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Effect of moisture on leaf litter decomposition and its contribution to soil respiration in a temperate forest

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[1] The degree to which increased soil respiration rates following wetting is caused by plant (autotrophic) versus microbial (heterotrophic) processes, is still largely uninvestigated. Incubation studies suggest microbial processes play a role but it remains unclear whether there is a stimulation of the microbial population as a whole or an increase in the importance of specific substrates that become available with wetting of the soil. We took advantage of an ongoing manipulation of leaf litter ^{14}C contents at the Oak Ridge Reservation, Oak Ridge, Tennessee, to (1) determine the degree to which an increase in soil respiration rates that accompanied wetting of litter and soil, following a short period of drought, could be explained by heterotrophic contributions; and (2) investigate the potential causes of increased heterotrophic respiration in incubated litter and 0–5 cm mineral soil. The contribution of leaf litter decomposition increased from 6 ± 3 mg C m^{-2} hr^{-1} during a transient drought, to 63 ± 18 mg C m^{-2} hr^{-1} immediately after water addition, corresponding to an increase in the contribution to soil respiration from $5 \pm 2\%$ to $37 \pm 8\%$. The increased relative contribution was sufficient to explain all of the observed increase in soil respiration for this one wetting event in the late growing season. Temperature (13°C versus 25°C) and moisture (dry versus field capacity) conditions did not change the relative contributions of different decomposition substrates in incubations, suggesting that more slowly cycling C has at least the same sensitivity to decomposition as faster cycling organic C at the temperature and moisture conditions studied.

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1. Introduction

[2] Soil respiration is a major component of ecosystem respiration [*Janssens et al.*, 2001] and consists of CO_2 derived from both plant (autotrophic) and microbial (heterotrophic) sources. On seasonal timescales, much of the variation in soil respiration fluxes can be explained by temperature variations. However, the covariance of soil temperature with moisture and with phenological patterns (i.e., root growth, seasonal availability of substrate) confounds the temperature-CO_2 flux relationship in many ecosystems [*Davidson et al.*, 1998; *Davidson and Janssens*, 2006]. Models that predict soil respiration are usually empirical and site-specific; process-based models of soil respiration are not yet adequate to explain short-term variations [*Davidson and Janssens*, 2006]. A key prospect for the improvement of process-based models are observations that target the response of specific components of soil respiration to temperature and moisture changes.

[3] The use of field manipulations and automated soil respiration chambers has demonstrated sudden and transient increases in soil respiration in response to wetting events following previously dry conditions [*Borken et al.*, 1999; *Savage and Davidson*, 2001; *Borken et al.*, 2002; *Goulden et al.*, 2004; *Scott-Denton et al.*, 2006]. These variations have been shown to be better correlated with leaf litter moisture rather than soil moisture [*Borken et al.*, 2003; *Hanson et al.*, 2003b]. Leaf litter normally contains few roots, so this finding suggests that at least some portion of the increased CO_2 fluxes reflect stimulation of heterotrophic decomposition. However, wetting of dry soils has also been shown to stimulate root respiration [*Burton et al.*, 1998]. A study using radiocarbon isotopes to partition respiration into autotrophic and heterotrophic respiration sources showed that both were reduced during prolonged drought [*Borken et al.*, 2006].

[4] A number of incubation studies have demonstrated that wetting of previously dry soil results in increased heterotrophic respiration, which could indicate stimulation of microbial consumption of cytoplasmic solutes, microbial consumption of killed, lysed cells or a shift in the utilization of substrates or a change in the kinetics of enzyme transport

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[*Fierer and Schimel*, 2003]. Understanding the cause of increased heterotrophic respiration in incubations may shed light on how repeated wetting and drying cycles influence longer-term decomposition rates.

[5] Several field methods have been applied in order to separate autotrophic from heterotrophic sources: (1) correlation of soil respiration fluxes with moisture and temperature conditions [*Yuste et al.*, 2003; *Epron et al.*, 2004] (2) manipulations such as girdling [*Högberg et al.*, 2001; *Bhupinderpal-Singh et al.*, 2003], trenching to remove the heterotrophic component [*Boone et al.*, 1998; *Lavigne et al.*, 2003; *Lee et al.*, 2003; *Bond-Lamberty et al.*, 2004; *Jiang et al.*, 2005] or removal of the leaf litter layer to determine leaf litter decomposition contribution [*Rey et al.*, 2002; *Lee et al.*, 2004] and (3) isotopic mass balance approaches [*Subke et al.*, 2004; *Ngao et al.*, 2005; *Borken et al.*, 2006; *Cisneros-Dozal et al.*, 2006].

[6] In this paper, we present the application of an isotope mass balance (^{14}C and ^{13}C) method to determine the role of leaf litter decomposition in causing the observed increase in soil respiration fluxes with increased water availability. Our approach took advantage of the differences in radiocarbon content between leaf litter (labeled versus unlabeled), soil organic matter, and root respiration, to partition soil respiration among leaf litter and other heterotrophic sources in both dry and wetted soils. We found that leaf litter decomposition can satisfactorily explain the increase in CO_2 fluxes after water addition, accounting for 37 ± 8% to soil respiration following a transient drought.

2. Methods

2.1. Site Description and Experimental Design

[7] The site is a temperate deciduous forest located in the U.S Department of Energy's Oak Ridge Reservation near Oak Ridge, Tennessee at 35°58 north and 84°17 west [*Johnson and Van Hook*, 1989]. Mean annual precipitation is 1352 mm and mean annual temperature is 14.2°C. The soils are Ultisols and the forest vegetation is dominated by *Quercus* spp and *Acer* spp [*Hanson et al.*, 2003a; *Huston et al.*, 2003]. This study was conducted as part of the Enriched Background Isotope Study (EBIS) experiment [*Trumbore et al.*, 2002; *Hanson et al.*, 2005; *Cisneros-Dozal et al.*, 2006] which uses labeled leaf litter produced after a whole ecosystem ^{14}C label caused by releases from hazardous waste incinerators in 1999. All measurements reported here were made at the Walker Branch watershed site in the central part of the Oak Ridge Reservation; a site that received low levels of plant ^{14}C labeling in the original 1999 ^{14}C release,. Field measurements took place in August (days 243, 248 and 250) 2003.

[8] A detailed description of the EBIS project and experimental design is given by *Hanson et al.* [2005] with additional details at http://ebis.ornl.gov/. Briefly, eight plots of 7 by 7 meters received ^{14}C-labeled leaf litter over three consecutive years replacing local litter fall. Starting in the fall of 2000, natural leaf litter fall was excluded from the plots and four plots received near background or 'low' ^{14}C-labeled litter (LL) that was ~215 per mil and the other four plots received enriched or 'high' ^{14}C-labeled leaf litter (HL) that was ~971 per mil. At the time of our observations, labeled leaf litter had been applied for a total of three years (May 2001, February 2002 and February 2003).

[9] Total soil respiration (CO_2) fluxes and collection of CO_2 for isotopic analyses were carried out at three levels of leaf litter moisture, on days 243, 248 and 250 in 2003. The initial and drier moisture contents measured on day 243 resulted from a transient late summer drought; surface leaf litter was very dry and brittle and rain had not reached the forest floor for 13 days prior to sampling. Field measurements were carried out just before a heavy rain event that occurred at the end of the afternoon (13 mm). Less dry conditions (our 'intermediate' moisture level) were attained on day 248 after a few rain events had wetted the litter layer (32 mm total) and it was starting to dry out again. The highest level of moisture on day 250 was attained by manually irrigating the area inside and around the chamber collars (a total area of 1 m^2). The irrigation took place after leaf litter moisture had decreased to levels close to those on day 243 (see below). We irrigated all collars with an amount of 7.5 litters of water per m^2 (7.5 mm) to simulate a heavy rain event. The water used was commercially available deionized water and was sprayed uniformly. Measurements took place a few minutes after the addition of water.

2.2. Field Moisture and Temperature Measurements

[10] Soil (0 to 15 cm) and leaf litter (Oi horizon) moisture and temperature were monitored with multiple sensors and a data logger (CR10X, Campbell Scientific, Inc.) coupled to a multiplexer (AM 16/32 Relay Analog Multiplexer, Campbell Scientific, Inc). Readings from all sensors were stored every 12 minutes. Litter water content of the Oi horizon was measured using the half bridge approach [*Hanson et al.*, 2003b] as modified by *Borken et al.* [2003]. A total of nine half bridge (HB) sensors were installed inside the plots in three different areas (3 sensors per m^2) and irrigated in the same manner as the collars used for soil respiration measurements on day 250 (see below). As a control, seven HB sensors were placed in an area with no irrigation. The voltage output from the HB sensors was converted to litter water content (LWC) using the calibration curve for the Oi horizon from *Borken et al.* [2003]. While this calibration curve is site-specific, the LWC we calculated provided a way to monitor the changes in litter moisture conditions and relate them to ^{14}C signatures of soil respired CO_2. Long-term LWC data from the Oi layer is also available at this site on an hourly basis from a different set of HB sensors [*Hanson et al.*, 2003b], hereafter referred to as 'HBL'. Additionally, moisture changes in the Oi layer were monitored with a Fuel Moisture Sensor (CS505 Campbell Scientific, Inc.) placed horizontally on the forest floor and manually irrigated on day 250 (see below). Litter temperature in the Oi horizon was monitored with a Temperature Probe (Vaisala HMP44) in an area without irrigation.

[11] Soil moisture changes were monitored using Water Content Reflectometers (CS616 Campbell Scientific, Inc.) installed at angle of ~20 degrees with the surface, using one sensor in dry or irrigated areas. We converted volumetric water content to water potential using equations developed for soils and leaf litter on the Walker Branch watershed [*Hanson et al.*, 2003a, 2003b]. Soil temperature was mea-

sured with four thermistors within each control (dry) or irrigated area and installed just below the O horizon.

2.3. Measurement of ^{13}C and ^{14}C in Respiration and Source Components

2.3.1. Total Soil Respiration

[12] Measurements of total soil respiration (CO_2) fluxes and collection of CO_2 for analyses of ^{13}C and ^{14}C were carried out in the field as described by *Cisneros-Dozal et al.* [2006] and *Gaudinski et al.* [2000]. Briefly, chamber collars (3 per litter treatment) were inserted ~2 to 5 cm into the mineral soil at least 24 hours before measurements began. We used closed dynamic chambers attached to an infrared gas analyzer (LI-800, LiCor, Inc. Lincoln, Nebraska) [*Davidson et al.*, 2002] for measurement of CO_2 fluxes. After placing the chamber lid on the collar, we monitored and recorded (LI-1400, data logger, LiCor, Inc. Lincoln, Nebraska) the increase in the CO_2 concentration in the headspace of the chamber for about 10 min. Following soil respiration measurements, we collected headspace CO_2 for ^{14}C and ^{13}C analysis using molecular sieve traps (mesh size 13X; Advanced by UOP, Specialty Gas Equipment). All soil respiration measurements took place between 11:00 and 16:00 hours.

[13] The ^{14}C signature of total soil respiration ($^{14}C_{total}$) per litter treatment (HL or LL) was estimated as the mean ± standard deviation of three measurements in each sampling day. The ^{13}C signature was estimated as the mean ± standard of all six chamber measurements.

2.3.2. Heterotrophic Respiration

[14] To estimate the isotopic signatures of leaf litter and soil (0–5 cm) decomposition, as well as their dependence on moisture and temperature conditions, we carried out incubations in the laboratory combining two levels of temperature and moisture. Six samples (3 per litter treatment) of the entire O horizon (labeled leaf litter plus semidecomposed leaf litter that predate the litter additions) in an area of 0.021 m^2 were collected on day 243 when leaf litter moisture was the driest and placed in air tight plastic bags. Soil samples representing the upper 5 cm of mineral soil were collected from the same area using a core (4.7 cm diameter) and stored in capped glass jars. Soil cores and leaf litter samples were refrigerated for transport to the laboratory and until the time of incubation (~3 months after collection). At the time of the incubation, each leaf litter sample was divided in four subsamples, each subsample was placed in aluminum foil (perforated) and inside sealed jars avoiding unnecessary disturbance. Similarly, soil cores were divided in four subsamples, large roots and stones were removed, and each was placed in a glass flask (uncapped) and inside a sealed1 L Mason jar outfitted with inlet and outlet valves on the lids. All four subsamples of leaf litter and mineral soil were incubated at 25°C for 6 days and these initial rates of CO_2 production which were to normalize rates under manipulated temperature and moisture conditions [*Dioumaeva et al.*, 2002].

[15] Following the initial period, two of the leaf litter subsamples were wetted to field capacity, then drained before placing them back inside the sealed jars. Similarly, water was added to two subsamples of soil core to reach a final moisture content of 20% by volume (chosen arbitrarily). Samples were incubated at two temperatures: 25°C (room temperature) and 13°C (using a temperature-controlled refrigerator), such that the four splits made from each sample were incubated under four conditions: 25°C, wet; 25°C, dry; 13°C, wet; 13°C, dry. Temperatures were monitored with Onset (R) temperature loggers.

[16] The CO_2 evolution inside the incubation jars was monitored every 1–2 days; when sufficient CO_2 was available, air in the jar was sampled using evacuated canisters for preparation for ^{14}C and ^{13}C analysis as described below. The ^{14}C signatures from decomposition of leaf litter and soil organic matter decomposition ($^{14}C_{leaf\ litter\ decomposition}$ and $^{14}C_{soil\ decomposition}$ respectively) are reported as the mean ± standard deviation of three replicate litter samples or cores, subsamples of which were incubated at each temperature and moisture condition. ^{13}C signatures were estimated as the mean ± standard of six separate incubations at each temperature and moisture condition.

2.3.3. Isotopic Measurements

[17] Carbon dioxide from evacuated canisters was purified cryogenically on a vacuum line. Carbon dioxide from molecular sieve traps was desorbed by heating to ~600°C under vacuum, and purified cryogenically. An amount of CO_2 equivalent to ~1 mg of carbon was sealed into a prepared tube (with catalyst and zinc as reducing agent) and reduced to graphite for accelerator mass spectrometry measurement of radiocarbon according to *Xu et al.* [2006]. An aliquot of CO_2 was removed and placed in a He-purged vial for measurement of ^{13}C using continuous flow isotope ratio mass spectrometry with a GasBench II interfaced to a Fisons mass spectrometer.

[18] All ^{14}C signatures are expressed in delta notation (Δ), the deviation of the $^{14}C/^{12}C$ ratio in the sample with respect to that of the standard (oxalic acid) in parts per thousand (‰), normalized to a common value of −25‰ in $\delta^{13}C$. ^{13}C signatures are expressed in delta notation (δ), the deviation of the $^{13}C/^{12}C$ ratio of the sample with respect to that of the standard (Pee Dee belemnite) in parts per thousand (‰).

2.3.4. Contribution of Leaf Litter Decomposition to Total Soil Respiration

[19] We determined the contribution of the entire O horizon to total soil respiration, hereafter referred to as FLD (i.e., fraction from litter decomposition), using the difference in the isotopic signature of CO_2 respired from the different litter treatment plots [*Cisneros-Dozal et al.*, 2006]. Briefly, the difference in the ^{14}C signature of total soil respiration ($\Delta^{14}C_{total}$) between HL and LL plots is proportional to the difference in the ^{14}C signature of leaf litter decomposition ($\Delta^{14}C_{leaf\_litter\_decomp}$, determined by incubation of the leaf litter layer) between HL and LL plots,

$$FLD = \frac{\Delta^{14}C_{total_{HL}} - \Delta^{14}C_{total_{LL}}}{\Delta^{14}C_{leaf\_litter\_decomp_{HL}} - \Delta^{14}C_{leaf\_litter\_decomp_{LL}}}. \quad (1)$$

[20] This method assumes that radiocarbon signatures of other potential soil respiration sources, including autotrophic respiration and soil organic matter decomposition, do not differ between treatment plots. No significant difference in $\Delta^{14}C_{total}$ between HL and LL plots means negligible

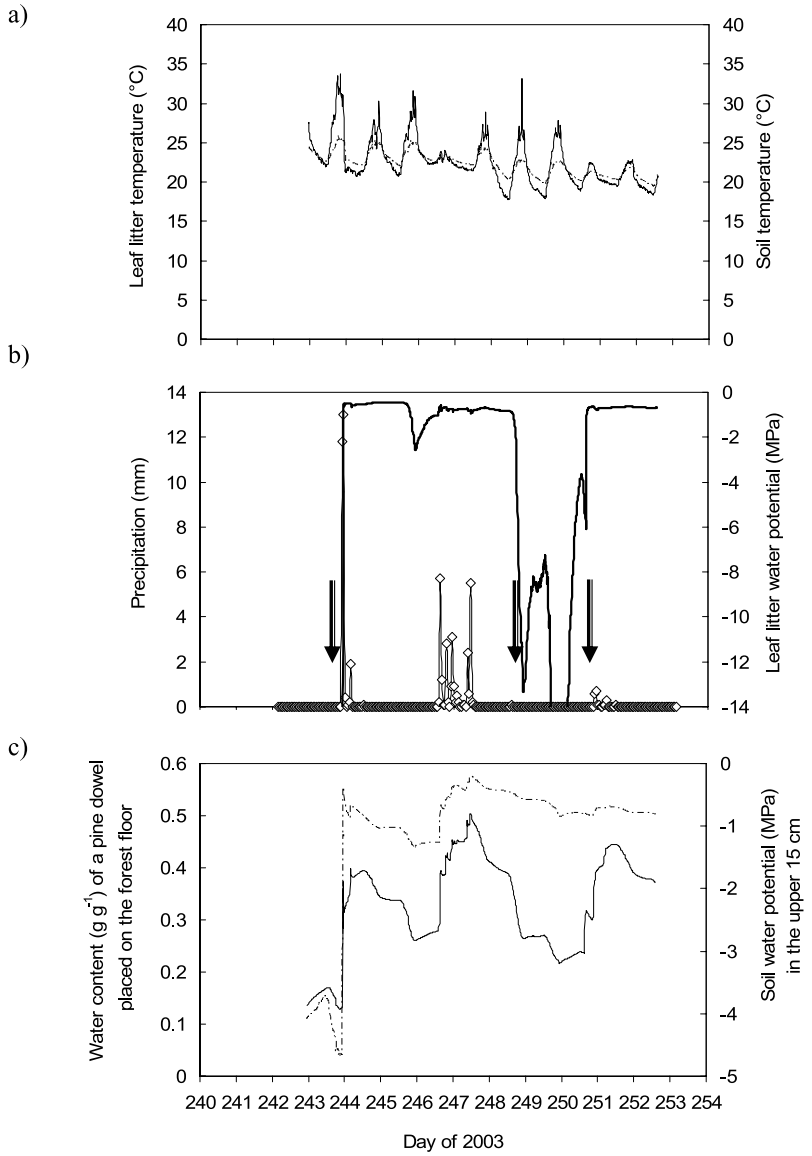

Figure 1. (a) Temperature of the Oi horizon (solid line) measured with a temperature probe (Vaisala HMP44) and of the upper 5 cm of mineral soil (dotted line) measured with thermistors. (b) Moisture content of the Oi horizon measured with nine half bridge sensors (solid line) and precipitation data (diamonds), days of CO_2 collection for radiocarbon analysis are indicated with arrows. Data from our newly installed (dry) half bridge (HB) litter moisture sensors were not reliable before the rain event on day 243, and are not shown. (c) Moisture changes in the Oi horizon (solid line) measured with a ponderosa pine dowel (Fuel Moisture Sensor, CS505 Campbell Scientific, Inc.) and in the upper 15 cm of mineral soil (dotted line) measured with a Water Content Reflectometers (CS616 Campbell Scientific, Inc.).

contribution from leaf litter decomposition, while a large difference indicates that leaf litter as an important source of total soil respiration.

2.3.5. Contribution of the Labeled Leaf Litter to Heterotrophic Respiration

[21] We estimated the contribution of the labeled leaf litter (as opposed to materials present prior to the 3 years of label addition) to CO_2 respired during incubations of the O horizon and the 0–5 cm of mineral soil, hereafter referred to as FLL_O and FLL_M respectively. These fractions would represent the decomposition of leaf litter that is $\leq$3 years old. The mass balance equations for the O horizon and mineral soil respectively are

$$FLL_O = \frac{\Delta^{14}C_{leaf\_litter\_decomp_{HL}} - \Delta^{14}C_{leaf\_litter\_decomp_{LL}}}{\Delta^{14}C_{labeled\_litter_{HL}} - \Delta^{14}C_{labeled\_litter_{LL}}} \quad (2)$$

$$FLL_M = \frac{\Delta^{14}C_{soil\_decomp_{HL}} - \Delta^{14}C_{soil\_decomp_{LL}}}{\Delta^{14}C_{labeled\_litter_{HL}} - \Delta^{14}C_{labeled\_litter_{LL}}}, \quad (3)$$

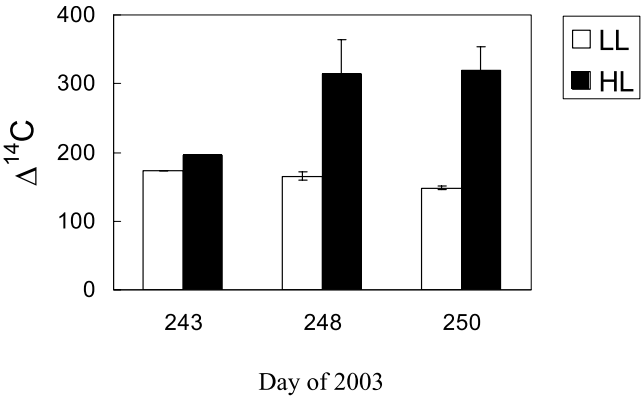

Figure 2. Radiocarbon signatures of total soil respiration by leaf litter treatment, HL and LL (high and low ^{14}C-labeled leaf litter, respectively) measured using manual chambers. Each value represents the mean of three measurements ± standard deviation (except for LL treatment on day 243 with only one value).

where $\Delta^{14}C_{leaf\_litter\_decomp}$ and $\Delta^{14}C_{soil\_decomp}$ are the ^{14}C signatures of CO_2 evolved in incubations of leaf litter and mineral soil respectively, for either HL or LL plots, and $\Delta^{14}C_{labeled\_litter\ HL}$ and $\Delta^{14}C_{labeled\ litter\ LL}$ are the average signatures of the added, labeled litter over the 3 years of the EBIS experiment (∼1000‰ and ∼230‰, respectively). The original litter used in the labeling experiments was not uniformly enriched with soluble and insoluble litter components having higher and lower than mean ^{14}C signatures, respectively [*Hanson et al.*, 2005]. Therefore these calculations may underestimate the ^{14}C signature of CO_2 respired from labeled leaf litter, and overestimate FLL_M and FLL_O to a small degree.

3. Results

3.1. Field Moisture and Temperature Conditions

[22] During the period of soil respiration measurements, soil water stress (water potential ≤ -4 MPa) in the upper 15 cm was observed only on day 243 prior to the heavy rainfall, reflecting the preceding transient drought (Figure 1c). Less limiting soil water conditions with values ranging from −1.3 to −0.2 MPa were observed over the next 7 days owing to several low-intensity rain events (Figure 1b). Soil water potential on day 250 was −0.8 MPa before a manual irrigation changed soil water potential to −0.5 MPa (data not shown).

[23] Leaf litter moisture was influenced by rain events and the manual irrigation on day 250, ranging from very low water potentials (<−10 MPa) during the transient drought (and during field measurements on day 243) to high values (−0.5 MPa) immediately after rainfall and the manual irrigation (Figure 1b). Litter water content as measured with the HB sensors on the second sampling day (day 248) declined continuously (from 0.9 to 0.1 g g^{-1}) during the time we measured soil respiration and thus it was difficult to assign one single value of litter water content for this period (Figure 1b). There was large variation among the 16 HB sensors which reflects both issues with sensor calibration and field heterogeneity. The Fuel Moisture Sensor placed on the forest floor responded more slowly than the HB sensors, but showed similar temporal patterns of wet-up and dry-down over the one week period (Figure 1c).

[24] Leaf litter temperature varied from 18°−34°C driven by diel air temperature changes of approximately 10°C. The highest temperatures were found in the afternoon (∼3 pm) and lowest in the early morning (5 to 8 am). Soil temperatures followed the same pattern with dampened diel oscillations of <2°C (Figure 1a). Throughout the week of measurements, there was a decline in daily average soil temperatures from 25 to 20°C.

3.2. Total Soil Respiration Fluxes and Isotopic Signatures

[25] Total soil respiration fluxes averaged 137 ± 27, 173 ± 16 and 170 ± 29 mg C m^{-2} hr^{-1} on days 243, 248 and 250 respectively. The means were significantly different ($p < 0.05$) between the first and second sampling day only, in part because of the large spatial variability in measured fluxes.

[26] Radiocarbon signatures of total soil respiration exhibited the expected pattern of increasing difference between litter treatments with higher leaf litter moisture on days 243, 248 and 250 (Figure 2). The difference between treatments in the ^{14}C signature of total soil respiration was 22 ± 10, 148 ± 51 and 170 ± 35 on days 243, 248 and 250 respectively. Owing to the large standard deviation in the HL treatment on day 248, the difference between treatments was only statistically significant on day 250 ($p < 0.05$). The ^{13}C signature of total soil respiration was −24.4 ± 0.2, −25.9 ± 0.3 and −26.2 ± 0.3 on days 243, 248 and 250 respectively.

3.3. Dependence of the ^{14}C and ^{13}C Signatures of Heterotrophic Decomposition Sources on Temperature and Moisture

[27] Radiocarbon signatures of leaf litter and mineral soil decomposition were unaffected by temperature and moisture (Figure 3). The mean ^{14}C signature at each of the manipulated incubation conditions was not significantly different ($p > 0.05$) from the mean signature of the CO_2 evolved at 25°C and field moisture. In contrast, the in vitro rates of CO_2 evolution inside the jars did show the effect of change in temperature and moisture, with fluxes increasing by 260% at the highest moisture levels (Figure 4a), and decreasing 27% with respect to base values at 13°C (Figure 4c) in the case of leaf litter. The combined effect of lower temperature and increased moisture had a mixed effect with some rates remaining unchanged (Figure 4e). Similar effects were observed in the incubated mineral soil (Figures 4b, 4d, and 4f) although the increase in the rates of CO_2 production after water addition was of lesser magnitude.

[28] The mean ^{13}C signature of the CO_2 evolved in the manipulated leaf litter incubations increased ∼1‰ with a change in the incubation temperature from 25°C to 13°C regardless of moisture condition (Table 1). In mineral soil incubations, the mean ^{13}C signatures of respired CO_2 were only significantly different for the combined 13°C and

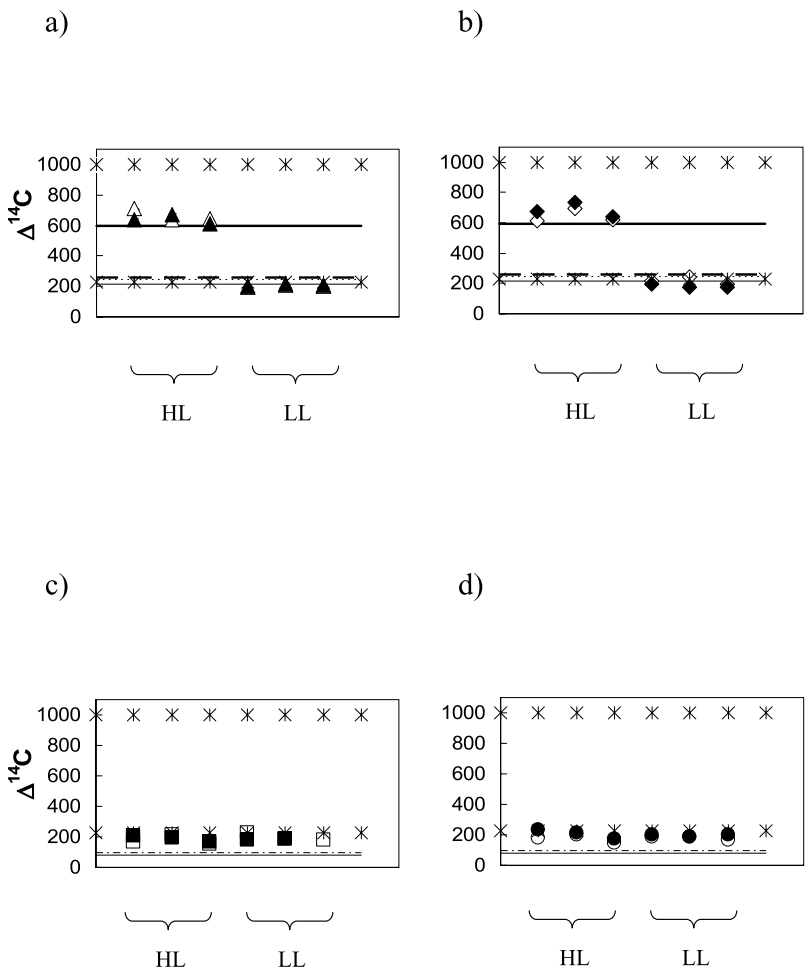

Figure 3. Radiocarbon signature of heterotrophic decomposition measured as the ^{14}C signature of the CO_2 evolved during incubations of leaf litter and soil cores at field moisture (open symbols) and at field capacity for leaf litter and 20% by volume for mineral soil (closed symbols). (a) Leaf litter samples incubated at 25°C, (b) leaf litter samples incubated at 13°C, (c) soil cores incubated at 25°C, and (d) soil cores incubated at 13°C. A total of six samples, three per litter treatment, HL and LL (high or low ^{14}C-labeled leaf litter, respectively) were incubated in each condition. The ^{14}C signatures of the O horizon and upper 15 cm of mineral soil (measured in February 2003 before the third litter addition) are indicated with lines as follows: in Figures 3a and 3b, coarse and fine solid lines correspond to the Oi horizon in HL and LL treatments, respectively, and coarse and fine dotted lines correspond to the Oe/Oa horizon in HL and LL treatments respectively; in Figures 3c and 3d, solid and dotted lines correspond to the mineral soil in HL and LL treatments, respectively. Stars denote the amount of ^{14}C label added to the HL and LL treatments, ~1000‰ and ~230‰, respectively.

increased moisture condition compared to the incubation at 25°C and field moisture.

3.4. Contribution From Leaf Litter Decomposition to Soil Respiration (FLD)

[29] Under dry conditions on day 243, we estimated leaf litter decomposition to account for only 5 ± 2% of total soil respiration. The contribution of leaf litter decomposition increased to 37 ± 8% with higher levels of leaf litter moisture (a change in water potential from ≤ -4 to -0.5 MPa). The corresponding absolute contributions (estimated as the product of FLD times total soil respiration flux) ranged from 6 ± 3 to 63 ± 18 mg C m^{-2} hr^{-1} under dry and moist conditions respectively (Figure 5).

3.5. Contribution From the Labeled Leaf Litter (FLL)

[30] We estimated that labeled leaf litter contributed at least 50% to the total decomposition in the O horizon with little or no contribution to CO_2 efflux from downward transport of dissolved organic compounds in the mineral soil (0–5 cm). This contribution was similar for 2002 and 2003 (no data were available for 2001), on average 54 ±

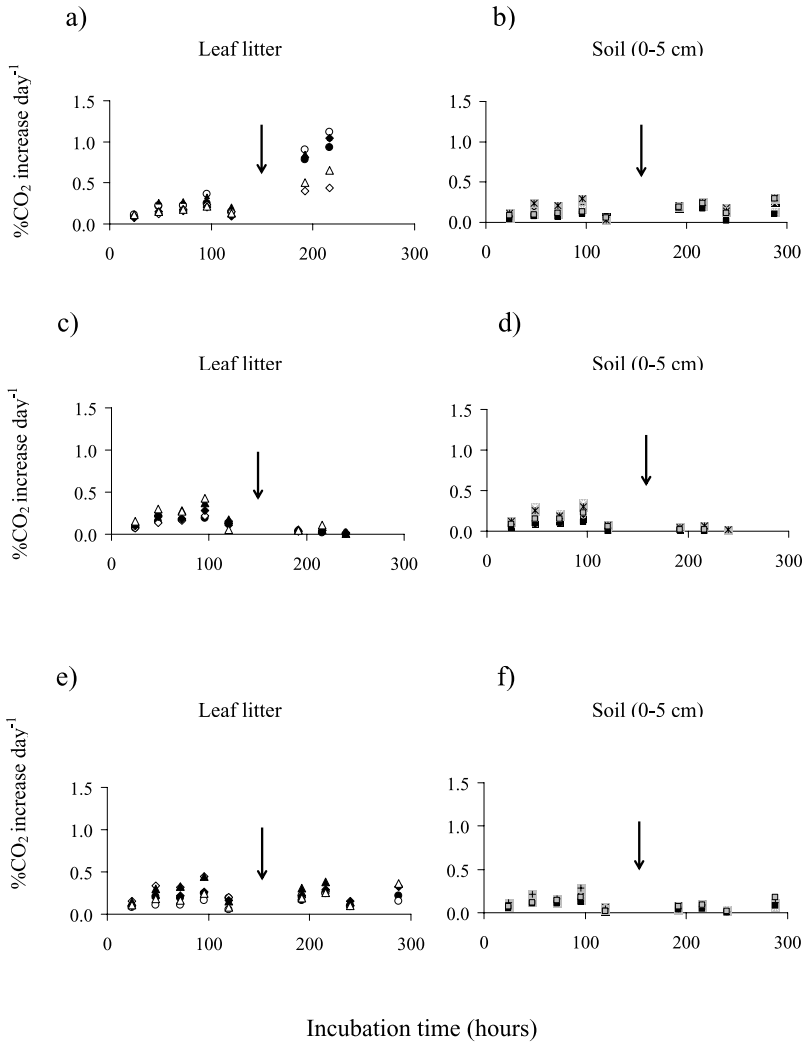

Figure 4. Daily change in CO_2 concentration (expressed in $\%CO_2$) in the headspace of sealed jars containing leaf litter and mineral soil (0–5 cm depth) samples (n = 6 for each). The rates from incubations of leaf litter are shown on the left hand side with the arrows indicating: (a) water addition to field capacity, (c) decrease in the incubation temperature from 25°C to 13°C and (e) combination of Figures 4a and 4c. The rates from incubations of soil samples are shown on the right hand side with the arrows indicating: (b) water addition to 20% by volume, (d) decrease in the incubation temperature from 25°C to 13°C, and (f) combinations of Figures 4b and 4d.

12% (O horizon; FLL_O) and 6 ± 4% (0–5 cm soil; FLL_M) of heterotrophically respired C was derived from labeled leaf litter. Given that the mean contribution from leaf litter decomposition to soil respiration under wet conditions was 37 ± 8% (see above), leaf litter ≤3 years old contributed from 15 to 30% to total soil respiration fluxes on that day. The incubation samples and respiration data were both taken in the latter part of the growing season, and may not be representative of annual averages or conditions at other times of the year.

Table 1. The $\delta^{13}C$ Signatures of the CO_2 Evolved in Manipulated Incubations of Leaf Litter and Mineral Soil Samples (0–5 cm)[a]

	25°C	13°C
	Leaf Litter	
Field moisture (dry)	−28.0 ± 0.4	−27.3 ± 0.6[b]
Field capacity	−27.7 ± 0.8	−27.1 ± 0.8[b]
	Soil	
Field moisture (dry)	−27.0 ± 0.5	−26.7 ± 0.4
Field capacity	−26.6 ± 0.4 (n = 3)	−26.3 ± 0.5[b]

[a]Data: the mean ± standard deviation (n = 6 separate incubations, except when otherwise indicated).
[b]Significantly different ($p < 0.05$) from means at field moisture and 25°C.

4. Discussion

4.1. Cause of Increased Soil Respiration When Rainfall Follows Temporary Drought

[31] For this forest in late August, the observed increase in soil respiration fluxes after rainfall following transient drought can be satisfactorily explained by an increase in heterotrophic respiration, primarily enhanced decomposition of the O horizon. Both total soil respiration and its radiocarbon signature increased when dry soils were wetted.

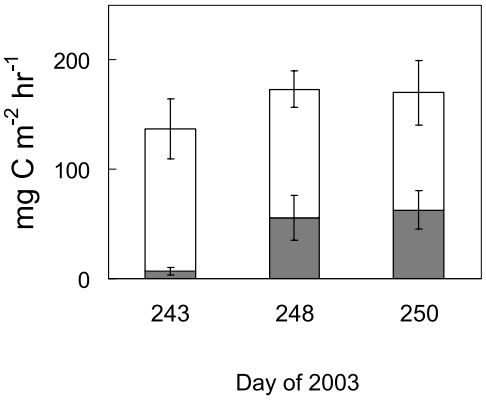

Figure 5. Absolute contributions of leaf litter decomposition to total soil respiration under dry (day 243) and moist (days 248 and 250) leaf litter. Fluxes were calculated as the product of soil respiration fluxes times the relative contribution from leaf litter decomposition (FLD). FLD was estimated using equation (1) and radiocarbon signatures of soil respiration and leaf litter decomposition.

The difference in the ^{14}C of total soil respiration between litter treatment plots, which was practically zero under dry conditions, increased dramatically when litter and surface soils were wetted. Given that this isotopic shift cannot be explained by a shift of C substrate for heterotrophic respiration (see below), it indicates greater contribution of decomposition in the O horizon, and particularly leaf litter $\leq$3 years old.

[32] The increase in total soil respiration fluxes from dry to wet conditions was roughly equal to the increased contribution from leaf litter decomposition (Figure 5), which seems to rule out a strong response of autotrophic origin. By contrast, *Borken et al.* [2006] observed a decrease in both autotrophic and heterotrophic respiration with simulated drought in the Harvard forest, Massachusetts. One explanation for the different results may lie in the vertical distribution of roots between the two sites: at the Harvard forest, the litter layer (Oi + Oea) is thicker and contains ~50% of the fine root biomass whereas at Oak Ridge, the Oi + Oea layer is thin and the majority of fine roots are found in the 0–30 cm layer of the soil [*Joslin and Wolfe*, 2003]. It is possible that more severe and prolonged droughts are needed for autotrophic respiration to be affected as tree root systems in this forest retrieve water throughout a deep soil profile. In addition autotrophic respiration may be more strongly controlled by aboveground factors such as site productivity [*Janssens et al.*, 2001; *Reichstein et al.*, 2003], photosynthetic activity [*Craine et al.*, 1998; *Högberg et al.*, 2001] and/or environmental conditions [*Irvine and Law*, 2002; *McDowell et al.*, 2004; *Ekblad et al.*, 2005] that require a time lag of several days before changes aboveground translate belowground [*Bowling et al.*, 2002; *Ekblad et al.*, 2005].

[33] *Lee et al.* [2004] estimated a linear relationship between the relative contribution from leaf litter decomposition to total soil respiration and leaf litter water content in a temperate forest. Fractional contributions were estimated to range from ~0.35 to 0.55 when leaf litter moisture varied from 5 to 15% by volume. Their measurements of water content however were recognized to be only an approximation of that of the leaf litter layer as they spanned a depth comprising the entire O horizon plus ~3 cm centimeters of mineral soil. While it is difficult to assign a fixed value of increase in leaf litter decomposition to a specific increase in litter water content (due to real heterogeneity in the field litter moisture and different water holding capacities between sites), this study suggests an increase of approximately 25% for an approximate 1.4 g g^{-1} increase in surface litter water content during the peak of the growing season. The percent increase could be lower during spring when cool temperatures limit decomposition as has been observed in earlier field measurements [*Cisneros-Dozal et al.*, 2006] and in model predictions [*Hanson et al.*, 2003b].

4.2. Causes of Increased Heterotrophic Respiration With Increased Temperature and Moisture

[34] Results from the manipulated incubations indicated no change in the ^{14}C-signature of CO_2 respired when we wetted dry litter or soils, or when we subjected dry or wet litter to different temperatures. Large changes in the rates of heterotrophic respiration under different incubation conditions indicate that the microbial community was responsive, but the lack of change in ^{14}C signature indicates that there was no discernable shift in the source of substrates being respired. For example, even though O horizon incubations contained a wide range of materials with different ^{14}C signatures, including C older than the 3 year manipulations as well as the enriched litter, the fraction of C derived from labeled leaf litter (54 ± 12%) remained constant for all conditions.

[35] Other recent studies have attempted to determine whether substrates for microbial respiration change with temperature, in an effort to determine if the temperature sensitivity of more slowly cycling C pools (which may contribute a minor fraction of heterotrophically respired CO_2) is the same as those of more rapidly cycling pools (which contribute most of the heterotrophic respiration). Results from the current work on the Oak Ridge Reservation indicate that the balance of sources of heterotrophically respired C remain the same even though rates of respiration change dramatically between 13°C and 25°C (Figure 4). *Dioumaeva et al.* [2002] observed a similar pattern of large increases in respiration rate with temperature but no change in the radiocarbon signature of the evolved CO_2 for boreal forest peat mosses incubated over a range of temperature conditions. Other studies however, have observed changes in the isotopic signature of the CO_2 evolved during incubations with changes in moisture or temperature, which these authors attributed to a shift of C substrate for decomposition. Using soil samples from a pineapple plantation and ^{13}C measurements, *Waldrop and Firestone* [2004] inferred the utilization of older C (>14 years) at 20°C versus 5°C although no change was observed with addition of water. Their samples were stored for 9 months and their incubations lasted for 103 days but an isotopic difference in the CO_2 produced between the two temperature conditions was seen throughout the experiment. In a multiyear incubation experiment, *Bol et al.* [2003] found increased temperature sensitivity for more recalcitrant pools. These studies suggest that the temperature dependence of more

recalcitrant substrates is at least the same as, and potentially greater than, that of more labile carbon pools.

[36] In this experiment a shift in the ^{13}C signature of respired CO_2 with temperature was observed, but not a shift in ^{14}C. This differential response suggests that the interpretation of changes in the ^{13}C of respired CO_2 in other incubation studies where temperature varies be undertaken with care. Since the radiocarbon results are corrected for mass-dependent fractionation effects (by reporting all data corrected to a common $\delta^{13}C$ value), the lack of a change in the ^{14}C of respired CO_2 with temperature indicates no change in balance of substrates with different ^{14}C signatures. Therefore the shifts we observed in the ^{13}C signature of respired CO_2 must reflect another process – such as a temperature-dependent change in the fractionation of ^{13}C by microbes. Another plausible explanation for the change in ^{13}C signature of leaf litter decomposition with temperature could be a change in composition of the microbial community. *Andrews et al.* [2000] found an isotopic enrichment (2.2–3.5‰) in the ^{13}C of the CO_2 evolved during incubations at 4°C versus 22°C and attributed it to the different type of microbial species present at each temperature. Similarly, *Biasi et al.* [2005] observed an isotopic depletion in the ^{13}C signature of heterotrophic decomposition with increasing incubation temperature in tundra soils and found shifts in the microbial community composition.

[37] There is no consensus on the specific mechanisms linking increased moisture to enhanced decomposition but several have been proposed including: high metabolic activity of young bacteria [*Birch*, 1958], the decomposition of microbial biomass killed under dry conditions and/or C release by microbial biomass perhaps through catabolism of internal solutes [*Bottner*, 1985], transport of solutes out of cells [*Fierer and Schimel*, 2003] or cell lysis [*Kieft et al.*, 1987]. The incubation results reported here would tend to rule out hypotheses requiring a shift in the age of microbial substrates and supports the suggestion by *Fierer and Schimel* [2003] that the short-term response is governed by internal microbial C sources.

5. Conclusions

[38] EBIS provided a very sensitive way to quantify the role of leaf litter decomposition in the observed CO_2 pulse after water addition and the role of labile C ($\leq$3 years old) in C cycling within the O horizon and surface mineral soils in this temperate forest. The contribution from leaf litter decomposition to soil respiration fluxes increased from 5 ± 2% to 37 ± 8% in response to water addition following transient drought. These results confirmed that leaf litter decomposition represents a substantial source of temporal variability in soil respiration fluxes and consequently in estimates of NEP in temperate forests as a result of sudden increases in leaf litter moisture. Recent C inputs (leaf litter $\leq$3 years old) dominated the response to water addition and was estimated to contribute from 15 to 30% to total soil respiration fluxes under moist conditions. In surface mineral soils, recent C sources were found to play a minor role to heterotrophic decomposition, with only 6 ± 4% of heterotrophically respired CO_2 being derived from carbon ($\leq$3 years old) leached from the leaf litter layer.

[39] Shifts in the carbon substrate utilized (i.e., older) with changes in moisture (dry versus field capacity) and/or temperature (13°C versus 25°C) conditions were not observed. Collectively, these results support the hypothesis that rapid changes in heterotrophic respiration following wetting are linked to the more rapid use of C sources already available to the microbes themselves rather than a shift in substrate use, and suggest that more slowly cycling C (which contributes less to soil respiration) has at least the same temperature sensitivity as faster cycling organic C.

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