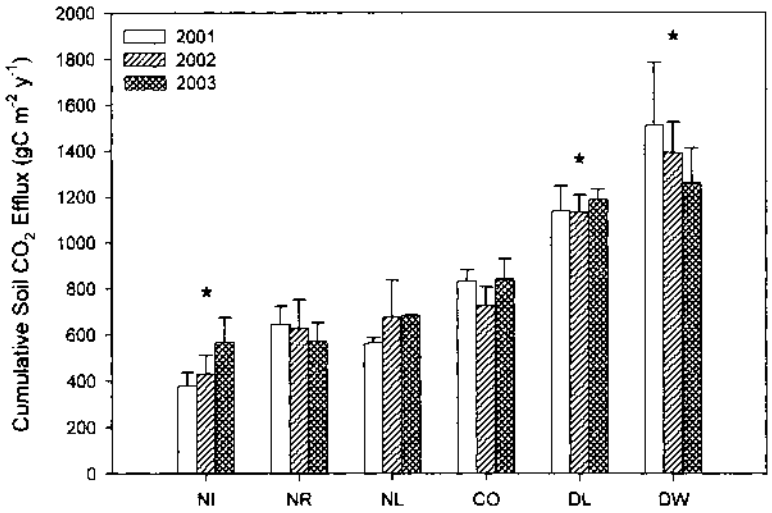


Figure 6. Annual DIRT soil CO_2 for each sampling year and litter treatment. Means ± SE calculated as sums of modeled daily values. Treatment was significant (p = 0.0002). Year was not significant. An asterix represents statistical difference from the Control using all three years of data.

forests in Japan; it is unlikely that their median reported value of 2.4 is representative of old-growth coniferous forests from an area with relatively mild winters.

In contrast to studies of crops and deciduous forests, field studies of coniferous evergreen vegetation in locations with a relatively mild winter typically yield lower Q_{10} values (e.g., Dalias et al. 2001; Xu and Qi 2001; Borken et al. 2002; Curiel Yuste et al. 2004). However, there are exceptions: Butnor et al. (2003) reported a Q_{10} of 2.57 for unfertilized ambient CO_2 plots of loblolly pine, and Campbell and Law (this issue) derived a Q_{10} of 2.46 for an old-growth stand at higher elevation than our site in Oregon. The generally lower Q_{10}s for conifers may be because phenology of coniferous vegetation is not as directly correlated with seasonal temperature as is phenology of deciduous vegetation. For example, there is no 'growing season' at low elevations of the H.J. Andrews Forest. Conifers are capable of photosynthesis all year, and the peak period of photosynthesis (late spring) typically precedes, or at least overlaps, bud break (Waring and Franklin 1979). The growth of new stemwood typically occurs after leaf growth, and the growth of roots occurs when stemwood and leaf growth have slowed (Weinstein et al. 1991). In the Pacific Northwest, USA, the weak relationship may also be driven by inverse relationships between soil temperature and moisture; when temperatures are high in summer months, water is limiting, and microbial growth may be limited.

Unlike Boone et al. (1998) we did not find differences in Q_{10}s between roots and soil organic matter. It is possible that temperature controls on roots and

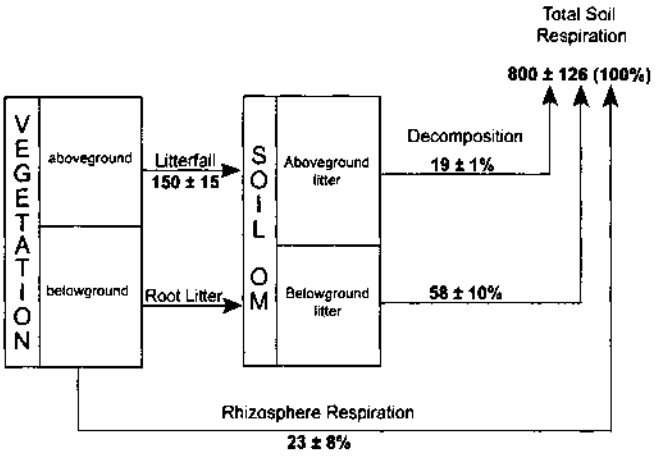


Figure 7. Annual soil respiration budgets for old growth coniferous forest at the H.J. Andrews Experimental Forest LTER site, central Oregon. Numbers are percentages of total soil CO_2 efflux averaged over the three study years (2001–2003), followed by the standard error. Litterfall and total soil CO_2 efflux are given in g C m^{-2} $year^{-1}$ with associated standard deviation. OM stands for organic matter.

Table 4. Proportions that each budget component contributes to total soil respiration in each of the three study years.

Component	2001	2002	2003
$R_{aboveground}$ (%)	19 (2)	21 (3)	19 (2)
$R_{belowground}$ (%)	59 (14)	65 (25)	49 (19)
$R_{rhizosphere}$ (%)	22 (12)	14 (21)	32 (15)
Total respiration (g C m^{-2} $year^{-1}$)	831 (53)	727 (81)	841 (88)

Errors associated with each source represent a propagation of standard errors of individual treatments. Data are means, standard error in parentheses.

soil organic matter operate fundamentally differently in western coniferous forests than in temperate deciduous forests. It may also be true that Q_{10} values cannot be established at sites where root growth, litterfall inputs, soil temperature, and soil moisture follow different seasonal patterns.

Our observed relationship between volumetric soil moisture content and CO_2 efflux was poor, perhaps because optimal water content is bimodal and out of phase with biologically optimal temperature. We suggest that the relationship between soil CO_2 efflux and soil moisture is weak except when water content is extreme (i.e., limiting to biological activity or physical diffusion). Bowden et al. (1998) reported reduced CO_2 and CH_4 fluxes under high and low water contents in a laboratory incubation with forest soil. Similarly, Progar et al. (2000) suggested that reduced respiration from coarse woody debris was attributable to high moisture content at HJA, and Davidson et al. (1998) found matric potential a more appropriate expression of biologically available water

content than volumetric water content. Transforming our moisture data into matric potentials (Brooks and Corey 1966) did not improve the relationship between flux and water content at our site, and we suggest that at best moisture content is only of local correlative value. Clearly, variables such as plant phenology and litter quality appear to be important drivers of soil CO_2 efflux at this site.

Modeling soil CO_2 efflux

As reported elsewhere (Bowden et al. 1998; Davidson et al. 1998; Epron et al. 1999; Maier and Kress 2000; Kutsch et al. 2001; Franzluebbers et al. 2002; Irvine and Law 2002; Rey et al. 2002), our ability to model the observed data improved substantially when both soil temperature and soil moisture were included in the predictive equation. However, unlike Rey et al. (2002), who found a positive linear increase in flux with added soil moisture at water contents below 20%, we observe a negative correlation with soil moisture at our site, where volumetric water contents rarely fall below 15% except in the Double Litter treatment in late summer, and where volumetric water contents near saturation are fairly common in the winter months. Davidson et al. (1998) also reported a negative correlation between efflux and volumetric water contents above a threshold (12% in that system).

Contributions of the components to total soil CO_2 efflux

Aboveground litter contribution

Based on the premise that the annual input of C from litterfall is equal to the annual soil CO_2 release from decomposing aboveground litter, we estimate that 19 ± 1% of soil CO_2 efflux was contributed by aboveground litter at our site. Our estimates are similar to published estimates by Rey et al. (2002: 22%) and Ewel et al. (1987: 19%). Even though we have assumed steady state soil C, soils are likely to be storing C. In support of this, Harmon et al. (2004) estimated long-term net total ecosystem production (including both aboveground and belowground components) at 20 g C m^{-2} $year^{-1}$ in the nearby Wind River Experimental Forest, Washington. Given that only a fraction of this C accumulation would be occurring in soil, and that these accumulation rates are within the errors of our measured C fluxes, annual soil accumulation would not meaningfully alter our partition estimates.

Rhizosphere contribution to total soil CO_2 efflux

Our estimated rhizosphere contribution ranges from 14% in 2002, the year with the lowest mean annual soil moisture of the three study years, to 32% in 2003, the warmest of the three study years. The three-year mean flux was 23 ± 8%. An analysis of the potential variance in the rhizosphere contribution was conducted by examining standard errors among the treatments, and

propagating those errors through the budget calculations. As expected, this error analysis results in considerable variability in our partitioning efforts (Figure 7, Table 4). Hanson et al. (2000) outlined shortcomings associated with each of the three major methods used to estimate the rhizospheric contribution to total soil CO_2 efflux (trenching, excision, and isotopic labeling), and indicated that there is a high variability both with season and with method used to estimate contributions; the isotope labeling approach generally yielded lower rhizosphere contributions (mean for forest studies 33.8%, $n = 9$, Table 1 of Hanson et al. 2000), and trenching studies tended towards higher values (mean 52.6% for forests, $n = 18$).

Our estimate falls within the wide range of values reported from a variety of ecosystems. In the earliest field study utilizing the root exclusion approach (i.e., trenching), Wiant (1967) calculated that 37–52% of annual respiration was root-derived in a hemlock forest. Recent studies bracket Wiant's results, ranging from 13% for an 80–100-year-old mixed forest in Russia (Larionova et al. 2003) to 65% in a boreal Scots pine forest in Sweden (Högberg et al. 2001). Many recent studies (e.g., Melillo et al. 2002; Rey et al. 2002; Lee et al. 2003) fall near the value that we calculated, although higher values have been reported by others (Epron et al. 1999, 2001; Maier and Kress 2000; Law et al. 2001; Lavigne et al. 2003). A statistical model based on 31 field studies predicts rhizosphere contributions of 30–50% for our site (Bond-Lamberty et al. 2004); however our values are within the range reported for a mesocosm-based study on Douglas-fir (Lin et al. 2001). In that study ^{13}C-labeled CO_2 taken up by young Douglas-fir was traced into roots and shoots; the authors concluded that the rhizosphere contributed 16–32% to total soil respiration in their constructed mesocosm, similar to our estimates in our intact Douglas-fir forest.

Studies that take place within months of trenching may underestimate the rhizospheric portion of soil CO_2 efflux because decomposition of newly killed roots may contribute to the estimate of respiration attributed to belowground litter. For example, one year after girdling, R_r estimates increased 11% compared to estimates made within a few months of girdling (Bhupinderpal-Singh et al. 2003). We used data from a decomposition study of Douglas-fir roots (Chen et al. 2002) to calculate that 30% of the roots killed in our plots in 1997 were likely to be present in 2003. This would represent a flux of approximately 5 g C m^{-2} $year^{-1}$ above that calculated by our partitioning. Unpublished data from Harmon suggest that 80% of the roots are within the top 30 cm of soil in old growth stands at H.J. Andrews; thus, we do not expect a large flux from roots below one meter that were never cut. We are confident that root re-growth is minimal. As mentioned previously, the Pennsylvania DIRT site showed no root re-growth 10 years post-trenching. Conversely, it is possible that we have overestimated rhizospheric respiration. By waiting four years after trenching, we have allowed time for an altered microbial community to develop in the No Roots plots (Brant 2005). Finally, we assumed that rhizosphere organisms die shortly after root trenching; however, if they instead are able to switch to alternative carbon sources (e.g., old organic matter), then

calculating R_r as the difference in respiration between Control plots and trenched plots would lead to overestimated values. Preliminary results from a laboratory incubation study employing isotopically labeled substrates suggest the microbial community does not shift to different carbon sources (Brant et al. 2004).

Seasonal variability in rhizospheric respiration

Our estimate of the rhizospheric contribution to total soil respiration is an annual summation; however, R_r clearly displays strong seasonality, as documented among a wide variety of ecosystems (Ewel et al. 1987; Ryan et al. 1997; Epron et al. 2001; Högberg et al. 2001, 2005; Widén and Madji 2001; Lavigne et al. 2003; Lee et al. 2003). In our plots, we can see seasonality in R_r by comparing soil respiration between Control and No Roots plots (Figure 8). In general, our data for 2002 (our period of most intense sampling) indicate root + rhizosphere activity is low before June, rises through August, and declines after October. Eventual inclusion of root + rhizosphere activity will be important as we attempt to better quantify the seasonality of autotrophic and heterotrophic respiration, especially given that there may be strong asynchronicity in factors that control rhizospheric respiration (e.g., root

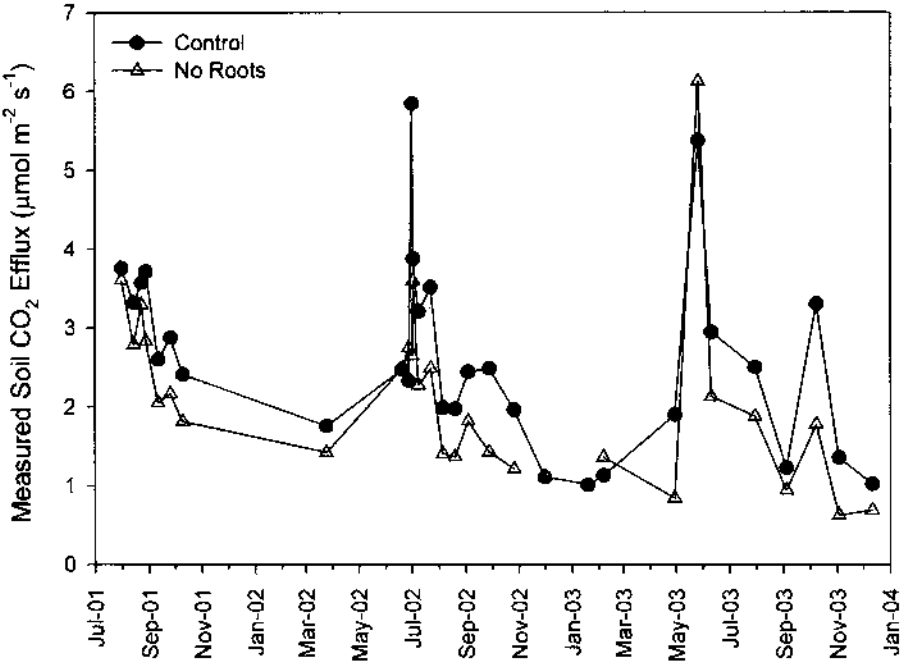


Figure 8. Measured fluxes from Control and No Root plots over the three study years. Highest rhizosphere respiration at this site appears to occur during late summer through fall (July–November). Both seasonal and interannual variability are apparent, but more data are needed.

growth, rhizodeposition) and organic matter decomposition (temperature, moisture).

Belowground litter contribution

The proportion of soil respiration derived from belowground litter ranges from 49% in 2003 (the wettest year) to 65% in 2002 (the driest year of the study), with a three-year mean of 58 ± 10%, which is within the wide range of estimates reported in other studies. For example, Edwards and Harris (1977), estimated a 48% belowground contribution in a yellow poplar forest in Tennessee, Rey et al. (2002) reported a belowground contribution of 55% in a coppiced oak forest in Italy, and Nadelhoffer and Raich (1992) estimated that 70–80% of total soil CO_2 efflux is due to belowground (litter plus root) components (see also Raich and Nadelhoffer 1989). Sun et al. (2004) used the integration of components method (Law et al. 2001) to measure heterotrophic respiration for an old growth stand at higher elevation than ours within the H.J. Andrews forest and reported rates 22% lower than ours obtained via the root exclusion method. It is likely that both inherent biases associated with each of the methods (exclusion may underestimate, while integration likely overestimates the rhizosphere contribution) and differences in the soils of the two stands explain the observed differences.

Our findings are in general agreement with the idea that in sites of low fertility, there is greater relative C allocation belowground than aboveground (Hendricks et al. 1993; Klopatek 2002). Soils at the H.J. Andrews are tremendously C-rich (122.5 Mg C ha^{-1}, Smithwick et al. 2002) but nutrient poor; the C:N of mineral soil from 0 to 20 cm in our Control plots is 35.9 (Keirstead 2004). In a temperate deciduous forest at the Harvard Forest LTER (HF), using a similar DIRT experiment, Bowden et al. (1993) found a lower contribution by belowground litter (30%) than we found at HJA and that site is more fertile than HJA (soil C:N at HF is 23: Nadelhoffer, unpublished data). Although average belowground contribution to total soil CO_2 efflux at HJA is 77%, comparable to the total of 63% at HF, our three-year average contribution of rhizospheric respiration is only 23%, compared to 33% at HF. This would suggest that even though rhizospheric respiration at HJA is lower than at the more nutrient rich temperate HF site, turnover of rhizospheric litter at HJA is higher than at HF.

The overall high belowground component may be driven by nutrient limitation. Coniferous forests are highly ectomycorrhizal (Allen 1991; Smith and Read 1997). Vogt et al. (1983) reported that 88% of Douglas-fir root tips were infected with mycorrhizal fungi in low fertility sites of western Washington, USA. The low nutrient status of these soils is likely a driver of the highly mycorrhizal nature of these systems, as mycorrhize greatly enhance the ability of infected hosts to access nutrients, and aid in decomposition of recalcitrant substances (Cairney and Chambers 1999; Molina et al. 2002; Read and Perez-Moreno 2003). It is very possible that at our site much of the belowground litter input comes not from roots directly, but from mycorrhizae associated

with roots. McDowell et al. (2001) and Hobbie et al. (2004) reported high net C accumulation in mineral soil as a result of rhizodeposition and turnover of mycorrhizal and other microbial biomass.

Evidence for priming?

The amount of respiration from decomposition of added aboveground litter over the six years since treatment installation was much greater than predicted. We calculated the amount of CO_2 efflux expected from the litter added to Double Litter plots each year for each of the six years of treatment using a first-order decay model for litter in a similar old-growth Douglas-fir – western hemlock dominated forest. Using the decay constant for Douglas-fir litter from Harmon et al. (2004), we calculated the expected amount of litter remaining in year 7 (2003) from that added during the first six years of the experiment (1997–2002) (a total of 55 g C m^{-2}). 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 in 2003 as an estimate of the expected flux from the Double Litter plots in that year. Finally, we subtracted the expected flux from the Double Litter plots (866 g C m^{-2} in 2003) from the measured flux (1145 g C m^{-2} in 2003) and expressed that as a percentage of the carbon added. Our calculations indicate that the six years of additional carbon inputs led to a 187% increase in respiration over that which would be expected based on the amount of carbon added, or a 34% increase in the total flux, leading us to conclude that the addition of labile energy sources is fueling decomposition of recalcitrant material.

Knowing that there are problems with litterbag-derived decay rates (Wieder and Lang 1982), we also used an alternative means to calculate the expected flux due to added aboveground litter. In this approach we first calculated the absolute CO_2 flux attributed to the rhizosphere (260 g C m^{-2}), aboveground litter (298 g C m^{-2}), and belowground litter (401 g C m^{-2}) using the CO_2 efflux values from Control plots and the percent contribution of each respiratory component (Figure 7). We assumed that these fluxes would remain constant in Double Litter plots but the flux from aboveground litter would double. We then compared the flux from aboveground litter based on partitioning (298 g C m^{-2}) to the flux from aboveground litter calculated by subtracting absolute values for roots and belowground litter from the measured flux from Double Litter plots (485 g C m^{-2}). This approach indicated a priming effect of 124%, or an increase in total flux of 23%, which is comparable to the result obtained using the method based on a simple exponential decay.

Instead of priming, the litter treatment might have merely increased total microbial or fungal biomass in the Double Litter plots relative to Control plots. Other studies report higher fungal biomass in plots with litter compared to those without litter (e.g., Subke et al. 2004). Neither our total biomass data nor our fungal biomass data indicate statistically significant differences between Double Litter and Control plots (data not shown; Brant 2005). Another

possible alternative to priming is that the added litter provided an insulating layer, damping diurnal temperature swings. Although the treatment did have this effect to a small degree (Figure 9), the lack of microbial biomass response again suggests that the added litter is indeed stimulating decomposition of older organic matter.

Our evidence of priming suggests a serious implication for future carbon storage in soils because the projected additional litter production resulting from elevated atmospheric CO_2 (e.g., Norby et al. 2002) could, rather than promoting additional storage of carbon in soils, cause a positive feedback to the atmospheric carbon pool by stimulating release of soil C (Pendall et al. 2004). How applicable our results are to other sites is not known. In a review of mechanisms and quantification of priming effects, Kuzyakov et al. (2000) noted that they were unable to find any references to priming effects induced by organic substrates with slow decomposition rates, although Fontaine et al. (2003) proposed that chemical diversity of substrates induces production of a diverse array of enzymes, increasing the likelihood of priming. Subke et al. (2004) documented priming using ^{13}C-labeled Norway spruce litter. Short-term labeling studies in other coniferous systems also document significant priming (e.g., Högberg and Ekblad 1996). Values reported for priming in model ecosystems range to well over 100% (e.g., Hamer and Marschner 2002; Waldrop and Firestone 2004).

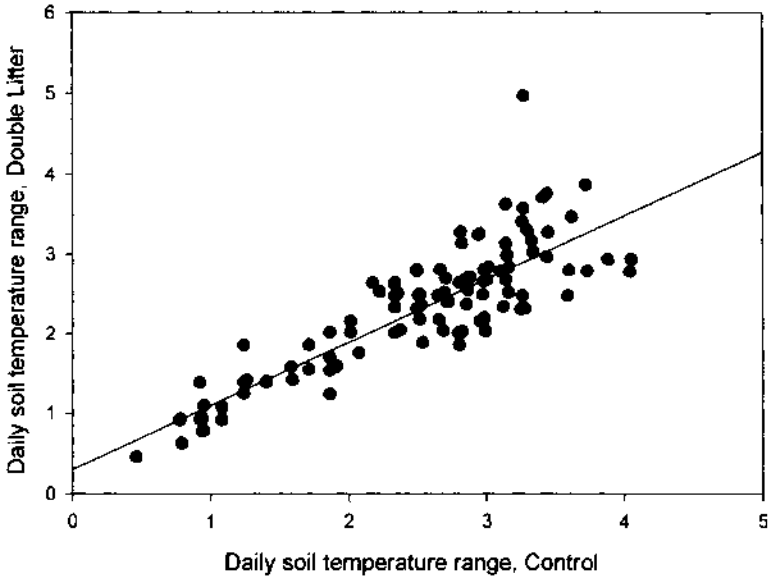


Figure 9. Daily range in soil temperature at 5 cm for June–September, 2001, for Control and Double Litter plots. The linear relationship is described by $y = 0.7947x + 0.3068$, $R^2 = 0.74$.

Summary and conclusion

At this mycorrhizally-associated old-growth Douglas-fir site in the Cascades, total soil respiration is dominated by belowground contributions. Our results suggest that rhizosphere activity is relatively low (23% on average), but that rhizospheric litter is a large pool with a relatively high turnover rate, as indicated by a large contribution to total soil respiration from belowground litter (three-year average 58%). In addition, we found strong evidence of a 'priming effect' by aboveground litter on total soil respiration in these C-rich, N-poor soils. If priming is relevant for other C-rich soils of the Pacific Northwest, it suggests that additional litter production resulting from elevated atmospheric CO_2 could cause a positive feedback to the atmospheric carbon pool.

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